UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

Ciências
ULisboa

Echinoderm Biodiversity and Biogeography in Oceanic Islands:

the Azores as a case study

"Documento Definitivo"

Doutoramento em Biologia
Especialidade de Biodiversidade

Patrícia Gomes Antunes Madeira

Tese apresentada nos termos do artigo 33º do regime jurídico dos graus e diplomas do Ensino Superior

Documento especialmente elaborado para a obtenção do grau de doutor

2019

UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

Echinoderm Biodiversity and Biogeography in Oceanic Islands:

the Azores as a case study

Doutoramento em Biologia

Especialidade de Biodiversidade

Patrícia Gomes Antunes Madeira

Júri:

Presidente:

- Doutora Maria Manuela Gomes Coelho de Noronha Trancoso, Professora Catedrática e Presidente do Departamento de Biologia Animal da Faculdade de Ciências da Universidade de Lisboa.

Vogais:

- Doutora Teresa Paula Gonçalves Cruz, Professora Auxiliar, Escola de Ciências e Tecnologia da Universidade de Évora
- Doutor Sérgio Paulo Ávila Campos Marques, Investigador Principal FCT, Instituto de Ciências, Tecnologias e Agroambiente da Universidade do Porto
- Doutor Mário Albino Pio Cachão, Professor Associado com Agregação, Faculdade de Ciências da Universidade de Lisboa
- Doutor Carlos António da Silva Assis, Professor Auxiliar, Faculdade de Ciências da Universidade de Lisboa
- Doutor José Lino Vieira de Oliveira Costa, Professor Auxiliar, Faculdade de Ciências da Universidade de Lisboa
- Doutora Romana Lopes Almeida dos Santos, Investigadora FCT de nível de desenvolvimento, Faculdade de Ciências da Universidade de Lisboa

Tese apresentada nos termos do artigo 33º do regime jurídico dos graus e diplomas do Ensino Superior

Documento especialmente elaborado para a obtenção do grau de doutor

CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores; Fundação para a Ciência e a Tecnologia - SFRH/BD/61146/2009.

2019

Nota prévia

A presente tese apresenta artigos científicos já publicados, submetidos ou em preparação para publicação (capítulos 5 e 7), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série — N.º 57 — 23 de Março de 2015. Uma vez que estes trabalhos foram realizados em colaboração, o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Janeiro de 2019

Patrícia Madeira

ACKNOWLEDGMENTS

Most sincere gratitude is expressed to Sérgio Ávila and Professor António Frias de Martins, for their guidance, constant encouragement, patience and support. Their dedication and enthusiasm for scientific research have been truly inspiring (and so as their insightful wisdom and unparalleled scientific knowledge).

I would like to gratefully and sincerely thank Andreas Kroh (Natural History Museum of Vienna, Austria) for his critical reviews, invaluable advises, and most importantly, his friendship. I would like also to thank Sérgio Stefanni (Stazione Zoologica A. Dohrn) for the support and guidance during my stay at the Department of Oceanography and Fisheries (University of the Azores).

I am extremely thankful to Nuno Lourenço (EMEPC, Estrutura de Missão para a Extensão da Plataforma Continental, Portugal), Alexandra Cartaxana (Museu Nacional de História Natural — Museu Bocage, Portugal), Felipe Porteiro (University of the Azores), and also João Paulo Constância (Museu Carlos Machado, Azores), for providing me access to the zoological collections and necessary institutional facilities (and for the support that went well beyond professional courtesy).

I would like to express my deepest gratitude to my PhD colleagues and comrades Ricardo Cordeiro, Carlos Melo and Ana Cristina Rebelo for their assistance and friendship. For their warm welcome and support, a warm-hearted, and much deserved thank you to all the lab fellows, fieldwork team members and technical staff of the above mentioned institutions and research facilities. I would like also to gratefully and sincerely thank all the participants of the numerous “Palaeontology in Atlantic Islands” workshops and expeditions that through the years helped convey the rich material that is now part of both fossil and extant echinoderm reference collection at the Faculty of Science and Technology (University of the Azores).

And finally (where words fail to express my appreciation), I am truly indebted to all my friends and family, who all helped me in numerous ways during various stages of my PhD.

This work was made possible by the financial support from SFRH/BD/61146/2009, by Fundação para a Ciência e Tecnologia (FCT) of the Portuguese Government.

I have also benefited from 3 SYNTHESYS Projects (AT-TAF-2563; AT-TAF-0260; BE-TAF-404), which is financed by European Community Infrastructure Action under the FP6 and FP7 programmes (http://www.synthesys.info/).

ABSTRACT

Oceanic Islands are natural laboratories for the study of the processes and patterns of dispersion, colonization and ultimately of the appearance of new species. In the Northeast Atlantic, the archipelago of the Azores meets all the requirements to be considered one of the most isolated oceanic island systems. In general terms, the Azorean biota, as other oceanic systems, derives from dispersal chance events. For shallow-water marine benthic organisms, the main mechanisms to overcome the isolation by distance are rafting by non-planktonic life stages and through planktonic larval stages, both of which rely heavily on sea-surface currents to travel. However, and in spite of being under the influence of the western-intensified Gulf Current, the Azorean biota shows an opposite trend, being predominantly derived from the NE Atlantic and the Mediterranean. This apparent paradox has startled many marine biogeographers, who search for answers in the present-day faunal patterns together with those reconstructed through the past geological history of the archipelago. The present study attempts to further contribute to the knowledge of the marine fauna of the Azores, and its biogeographical relationships, using the echinoderms as a model. This animal phylum encloses a diverse group of strictly marine invertebrates found at all latitudes and depths. Furthermore, the echinoderms form one of the most conspicuous elements of both shallow- and deep-sea fauna in the Azores, and both in extant waters and among the fossiliferous outcrops of Santa Maria (37°N23’ 24°45’W), the oldest island in the archipelago. Thus, for a clear biogeographical background it was necessary to construct an updated catalogue of both local extant and fossil echinoderm fauna.

During the International Workshops ‘Palaeontology in Atlantic Islands’, held in Santa Maria Island between 2002-2013, new material was collected from Lower Pliocene and Pleistocene deposits. The early Pliocene beds encompass the following taxa: *Eucidaris tribuloides*, *Echinoneus* cf. *cyclostomus*, *Clypeaster altus*, *Echinocyamus pusillus*, *Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids. The Pleistocene outcrops (MISS 5e) included three regular echinoid species, *Sphaerechinus granularis, Arbacia lixula* and *Paracentrotus lividus*. The small

irregular echinoid *Echinocyamus pusillus* was also present in the Azorean Pleistocene fauna, a species common as well in the extant coasts of the archipelago. The presence of tropical taxa in the early Pliocene sediments clearly contrasts with the warm temperate taxa found in the Pleistocene and present coasts of the Azores.

Updated faunal lists are fundamental in biodiversity and biogeographical studies. *Arbaciella elegans* is a small cryptic echinoid species that was believed to have a large geographical range from the tropical Atlantic waters of Central Africa to the northern shores of the Azores, Canaries, Northwest Africa and Mediterranean Sea. However, and unlike the Central African material, individuals from the warm temperate waters present a uniform dark color. A morphological and genetic characterization of specimens from the Azores shows that the dark *Arbaciella* phenotype represents in fact juvenile stages of *Arbacia lixula*, which implies that *A. elegans* is circumscribed to the tropical African waters from where it was first described. This study emphasizes the difficulty of constructing faunal lists mirroring true distributions of species or local biodiversity, when rare or cryptic species are involved.

The Faculty of Sciencie and Tecnology (University of the Azores), houses hundreds of echinoderm specimens collected over more than 20 years of activity by the former Department of Biology. Three young specimens of the Mediterranean sea star *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882), a species previously not known to the Azores, were found among the echinoderm material. These animals were dredged off the south coast of São Miguel Island, at 135 m depth. *Sclerasterias richardi* is one of two sea star species known to reproduce asexually through fission in the Azores, the other being the shallow-water *Coscinasterias tenuispina* (Lamarck, 1816). However, *S. richardi*, though a shelf species, lives at much deeper waters than the latter. *S. richardi* is also capable of producing long-lived planktotrophic larvae with high dispersal potential to reach remote areas such as the Azores. The presence of *S. richardi* in Azorean waters in an otherwise thoroughly investigated area does not necessarily imply a recent arrival, as the depths in consideration (80-700 m) are also the least studied in the archipelago.

The review of the extant echinoderm fauna of the Azores, based on the related bibliography that has been accumulating over 150 years, complemented with the construction of an important local echinoderm reference collection in the University of the Azores, resulted in a critical reassessment of this significant component of the Azorean marine fauna. Herein are reported 172 species of echinoderms (6 crinoids, 55 ophiuroids, 45 asteroids, 36 holothuroids and 30 echinoids) to the archipelago, most of them inhabiting deep-waters. Although 65 species could be classified as shelf species (<200 m), only 29 occur in shallow-water (≤50 m depth). In general, the echinoderm species from the Azores are characterized by a wide geographical distribution in the Atlantic Ocean, with an additional 37 species occurring as well outside the Atlantic. Only 9 taxa (all deep-water species, >840 m) appear to be restricted to the Azorean waters. Though relatively poorer in number of species, the Azores show similar general trends to what is observed in other Macaronesian archipelagos (*i.e.* Madeira, Canaries and Selvagens): lack of endemic species, dominance of echinoderm fauna generally associated with rocky shores and species capable of producing planktonic feeding larvae. The relatively low echinoderm diversity could be attributed to the archipelago remoteness, the northern geographical position and to other local features attributed to their relative young volcanic age (*e.g.,* lower habitat diversity).

The echinoderm fauna of the Azores encompasses several edible species, though none known to be traditionally harvested. In recent years, fisheries targeting holothurian species have developed dramatically in several European and North African countries, and two of the most common sea-cumber species in the Azores, *Holothuria mammata* and *H. sanctori*, are now being commercially harvested in the Northeast Atlantic and in the Mediterranean Sea. The identification of *Holothuria* species tends to be difficult and time-consuming, and in many cases requires experienced taxonomists. Conversely, the use of PCR-RFLPs to rapidly and inexpensively identify species with no need for taxonomical or genetic expertise could prove a valuable asset. The present work introduces a simple and fast method, using restriction nuclease Sau3AI on 16S rRNA fragments. A simple non-destructive DNA sampling is also presented, using tube feet or oral tentacles, to be applied in genetic studies.

The updated faunal list of the echinoderms of the Azores was combined with those from the other areas in an updated distributional catalogue of the shallow-water echinoderms (≤200 m depth) from the North and Central Atlantic, and the

Mediterranean Sea, providing the basic framework for the analysis of biodiversity patterns and the construction of a biogeographical model. A total of 891 species belonging to 341 genera of shallow-water echinoderms are presently recorded in the studied areas. The tropical West Atlantic was by far the most biodiverse region (483 species, 210 of which were endemic). The Mediterranean Sea did not emerge as a biodiversity hotspot, revealing similar biodiversity rates as the neighbouring regions of Iberian and NW Africa, but presented significant endemism rate. Among the insular systems, Canaries presented the highest echinoderm biodiversity with 85 species, followed by Cabo Verde with 76. A positive correlation between latitude and the species' depth range was detected, confirming the Rapoport's latitudinal gradient. The most common larval development was planktotrophic (119 species), followed by the lecithotrophic (71 species) and aplanktonic (47 species). The relative representation of lecithotrophic and aplanktonic larval development increased towards high latitude areas and decreased as species geographical range increased. Also, the asexual reproduction decreased towards high latitude colder areas and this reduction was correlated with the relative increase of aplanktonic larval mode of development in the same areas. Endemic species were particularly numerous among sediment-associated habitats and broadly distributed species showed no preference for either soft or hard bottoms. Most areas showed a natural decrease of shared species with increasing geographical distance and this was particularly evident in oceanic systems. In these, faunal affinities tended to be related with the nearest continental shores, regardless of the prevailing sea-surface currents. In general, echinoderms proved to be good models for testing biodiversity and biogeographical patterns, though significant gaps were found on the available information.

Keywords: Echinodermata, Biodiversity, Biogeography, Azores, NE Atlantic.

RESUMO

As ilhas oceânicas são laboratórios naturais para o estudo de processos e padrões de dispersão, de colonização e do aparecimento de novas espécies. No Atlântico Nordeste, o arquipélago dos Açores preenche todos os requisitos para ser considerado um dos sistemas insulares mais isolados do hemisfério norte. Em termos gerais, a origem do biota açoriano, tal como noutras ilhas oceânicas, deriva de eventos de dispersão ocasionais. Nos animais bentónicos, os principais mecanismos de dispersão são o '*rafting*' por estádios de vida não planctónicos ou dispersão por estádios larvares planctónicos, ambos dependentes em larga medida das correntes oceânicas. Todavia, apesar de estar sob a influência da Corrente do Golfo que se move de oeste para leste, o biota açoriano exibe uma tendência oposta, estando mais próximo das costas a este *i.e.* do Atlântico Nordeste e do Mar Mediterrâneo. Este aparente paradoxo surpreendeu biogeógrafos que procuram respostas nos padrões faunísticos presentes juntamente com os reconstruídos ao longo da história geológica do arquipélago. O presente estudo tem como principal objetivo contribuir para o conhecimento da fauna marinha açoriana e suas relações biogeográficas, recorrendo aos equinodermes como modelo. Este filo animal abrange um grupo diverso de invertebrados, estritamente marinhos, encontrados em todas as latitudes e profundidades. Estes animais constituem um dos elementos faunísticos mais visíveis, não só das águas litorais e de profundidade dos Açores, como também dos afloramentos fossilíferos de Santa Maria (37°23'N 24°45'W), a ilha mais antiga do arquipélago. Desta forma, para obter um cenário biogeográfico claro, foi necessário construir um catálogo atualizado da fauna local de equinodermes, tanto fóssil como extante.

Durante os *workshops* internacionais "Paleontologia em Ilhas Atlânticas", realizados em Santa Maria entre os anos 2002-2013, foram coletados espécimes novos provenientes dos depósitos do Pliocénico e do Plistocénico. Os taxa presentes no Pliocénico de Santa Maria compreendem os equinóides *Elucidares tribuloides*, *Echinoneus* cf. *cyclostomus, Clypeaster altus, Echinocyamus pusillus, Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. e espatangóides indeterminados. O material coletado nos afloramentos do Plistocénico Superior (MISS 5e) incluiu três espécies de

equinóides regulares: *Sphaerechinus granularis, Arbacia lixula* e *Paracentrotus lividus*. O pequeno equinóide irregular *Echinocyamus pusillus* foi também identificado na fauna plistocénica dos Açores, sendo esta uma espécie extante igualmente comum no litoral do arquipélago. A presença conspícua de taxa típicos de mares tropicais nos sedimentos do Pliocénico contrasta com a fauna encontrada no Plistocénico, típica de climas temperados quentes e com uma composição bastante próxima da que se observa atualmente nas costas açorianas.

Em estudos biogeográficos ou sobre biodiversidade, listas faunísticas atualizadas são fundamentais. *Arbaciella elegans* é um pequeno equinóide críptico, que se acreditava ter uma ampla distribuição geográfica desde as águas tropicais da África central até às costas a norte dos Açores, das Canárias, do noroeste africano e do mar Mediterrâneo. No entanto, e ao contrário do material tipo, indivíduos provenientes das águas temperadas quentes apresentam uma cor uniforme escura. A caraterização morfológica e genética com base em espécimes dos Açores mostrou que o fenótipo escuro de *Arbaciella* é de facto representativo de estádios juvenis de *Arbacia lixula*, o que sugere que *A. elegans* está circunscrita às águas tropicais na qual foi descrita. Este estudo sublinha a dificuldade em construir listas faunísticas que reflitam as distribuições das espécies ou a biodiversidade local quando espécies raras ou crípticas estão envolvidas.

A Faculdade de Ciências e Tecnologia da Universidade dos Açores alberga centenas de exemplares de equinodermes coletados durante mais de 20 anos de atividades pelo antigo Departamento de Biologia. Três espécimes jovens da estrela-do-mar Mediterrânica, *Sclerasterias richardi* (Perrier, em Milne-Edwards, 1882), uma espécie anteriormente desconhecida nos Açores, foram encontrados entre este material. Estes animais foram dragados a 135 m de profundidade, a sul da ilha de São Miguel. *Sclerasterias richardi* é a segunda espécie de estrela-do-mar registada nos Açores que pode reproduzir-se assexuadamente através de fissão, sendo a outra *Coscinasterias tenuispina* (Lamarck, 1816). Não obstante, *S. richardi* vive tipicamente em águas muito mais profundas do que *C. tenuispina*. *S. richardi* também é capaz de produzir larvas planctotróficas com alto potencial de dispersão para alcançar áreas remotas, como os Açores. Este novo registo da *S. richardi* não significa necessariamente que esta espécie seja recente nas águas açoreanas, pois as profundidades em que vive tipicamente (80-700 m), são também as menos estudadas no arquipélago.

A revisão bibliográfica da fauna recente de equinodermes dos Açores, complementada com a construção de uma coleção local de referência de equinodermes na Universidade dos Açores, permitiu uma reavaliação de forma crítica e exaustiva deste importante componente faunístico. No total, registaram-se 172 espécies de equinodermes (6 crinóides, 55 ofiuróides, 45 asteróides, 36 holoturóides e 30 equinóides) para o arquipélago, na sua maioria habitantes de águas profundas. Embora 65 espécies possam ser classificadas como espécies costeiras (≤200 m), apenas 29 ocorrem localmente em águas pouco profundas (≤50 m de profundidade). Em geral, as espécies de equinodermes presentes nos Açores caraterizam-se por uma ampla distribuição geográfica no Atlântico, com outras 37 espécies ocorrendo também fora do Atlântico. Apenas 9 espécies (todas de águas profundas, >840 m) aparentam ter uma distribuição geográfica restrita às águas açorianas. A fauna de equinodermes dos Açores, embora relativamente pobre em número de espécies, enquadra-se na tendência geral observada em outros arquipélagos da Macaronésia (*i.e.* Madeira, Selvagens e Canárias): ausência de espécies endémicas, predominância de espécies associadas a costas rochosas e de espécies capazes de produzir larvas planctotróficas. A diversidade relativamente baixa de equinodermes nos Açores pode ser atribuída ao grau de isolamento das ilhas açorianas, à sua posição geográfica mais a norte e a outros atributos associados à origem vulcânica relativamente jovem do arquipélago (*e.g.,* menor diversidade de habitats).

Nas águas dos Açores vivem várias espécies de equinodermes comestíveis, com potencial económico. Nos últimos anos, a apanha comercial de holotúrias desenvolveu-se dramaticamente em vários países da Europa e do norte de África. Duas das espécies mais comuns do litoral Açoreano, *Holothuria mammata* e *H. sanctori*, são agora comercializadas. A identificação das espécies de *Holothuria* tende a ser difícil e demorada e, em muitos casos, requer taxonomistas experientes. Em alternativa, o desenvolvimento de kits de identificação recorrendo a técnicas de PCR-RFLPs permite a discriminação de espécies de forma rápida e pouco dispendiosa, dispensando a perícia taxonómica ou genética. O presente trabalho introduz um método simples de diagnose de *H. mammata* e *H. sanctori*, empregando a nuclease de restrição Sau3AI em fragmentos de ARNr 16S. É também apresentado um procedimento de amostragem de DNA não destrutivo, usando os pés ambulacrários ou os tentáculos orais, indicado para estudos genéticos.

A lista de espécies produzida para os Açores foi combinada com a de outras áreas, numa matriz atualizada de distribuições geográficas dos equinodermes de águas costeiras (≤200 m de profundidade) do Atlântico Norte e Central e do Mar Mediterrâneo. Esta matriz serviu como base para a análise de padrões de biodiversidade e construção de um modelo biogeográfico, ao incluir também especificidades sobre os ciclos de vida, amplitude batimétrica e tipo de substrato de cada espécie. Nas águas litorais estudadas registou-se um total de 891 equinodermes pertencentes a 341 géneros. A região tropical oeste do Atlântico foi, de longe, a mais biodiversa (483 espécies, das quais 210 são endémicas). O mar Mediterrâneo não emergiu como um 'hot spot' de biodiversidade, apesar de apresentar níveis significativos de endemismo, revelando taxas de biodiversidade semelhantes às das regiões vizinhas do Norte de África e da Península Ibérica. Entre os sistemas insulares, as Canárias apresentaram os níveis de biodiversidade mais elevados, com um total de 85 espécies, seguidas por Cabo Verde com 76 espécies. Foi detetada uma correlação positiva entre a latitude e amplitude batimétrica das espécies, confirmando o gradiente latitudinal de Rapoport. O desenvolvimento larvar mais comum foi o planctotrófico (119 espécies) seguido do lecitotrófico (71 espécies) e do não-planctónico (47 espécies). A representação relativa do desenvolvimento larvar lecitotrófico e não-planctónico aumentou em direção às áreas de maior latitude e diminuiu à medida que a amplitude geográfica das espécies aumentou. A reprodução assexuada diminuiu com a latitude e esta redução foi correlacionada com o aumento relativo da incidência do desenvolvimento não-planctónico entre os habitantes dessas mesmas áreas. As espécies endémicas foram particularmente numerosas entre os habitats associados ao substrato móvel. Em oposição, as espécies com grande amplitude geográfica não apresentaram uma preferência clara, seja por substratos móveis ou duros. A maioria das áreas mostrou uma diminuição relativa do número de espécies comuns com o aumento da distância geográfica entre estas. Esta tendência foi particularmente evidente nos sistemas oceânicos. Nestes, as afinidades faunísticas demonstraram estar orientadas para as margens continentais mais próximas,

independentemente do padrão de correntes oceânicas de superfície. Em geral, os equinodermes provaram ser bons indicadores para a análise de padrões de biodiversidade e modelos biogeográficos, muito embora se tenham detetado lacunas significativas na informação base atualmente disponível.

Palavras-chave: Echinodermata, Biodiversidade, Biogeografia, Açores, Atlântico Nordeste.

LIST OF FIGURES:

LIST OF TABLES:

Abbreviations and Acronyms

Institutions and Zoological Collections:

DBUA-ECH – recent echinoid reference collection of the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island, Azores); **DBUA-F –** fossil reference collection of the Department of Biology of the University of the Azores, Ponta Delgada, São Miguel, Azores, Portugal; **DOP** – recent reference collection of the Department of Oceanography and Fisheries of the University of the Azores (Horta, Faial Island, Azores); **EMEPC** – Portuguese expeditions 'Estrutura de Missão para a Extensão da Plataforma Continental Portuguesa' (Paço de Arcos, Portugal); **LUSO** – Remotely operated underwater vehicle operated by EMEPC; **MB–NMHN** – Museu Bocage, Natural History Museum (Lisbon, Portugal); **MG–LNEG** – Museu Geológico (Laboratório Nacional de Energia e Geologia, Lisbon), Portugal; **NHMW** – Natural History Museum of Vienna, Vienna, Austria.

Measurements and Animal Structures:

AL – arm length (Crinoidea); **D** – diameter; **IBr** – division series (Crinoidea); **P** – pinnules (Crinoidea); **R** – major radius, from the centre to the arm tip (Asteroidea); **r** – minor radius, from the centre to the interradius (Asteroidea); **Rmax** – major radius from centre of disc to tip of longest arm (Asteroidea); **TD** – test diameter (Echinoidea); **% TD** – percentage of the test diameter; **TH** – test Height (Echinoidea); **TL** – total length (Echinoidea); **%TL** – percentage of the total length; **%D** – Percentage of the diameter.

Localities:

AZO – Azores; **FAY** – Faial island; **FLS** – Flores island; **FRM** – Formigas Islet; **GRA** – Graciosa Island; **PIX** – Pico Island; **SJG** – São Jorge island; **SMA** – Santa Maria island; **SMG** – São Miguel island; **TER** – Terceira Island.

Other:

bt(s) – bare test(s) (Echinoidea); **PCR** – polymerase chain reaction; **RFLP** – restriction fragment length polymorphism; **RV** – research vessel; **ROV** – Remotely operated underwater vehicle; **Sta(s)** – station(s); **spm(s)** – specimen(s).

TABLE OF CONTENTS

Chapter 1. General Introduction

1.1. Introduction

True oceanic islands are those that have formed over oceanic plates and have never been connected to continental landmasses (Whittaker & Fernández-Palacios 2007). Since Darwin's (1859) essay on "The Origin of Species", islands have fascinated the scientific community and general public alike. In simple terms, the biota inhabiting oceanic islands must have derived from species that arrived from elsewhere, and later enriched by speciation if given enough time. Consequently, these relatively small, short-lived and isolated entities have served as natural laboratories for the study of the processes and patterns of dispersion, colonization and ultimately of the appearance of new species (Ávila 2013).

The Azores archipelago is composed of nine volcanic islands and several islets, with ages ranging from *c.* 6 Ma (Santa Maria Island; Ramalho *et al*. 2017) to 0.27 Ma (Pico Island; Demand *et al*. 1982). It is located in the North Atlantic, nearby the Mid-Atlantic Ridge, along the tectonic zone where the European, American and Nubian plates meet, some 1,400 km from the nearest European continental shores (Portugal) and about 840 km from Madeira Archipelago, the closest insular system (Ávila *et al*. 2018). The Azores is thus one of the most remote oceanic systems of the North Atlantic, a textbook example to test biogeographic models and theories.

The echinoderms are a group of diverse marine animals, mostly benthic, encompassing the brittle stars (class Ophiuroidea), sea stars (class Asteroidea), sea cucumbers (class Holothuroidea), sea urchins (class Echinoidea), sea lilies and feather stars (class Crinoidea) (Pawson 2007). Though strictly marine, they are found in all latitudes and depths, occurring in virtually any marine habitat (Pawson *et al*. 2009). Many echinoderm species are perceived as useful indicators of environmental degradation, either by playing key functions in structuring marine communities and ecosystems or by their destructive potential as those observed under echinoid or sea-star population outbreaks (Uthicke *et al.* 2009). Many species are also viewed as an economic asset, being used directly for human consumption (mainly holothurians and echinoids) or as additives in pharmaceutical, nutraceutical, and cosmetic products, or even sold as souvenir memorabilia and decoration trinkets (Micael *et al.* 2009; Purcell *et al.* 2012). For these reasons, extensive data is available on their biology, ecology, behaviour and geographic and bathymetric ranges, making the echinoderms a perfect choice for biogeographic studies.

The echinoderms are a conspicuous presence in the Azores, both in shallow and deep-waters, and have been the subject of interest since the beginning of natural studies in the islands, over 150 years ago. The early studies characterised the shallow-water echinoderm fauna of the Azores as relatively poor, derived exclusively from European waters, particularly from the Mediterranean Sea, with no new elements endemic to the area (*e.g.,* Drouët 1861). From this rather dismal portrait, the Azores later emerged as world reference following the retrieval from the archipelago's deep-waters of echinoderm material unknown to science, during the 'Golden Age' of oceanographic surveys in the late 19th century (*e.g.,* Koehler 1909; Perrier 1894). In more recent years, the oceanographic cruises have returned to the area and the use of modern techniques of capture such as Remote Operated Vehicles (ROV), together with more traditional collecting forms (*e.g.,* dredge, trawl or sledge) led to the inclusion of several new species to the archipelago's deep-water echinoderm fauna, some of which proved to be new to science (*e.g.,* Stöhr & Segonzac 2005; Gebruk 2008).

The first echinoderm studies on fossil fauna of the Azores are also from the late 19th century (*e.g.,* Mayer 1864). Echinoid remains are also a conspicuous presence in the fossiliferous deposits from the early Pliocene and from the Pleistocene of Santa Maria Island (Ávila *et al.* 2008, 2015). However, and unlike the recent fauna, the Neogene echinoid fauna of Santa Maria is poorly known, as lists of reported species remained almost unchanged in over 150 years of palaeontological research on the island.

1.2. Objectives

The main objectives of the present thesis are as follows: to contribute to the knowledge of the fossil and extant biodiversity of the archipelago, with the production of an updated list of echinoderm species from the Azores; to study the rich echinoderm extant (DBUA-ECH) and fossil material (DBUA-F) housed at the reference collection of the Faculty of Sciences and Technology (University of the Azores); to analyse biodiversity and biogeographic patterns and the underlying processes in the

Atlantic Ocean, using the shallow-water echinoderms as model' subjects. Additionally, among the echinoids and holothurians living in the shallow-waters of the Azores, several species are commercially harvested in the Atlantic and Mediterranean. The holothurian species are notoriously difficult to identify without adequate expertise, and in many instances require the use of time-consuming laboratory methods. PCR-RFLP based methods are viewed as a rapid and relatively inexpensive technic and can be applied without the need for expertise personal. The construction of PCR-RFLP protocols to discriminate shallow-water holothurian species from the Azores was explored. It also targeted a non-destructive tissue sapling method for future genetic studies whether to be used in fisheries or in other studies involving rare or reference collection specimens.

1.3. Thesis structure

The interpretation of the processes and patterns underlying the biodiversity and biogeography of the echinoderm fauna of the Azores was structured into seven chapters, and ordered by subject area as follows (* - refers to papers already published in peer-reviewed journals):

Fossil Fauna of the Azores

- Chapter 2) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean)

***Madeira, P.**, Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61 (3), 243–264. **[IF2016=1.46]**

Extant Fauna of the Azores

- Chapter 3) Species distribution: virtual or real – the case of *Arbaciella elegans* (Echinoidea: Arbaciidae)

*Kroh, A., **Madeira, P.** & Haring, E. (2011) Species distribution: virtual or real – the case of *Arbaciella* elegans (Echinoidea: Arbaciidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 99–105. **[IF=3.286]**

- Chapter 4) First report of a new Mediterranean species in the Azores: *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) (Asteroidea: Echinodermata).

***Madeira, P.**, Martins, A.M.F. & Ávila, S.P. (2017) First record of the Mediterranean asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) in the Azores Archipelago (NE Atlantic Ocean). *Arquipelago*. *Life and Marine Sciences*, 35, 11–18.

- Chapter 5) The Echinoderm Fauna of the Azores (NE Atlantic Ocean).

Madeira, P., Kroh, A., Martins, A.M.F., Cordeiro, R. & Ávila, S.P. (*submitted*). The Echinoderm Fauna of the Azores (NE Atlantic Ocean). *Zootaxa*.

- Chapter 6) Non-destructive tissue sampling and the use of PCR-RFLP's in two edible sea cucumbers, *Holothuria mammata* Grube, 1840 and *H. sanctori* Delle Chiaje, 1823 (Echinodermata: Holothuroidea)

***Madeira, P.**, Stefanni, S. & Ávila, S.P. (2018). Non-destructive tissue sampling and the use of PCR-RFLP's in two edible sea cucumbers from the Northeastern Atlantic, *Holothuria mammata* Grube, 1840 and *H. sanctori* Delle Chiaje, 1823 (Echinodermata: Holothuroidea). *The European Journal of Zoology* (formerly known as *Italian Journal of Zoology*), 10.1080/24750263.2018.1438529. **[IF2015=1.16]**

Biodiversity and Biogeographic patterns

- Chapter 7) Biodiversity and biogeographic patterns of Echinodermata in the North and Central Atlantic Ocean and the Mediterranean Sea.

Madeira, P., Kroh, A., Martins, A.M.F., Johnson, M.E. & Ávila, S.P. (*submitted*). Biodiversity and biogeographic patterns of Echinodermata in the North and Central Atlantic Ocean and the Mediterranean Sea. .*Zoological Journal of the Linnean Society*

The Annex chapters contain additional material related to the chapter 2 (Annex I) and chapter 5 (Annex II):

Annex I) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic).

Madeira, P., Kroh, A., Melo, C., Cordeiro, R. & Ávila, S.P. (2017) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic). *In*: Ávila, S.P. & Melo, C. (Eds.). RCANS *2017 - 6th Regional Committee on Neogene Atlantic Stratigraphy, Ponta Delgada, São Miguel Island, Azores, July, 10-13, University of the Azores (Abstract Book)*, p. 44.

Annex II) Extant echinoderm fauna of the Azores (species list), containing a list of all species native to the Azorean waters

1.4. References

Ávila, S.P. (2013) Unravelling the patterns and processes of evolution of marine life in oceanic islands: a global framework. *In*: Fernández-Palacios, J.M., de Nascimento, L., Hernández, J. C., Clemente, S., González, A., & Díaz-González, J.P. (Eds.) *Climate Change perspectives from the Atlantic: past, present and future*. Universidad de La Laguna, 85–116.

Ávila, S.P., Madeira, P., Mendes, N., Rebelo, A., Medeiros, A., Gomes, C., García-Talavera, F., Marques Da Silva, C., Cachão, M., Hillaire-Marcel, C. & de Frias Martins, A.M. (2008) Mass extinctions in the Azores during the last glaciation: fact or myth? *Journal of Biogeography*, 35, 1123–1129.

Ávila, S.P., Ramalho, R.S., Habermann, J.M., Quartau, R., Kroh, A., Berning, B., Johnson, M., Kirby, M.X., Zanon, V., Titschack, J. & Goss, A. (2015) Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores). *Palaeogeography, Palaeoclimatology, Palaeoecology,* 430, 57–73.

Ávila, S.P., Cordeiro, R. Madeira, P., Silva, L., Medeiros, A., Rebelo, A.C., Melo, C., Neto, A.I., Haroun, R., Monteiro, A., Rijsdijk, K. & Johnson, M.E. (2018) Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands. *Marine Pollution Bulletin*, 126, 101–112.

Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London, 502 pp.

Demand, J., Fabriol, R., Gerard, F. Lundt, F. & Chovelon, P. (1982) Prospection géothermique, íles de Faial et de Pico (Açores). Rapport géologique, geochimique et gravimétrique. Technical report, BRGM 82 SGN 003 GTH.

Drouët, H. (1861) *Elément de la Faune açoréenne*. J.B. Bailliere & Fils, Lubaires de L'Academie de Médicine, Paris, 245 pp.

Gebruk, A.V. (2008) Holothurians (Holothuroidea, Echinodermata) of the northern Mid-Atlantic Ridge collected by the G.O. Sars MAR–ECO expedition with descriptions of four new species, *in*: Gebruk, A.V. (Ed.) (2008). Benthic fauna of the northern Mid-Atlantic Ridge: results of the MAR–ECO expedition. *Marine Biology Research*, 4(1–2), pp. 48–60.

Koehler, R. (1909) Echinodermes provenant des campagnes du yacht Princesse-Alice (Astéries, Ophiures, Echinides et Crinoïdes). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 34, 1–317.

Mayer, K. (1864) SystematischesVerzeichniss der fossilen reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. *In*: G. Hartung, *Geologische Beschreibung der Inseln Madeira und Porto Santo*. W. Engelmann, Leipzig, pp. 183–298.

Micael, J., Alves, M.J., Costa, A.C. & Jones, M.B. (2009) Exploitation and Conservation of Echinoderms. *Oceanography and Marine Biology: An Annual Review*, 47, 191–208.

Pawson, D.L. (2007) Phylum Echinodermata. *Zootaxa*, 1668, 749–764.

Pawson, D.L., Vance, D.J., Messing, C.G., Solís-Marin, F.A. & Mah, C.L. (2009) Echinodermata of the Gulf of Mexico. *In*: Felder D.L. & Camp, D.K. (Eds.) *Gulf of Mexico: origin, waters, and biota, vol. 1, Biodiversity*. Texas A & M University Press, College Station, pp. 1177–1204.

Perrier, M.E. (1894) Stellérides. *Expéditions Scientifiques du Travailleur et du Talisman*, Masson, Paris, 1–431.

Purcell, S.W., Samyn, Y. & Conand, C. (2012) Commercially important sea cucumbers of the world. *FAO Species Catalogue for Fishery Purposes*, Rome, 6, 150 pp.

Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Thomas, C., Quartau, R., Hipólito, A., Rovere, A., Hearty, P.J. & Ávila, S.P. (2017) The emergence and evolution of Santa Maria Island (Azores) – the conundrum of uplifting islands revisited. *Geological Society of America Bulletin*, 129 (3-4), 372–390.

Stöhr, S. & M. Segonzac (2005) Deep-sea ophiuroids (Echinodermata) from reducing and non-reducing environments in the North Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 84, 4722/1–20.

Uthicke, S., Schaffelke, B. & Byrne, M. (2009) A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs*, 79(1), 3–24.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: ecology, evolution and conservation*, 2nd edn. Oxford University Press, Oxford, 416 pp.

Chapter 2. The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean)

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61 (3), 243–264.

Abstract

In the relatively young archipelago of the Azores, fossiliferous deposits are restricted to the oldest island (Santa Maria), mainly from Late Miocene-Early Pliocene deposits, and a few from the Pleistocene. echinoid material collected from these deposits comprises mainly disarticulated skeletal material (primary spines and coronal fragments) and a few complete tests. The taxa present in the Upper Miocene to Lower Pliocene beds comprise *Eucidaris tribuloides*, *Echinoneus* cf. *cyclostomus*, *Clypeaster altus*, *Echinocyamus pusillus*, *Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids. The spatangoids and *E.* cf. *cyclostomus*, are new records for the Miocene-Pliocene strata of the island. The material collected from Upper Pleistocene outcrops (MISS 5e) included three regular echinoid species, *Sphaerechinus granularis*, *Arbacia lixula* and *Paracentrotus lividus*. The two latter species are recorded for the first time from the Pleistocene deposits of the island. Compared to the older deposits, the Pleistocene record represents a very narrow range of environments and is basically restricted to deposits associated with an ancient rocky shore. Moreover, the conspicuous presence of taxa typical of tropical seas in the Mio-Pliocene sediments contrasts with the Pleistocene and modern echinoid fauna, which is warm temperate in composition.

Key words: Northeastern Atlantic; Azores; Santa Maria Island; Late Miocene-Early Pliocene; Late Pleistocene; MISS 5e.

2.1. Introduction

The Azores is one of the most remote archipelagos of the North Atlantic. This relatively young oceanic island system is composed of nine volcanic islands and several islets, located midway between the North American and european shores. reports on marine fossiliferous outcrops are restricted to the oldest island of Santa Maria (lat. 37°23’N; long. 24°45’W), mostly from deposits of Late Miocene to Early Pliocene age and from a few Pleistocene deposits (Madeira *et al.* 2007). exceptionally, very small fossiliferous deposits from the Late Miocene-Early Pliocene are also known from the islet of Formigas, 30 km NE of Santa Maria (Zbyszewski *et al.* 1961b; Abdel-Monem *et al.* 1975).

The fossiliferous deposits of Santa Maria Island have long attracted the attention of researchers, and several studies devoted to the fossil faunas were published, particularly on the fossil malacofauna (García-Talavera 1990; Callapez & Soares 2000; Ávila *et al.* 2002, 2009; for older references see Madeira *et al.* 2007). However, the Neogene echinoid fauna of Santa Maria is poorly known. The list of reported species remained almost unchanged in over 150 years of palaeontological research on the island. In the first publications (*e.g.,* Bronn 1860a; Mayer 1864 and Cotter 1892) a total of three echinoid species was reported from the Mio- Pliocene outcrops: *Eucidaris tribuloides* (Lamarck, 1816), *Echinocyamus pusillus* (O.F. Müller, 1776) and *Clypeaster altus* (Leske, 1778).

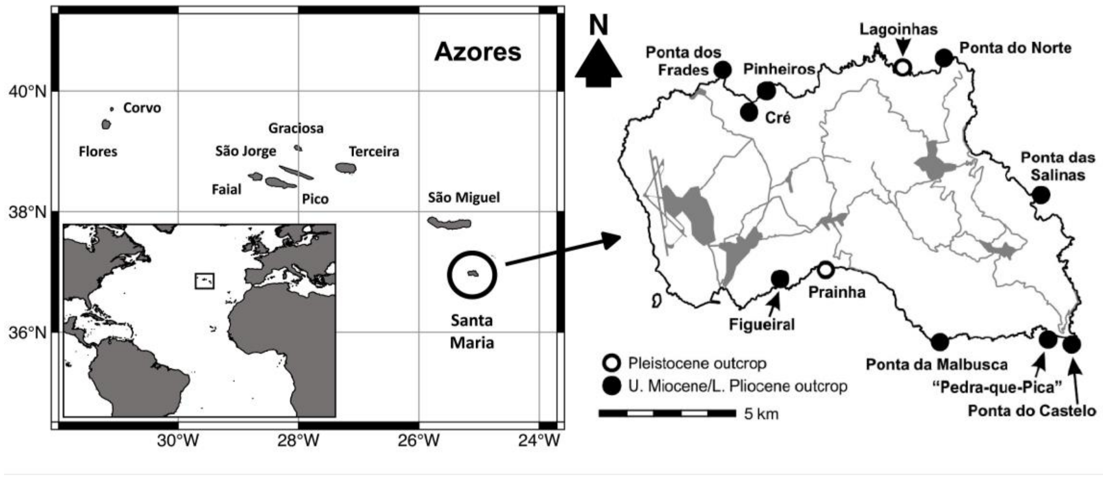


Figure 2.1. Locations of Upper Miocene/Lower Pliocene and Pleistocene outcrops studied. Inset (left hand side) shows the position of Santa Maria Island. For coordinates and alternate names of the outcrops see Table 2.1.

The last addition was *Prionocidaris avenionensis* (Des Moulins, 1837) (but see remarks below under *Eucidaris tribuloides*) by Ferreira (1955), making a reported total of four species from the older outcrops of Santa Maria. *Sphaerechinus granularis* (Lamarck, 1816) reported by Callapez & Soares (2000), is the only record from the Pleistocene outcrops.

The rediscovery of the fossiliferous outcrops made during the international workshops "*Palaeontology in Atlantic Islands*" (2002, 2005-2009), and the retrieval of new echinoderm fossil specimens, clearly shows that this subject is in need of revision.

2.2. Study area

Santa Maria is a relatively small island, with an area of 97 km^2 and a maximum length of 16.8 km (França *et al.* 2003). Radiometric (K-Ar) analysis has shown that this most south-eastern island of the Azores began its rise above the sea at a maximum estimate of 8.12 Ma (Abdel-Monem *et al.* 1975). The sedimentary deposits are exposed mainly along coastal sections and up valleys, rarely extending higher than 200 m above the present sea level. These deposits consist of sedimentary layers intercalated by volcanic material, and are represented by limestone, breccia, sandstone, conglomerate and subaerial deposits (Agostinho 1937; Ferreira 1955; Mitchell-Thomé 1974). Pure calcareous units are rare and poorly developed, being restricted to thin beds of bioclastic rud- and wackestone in most outcrops (Madeira *et al.* 2007). These deposits were grouped in two basic units by Serralheiro *et al.* (1987, 1990) and Serralheiro (2003): the Touril complex and the Facho- Pico Alto complex. The older fossiliferous outcrops studied here fall in the second group. Recent Sr-isotope data by Kirby *et al.* (2007) and biostratigraphic data by Janssen *et al.* (2008) dated them as early Pliocene (Zanclean), although a latest Miocene age cannot be completely ruled out.

Pleistocene marine fossiliferous deposits are locally exposed on the north and south coasts of the island, consisting mainly of poorly consolidated bioclastic sands resting either on a layer of algal crust or directly on basaltic marine terraces. recent dating estimates by Ávila *et al.* (2008a) suggest that the Pleistocene outcrops of Santa Maria Island correspond to Marine Oxygen Isotope Substage 5e (MISS 5e), with an absolute age of 130-120 ky.

Table 2.1. Reported fossiliferous outcrops of Santa Maria islands, their location, and other names used in the literature (for references see Madeira *et al*. 2007).

Outcrop	**Location**	**Other given names**
Cré	N37°00'03.76" W25°08'10.78"	Bocca do Crè; Forno do Cré; Furna da Cré; Casa da Cré; Escarpa da Cré; Pedreira dos Frades
'Pedra-que-Pica'	N36°55'48.37" W25°01'29.23"	–
Ponta da Malbusca	N36°55'46.10" W25°04'08.14"	Forno da Cré; Furna da Cré; Boca da Cré; Ponta da Piedade
Ponta do Castelo	N36°55'43.93" W25°00'58.35"	Ponta da Maia
Ponta dos Frades	N37°00'41.67" W25°08'44.68"	–
Ponta das Salinas*	N36°58'22.97" W25°01'43.38"	Feiteirinhas; Feteirinha
Ponta do Norte*	N37°00'57.76" W25°03'50.80"	–
Pinheiros*	N37°00'21.45" W25°07'48.87"	Pinheiras
Figueiral	N36°56'53.82" W25°07'40.31"	–
Prainha	N36°57'07.46" W25°06'17.89"	Prainha; Praia Formosa
Lagoinhas	N37°0'407.05" W25°04'58.23"	–

(*)Historical outcrops from which it we were unable to retrieve new material.

A review of the palaeontological research on the island can be found in Madeira *et al.* (2007). Further details on the litho- and bio-stratigraphy of the Miocene-Pliocene outcrops can be found in Kirby *et al.* (2007), Janssen *et al.* (2008) and Kroh *et al.* (2008). Detailed descriptions of the Pleistocene fossiliferous deposits can be found in Ávila *et al.* (2002, 2009, 2010) and Ávila (2005).

The echinoid material was collected from seven locations scattered along the coastal areas of Santa Maria (Fig. 2.1): Cré, Ponta dos Frades, "Pedra-que-Pica", Ponta da Malbusca, Ponta do Castelo, Praia do Calhau (Praia Formosa) and Lagoinhas. The outcrop names used herein are based on the geological map by Serralheiro *et al.* (1987) and, with few exceptions, are consistent with the historical studies (see Table 2.1).

2.3. Materials and methods

All of the specimens were collected during the International Workshops "*Palaeontology in Atlantic Islands*", held in Santa Maria Island, in June 2002, 2006, 2007 and 2008. Individual echinoid specimens were collected from the surface by bed-to-bed collecting. Additionally, beds with suitable lithology were subject to bulk sampling. These bulk samples were treated with H_2O_2 and processed by wet sieving. Both whole specimens and fragments were picked from the residues using a binocular microscope. The specimens are deposited in the fossil collection of the Department of Biology of the University of the Azores (DBUA-F collection).

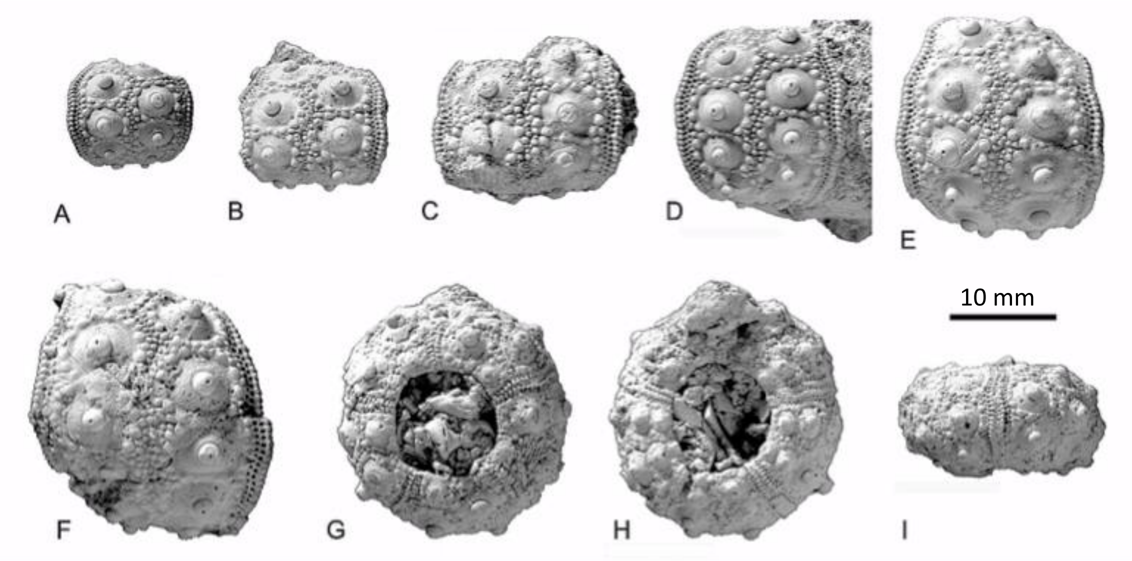


Figure 2.2. *Eucidaris tribuloides* (Lamarck, 1816); A - DBUA-F 343-1; B - DBUA-F 455; C - DBUA-F 272; D - DBUA-F 305; E - DBUA-F 448; F - DBUA-F 346; g-I - DBUA-F 445. A, E and G-I from Ponta da Malbusca, B-D and F from Pedra-que-Pica.

Abbreviations

DBUA-F – fossil collection of the Department of Biology of the University of the Azores, Ponta Delgada, São Miguel Island, Azores, Portugal; MG-LNEG – Museu Geológico (Laboratório Nacional de Energia e Geologia, Lisbon), Portugal; NHMW – Natural history Museum of Vienna, Vienna, Austria; TL - Test length; TD - Test diameter; % TL - Percentage of the test length; % TD - Percentage of the test diameter.

2.4. Systematic palaeontology

(following Kroh & Smith 2010)

Class Echinoidea Leske, 1778

Subclass Cidaroidea Smith, 1984

Order Cidaroida Claus, 1880

Family Cidaridae Gray, 1825

Genus *Eucidaris* Pomel, 1883

Eucidaris tribuloides (Lamarck, 1816)

(Figs. 2.2A–I, 2.3A–C)

1816. *Cidaris tribuloides*; Lamarck, p. 56.

1862. *Cidaris* ?*tribuloides* Lmk.; Bronn, *in* Reiss, p. 47, pl. 1, fig. 20 [3 spines].

1864. *Cidaris tribuloides* Lamarck; Mayer, p. 11.

1898. *Cidaris tribuloides* Lamarck; Koehler, pp. 7–9

1928. *Eucidaris tribuloides* (Lamarck.); Mortensen, pp. 400–408, fig. 119; pl. 41, figs. 9–16; pl. 48, fig. 1; pl. 73, fig. 1; pl. 86, fig. 16 [cum syn.].

1955. *Cidaris avenionensis* Desmoulins; Ferreira, p. 15; pl.10, fig. 71 [misidentification].

1961. *Cidaris tribuloides* Lamarck; Ferreira, pp. 532–533; pl. 1, fig. 5; pl. 2, fig. 11.

1961a. *Eucidaris trïbuloides* Lam.; Zbyszewski, Ferreira & Assunção, p. 14.

1962a. *Cidaris tribuloides* Lam.; Zbyszewski & Ferreira, p. 224.

1962a. *Eucidaris tribuloides* Lam.; Zbyszewski & Ferreira, pp. 226, 231.

1962b. *Cyathocidaris avenionensis* Desm.; Zbyszewski & Ferreira, p. 251 [following the misidentification by Ferreira 1955].

1962b. *Cidaris tribuloides* Lam.; Zbyszewski & Ferreira, p. 251, pl. 1, figs. 7–8.

1976. *Cyathocidaris avenionensis* Desm.; Mitchell-Thomé, p. 89 [following the misidentification by Ferreira 1955].

1976. *Eucidaris tribuloides* Lamarck; Mitchell-Thomé, p. 89.

Material: Late Miocene-Early Pliocene: a single complete specimen from Ponta da Malbusca (DBUA-F 445); 32 corona fragments from Cré (three fragments; DBUA-F 444), 'Pedra-que-Pica' (23 fragments, DBUA-F 107–4, 272, 305, 346, 352, 367, 448, 449, 450, 451, 452, 453, 455 and 461–1) and from Ponta da Malbusca (four fragments, DBUA-F 335, 336, 343–1 and 343–3); three primary spine fragments from Cré (DBUA-F 443), 'Pedra-que-Pica' (one complete spine, DBUA-F290; 102 fragments, DBUA-F 266–2, 274, 290, 454, 456), Ponta da Malbusca (32 fragments, DBUA-F 192–14, 250–2, 343–5, 446, 447), and Ponta do Castelo (four complete spines, DBUA-F 294–1; 35 fragments, DBUA-F 266–02, 345–5, 442).

Description: corona - apart from one complete corona from Ponta Malbusca (DBUA-F 445), the specimens usually comprise a full interambulacrum and adjoining half ambulacra. The ambulacra are narrow, with a sinuous, double row of marginal tubercles (one on each plate). In the ambital region of larger specimens (TH > 15 mm) a small internal tubercle is added on each plate. The pores are C1 isopores (*sensu* Smith 1978). Each interambulacral plate is bordered by 7 to 9 ambulacral plates ambitally. Each interambulacral plate bears one large, noncrenulate, perforate primary tubercle, the areole of which takes up the whole plate height. Adorally the areoles are confluent, ambitally adjoining areoles are separated by a narrow band of tubercles. The scrobicular tubercles are distinctly larger than the other secondary tubercles. The latter are generally rare in small specimens, but increase in number during growth. In the largest specimens observed (TH ≈25 mm) there are up to two rows of secondary tubercles interradially (per interambulacral plate), forming a moderately wide median zone. In small specimens the median zone is narrow. In the sole whole corona observed (DBUA-F 445, TD 19.4 mm), peristome diameter and apical region are subequal and *c*. 8.5 mm wide (≈44 % TD). Primary spines – numerous primary spines have been found in most of the outcrops studied. They are up to 21 mm in length, but most lie in a range from 11 to 17 mm. They are slightly widened just above the collar, giving the spines a stout appearance. The ornamentation consist of small nodulae arranged in vertical rows (22 to 26), forming a uniform surface. No thorns or spikes are formed. The acetabulum has a non-crenulate margin, the milled ring is finely striated, and both the collar and the neck are short. At the distal end a blunt point is developed, the most distal nodulae forming low ridges and a weakly developed crown with a small central projection. Traces of the original coloration, namely a coarse brown to lilac horizontal banding, are commonly still visible. cross sections reveal a thick cortex layer and a comparatively small medulla.

Remarks: comparisons of the abundant fossil material from Santa Maria Island with extant specimens of *Eucidaris tribuloides* in the NHMW collection confirm that they are conspecific. This also confirms earlier reports of that species by Bronn (*in* Reiss 1862), Mayer (1864) and others. The occurrence of this species in the early to Middle Miocene of the Mediterranean, although mentioned by Philippe (1998, pp. 46-48, p. 274, pl. 4, figs 16-18), is doubtful (see Kroh 2005, p. 8). There, another species of *Eucidaris* occurred, namely *E. zeamays* (Sismonda, 1842). It differs from *E. tribuloides* in its smaller size, well separated areoles, narrower median zone, and spines coarsely ornamented by whorls of thorns. *E. desmoulinsi*, described by Borghi (1999, pp. 110-111, pl. 3, figs 1-9, pl. 5, figs 1-2) from the Italian Pliocene, closely resembles the specimens collected in Santa Maria, particularly regarding spine size and ornamentation.

Ferreira (1955, p. 15, pl. 10, fig. 71) reported the presence of some small and poorly preserved spines of "*Cidaris avenionensis* Desmoulins" [now *Prionocidaris avenionensis* (des Moulins, 1837)], in the Santa Maria fossil collection of Serviços Geológicos de Portugal (now allocated to the geological Museum, in Lisbon). We were unable to trace the original specimens in the Portuguese collection. however, based on Ferreira's illustrations, the referred spines are very similar to the ones here described and assigned to *E. tribuloides*, with no indication of the ornament series of thorns seen typically in *Prionocidaris avenionensis* (compare Philippe 1998, pp. 34-42, pl. 1, pl. 3, figs 1-19; Kroh & Nebelsick 2003, figs 3f-g). We thus dismiss the record of *P. avenionensis* from the Azores as misidentification, especially as this species is

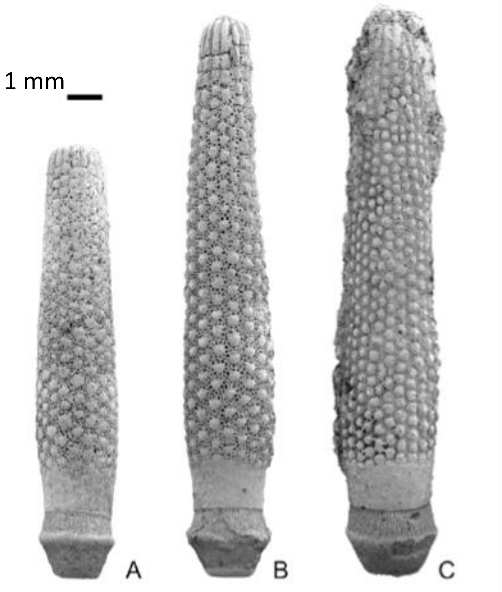


Figure 2.3. *Eucidaris tribuloides* (Lamarck, 1816); A - DBUA-F 446-1 (Ponta Malbusca); B - DBUA-F 456-1 (Pedra-que-Pica); C - DBUA-F 294-1 (Ponta do costelo).

restricted to the Burdigalian and Early Langhian elsewhere (Philippe 1998, p. 42).

Occurrence: this species was reported from the late Miocene-Early Pliocene of Santa Maria Island, from the outcrops of Figueiral (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski & Ferreira 1962a, b), Ponta da Malbusca (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski & Ferreira 1962a, b), Ponta das Salinas (Mayer 1864; Zbyszewski & Ferreira 1962a, b) and Cré (Ferreira 1961; Zbyszewski & Ferreira 1962b). This species is also known to occur in the Pleistocene of the Caribbean islands (Donovan 2003) and also the Bermuda Archipelago (Olson & Hearty 2009). At present, this species occurs in tropical waters of the East Atlantic, in the Guinea Gulf and Cape Verde Islands (see Kroh & Mooi 2010 for more extensive distribution records). In the Western Atlantic, it occurs in the warmer waters of the American coasts, from South Carolina (USA) to Northern Brazil, including the Caribbean archipelagos. It can be found in small crevices on coral reefs, under rocks and boulders in back reef lagoon areas, though it is particularly abundant in turtle grass beds, from the littoral to a depth of 450 m (Schultz 2005). Koehler (1898, pp. 7-9) reported this species (= *Cidaris tribuloides* Lamarck) from the Azores, based on a single specimen dredged from the Pico-Faial Channel at 130 m depth, a record that later surveys failed to confirm.

Subclass Euechinoidea Bronn, 1860b

Echinacea Claus, 1876

Order Arbacioida Gregory, 1900

Family Arbaciidae Gray, 1855

Genus *Arbacia* Gray, 1835

Arbacia lixula **(Linnaeus, 1758)**

(Figs. 2.4A–D, 2.5A, 2.6A)

1758. *Echinus lixula*; Linnaeus, p. 664.

1935. *Arbacia lixula* (Linnaeus); Mortensen, pp. 566–572; pl. 70, fig. 13; pl. 87, figs. 11–12 [cum syn.]

Material: Pleistocene of Prainha: one complete corona from (DBUA-F 271); 6 corona fragments (DBUA-F 354); Pleistocene of Lagoinhas: 22 corona fragments (DBUA-F 327; 438); numerous primary spines fragments (DBUA-F 149–7, 438).

Description: corona - the complete corona is *c*. 29 mm (DBUA-F 271) in horizontal diameter. In profile, the corona is flattened, test height 52 %TD. Apical disc dicyclic, enclosing an oval periproct with maximum width 3.5 mm. genital and ocular plates are almost devoid of tubercles, the remaining surface covered by epistromal ornament. The ambulacra are formed by trigeminate plates of the arbacioid compound type. The ambulacral pores belong to the C1 type (*sensu* Smith 1978) and form more or less straight, vertical rows. Each ambulacral plate bears one large primary tubercle. On adapical plates, however, these are less distinct.

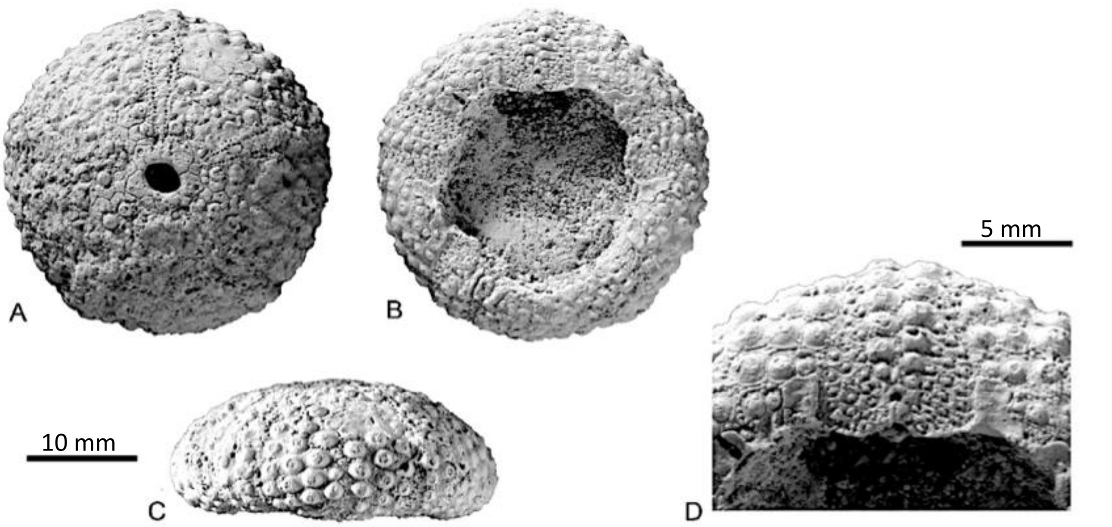


Figure 2.4. *Arbacia lixula* (Linné, 1758); DBUA-F 271 (Pleistocene of Praia do calhau).

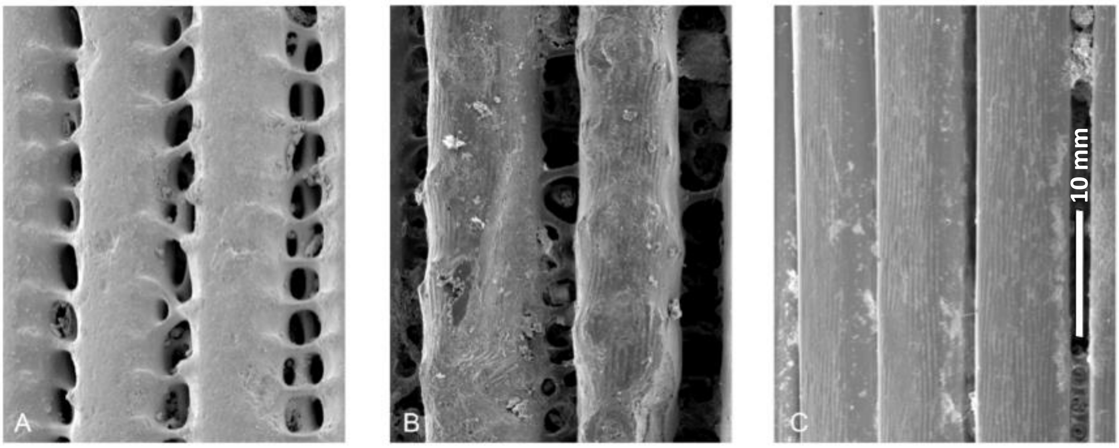


Figure 2.5. Microstructure of echinoid spines from the Pleistocene of Lagoinhas (bulk sample DBUA-F lh06-7): A – *Arbacia lixula* Linné, 1758; B - *Sphaerechinus granularis* (Lamarck, 1816); C - *Paracentrotus lividus* (Lamarck, 1816).

Ambitally and orally the interambulacra bear large, multiple subequal primary tubercles in horizontal rows. Up to four imperforate, non-crenulate tubercles per plate are present at the ambitus. Secondary tuberculation is generally sparse, but plates are covered by epistromal ornament in between the tubercles. On the two most adapical plates in each interambulacral column there are no primary tubercles along the interradial suture. A pronounced naked zone, however, is not formed. Peristome large (55.9 % TL in DBUA-F 271), with ambulacra expanding adorally forming phyllodes facilitating enlarged pore pairs. Primary spines – primary spine fragments associated with the test fragments could be attributed to *Arbacia* based on their surface microstructure (Fig. 2.5A) and cross sections (Fig. 2.6A) and on comparison with extant material. The wedges on the surface of the spines are typically finely jagged, and the furrows between the ridges show the irregular mesh that fills most of the cross section of the spines (Fig. 2.6A).

Remarks: The features outlined above enable confident assignment of the fossil material from Santa Maria to the genus *Arbacia*. The lack of a pronounced naked zone in the adapical interambulacra suggests attribution to *A. lixul*a, which still occurs in the area. This species has not previously been reported from the Santa Maria fossil fauna.

Occurrence: on Santa Maria Island *A. lixula* was present in both Pleistocene outcrops, Lagoinhas (north shore) and Prainha (south shore). This species occurs presently in shallow-waters (0-40 m depth) of the Mediterranean and adjacent Atlantic waters to the Gulf of Guinea, including the archipelagos of the Azores, Madeira, Canaries and

Cape Verde (Mortensen 1935; Schultz 2005). In the western Atlantic, it is also known to occur in Brazil (Schultz 2005), which represents a genetically distinct population (Palumbi & Lessios 2005). Together with *Paracentrotus lividus*, it is one of the most conspicuous echinoid species of the Azorean shallow waters, commonly forming dense patches on the rocky shores of the islands (Marques 1983; Morton *et al.* 1998). Despite its common occurrence throughout the Lusitanian Province today, fossil records of *Arbacia lixula* are rare. To our knowledge, fossil *A. lixula* has only been reported from the lower Pleistocene ("Postpliocene/Piano Siciliano") of the Livorno area in western Italy and the Pleistocene of Madeira (Stefanini 1911; under the name *A. pustulosa*, a junior synonym of *A. lixula*). Based on these occurrences, Mortensen (1935, p. 572) concluded that *A. lixula* had migrated from the Atlantic to the Mediterranean in 'postglacial' times (at that time the absolute dating of the glaciation periods was poorly known).

Order Camarodonta Jackson, 1912
Infraorder Echinidea Kroh & Smith, 2010
Family Parechinidae Mortensen, 1903
Genus *Paracentrotus* Mortensen, 1903

***Paracentrotus lividus* (Lamarck, 1816)**

(Figs. 2.5c, 2.6, 2.7)

1816. *Echinus lividus*; Lamarck, pp. 50.

1943b. *Paracentrotus lividus* (Lamarck); Mortensen, pp. 157–168, pl. 17, figs. 2–3; pl. 22, figs. 1–9; pl. 57, figs. 1–3,11, 12, 20. [cum syn.]

Material: Pleistocene of Lagoinhas – one test fragment (DBUA-F 327–1), numerous primary spine fragments (DBUA-F 149–7).

Description: Corona - coronal material is represented by a single fragment of a supraambital ambulacrum only. This fragment consists of polygeminate ambulacral plates (4 or 5 pores per plate respectively), which belong to the echinoid compound type. The pores are P2 type pores (*sensu* Smith 1978). They are arranged in arcs, forming oblique rows, separated by secondary tubercles. The tubercles are imperforate and non-crenulate, each ambulacral plate bears one primary tubercle and several secondary tubercles. Primary spines - though much more common that the coronal material, they are usually highly fragmented. The spines have a glassy smooth

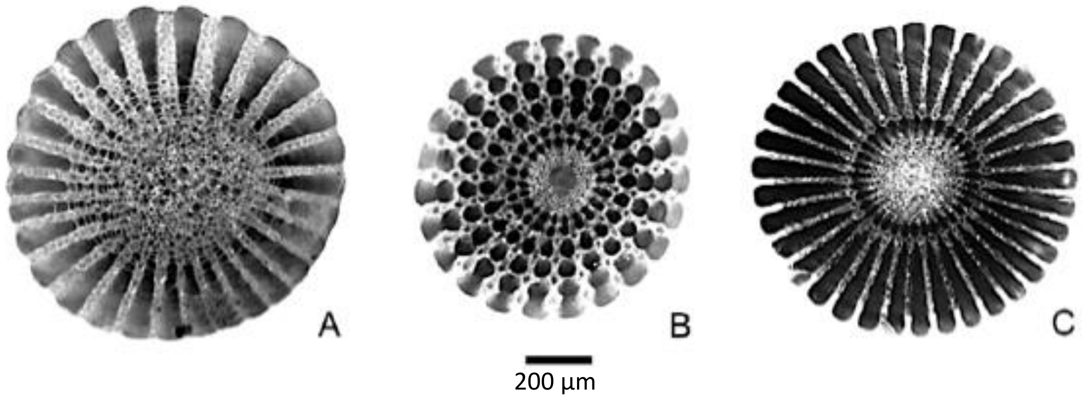


Figure 2.6. Cross sections of echinoid spines from the Pleistocene of Lagoinhas (bulk sample DBUA-F lh06-7): A – *Arbacia lixula* (Linné, 1758); B - *Sphaerechinus granularis* (Lamarck, 1816); C - *Paracentrotus lividus* (Lamarck, 1816).

uniform appearance, with the wedges joining closely together (Fig. 2.5c). The wedges have a very fine longitudinal striation and extend deep into the spine, reducing the irregular meshwork to the centre of the cross section, with no central cavity (Fig. 2.6c).

Remarks: albeit fragmentary, the present specimen can clearly be assigned to the genus *Paracentrotus*, based on the characters of the aboral ambulacrum. Comparison with extant material of *P. lividus* from the Mediterranean and the Northern Atlantic showed a high degree of similarity. Another species of this genus occurs at present in the Atlantic, *P. gaimardi* (reported from the Brazil, Angola and Eloby Islands of the Gulf of Guinea; Mortensen 1943b, p. 168). This species was described by Mortensen (1943b), who stated that the only significant difference between these two species was the radiating striation on the apical disc, albeit *P*. *lividus* tended to attain bigger sizes than *P. gaimardi*. The fossil specimens do not preserve the features used for distinguishing *P. lividus* and *P. gaimardi*. However, comparing the extant geographical ranges of both species, *P. lividus* being a common element of the extant Azorean fauna, is the most likely candidate. Thus, until new data allows further comparisons, we assume that the remains found at Lagoinhas belong to this later species.

Occurrence: in the Pleistocene of Santa Maria, it is only known from the locality of Lagoinhas. *P. lividus* is a rock-boring shallow-water species (0-100 m depth) presently known to occur in the Mediterranean and in the Northeast Atlantic from Ireland and the English Channel southwards to the Western Sahara, including the archipelagos of

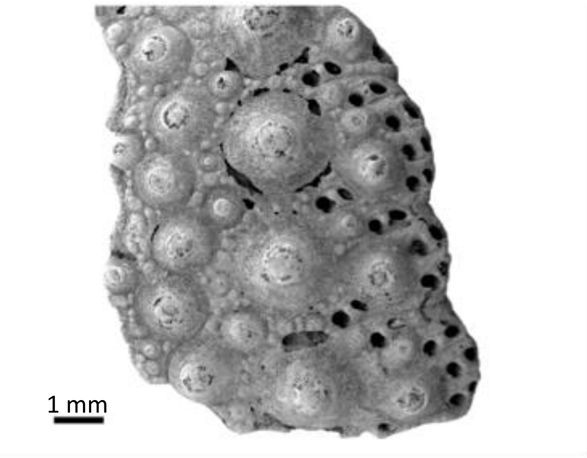


Figure 2.7. *Paracentrotus lividus* (Lamarck, 1816), ambulacral test fragment (DBUA-F 327-1, Lagoinhas).

Azores, Madeira, Canaries and Cape Verde (Schultz 2005; Kroh & Mooi 2010). *P. lividus*, together with *A. lixula*, is one of the most conspicuous grazers of the Azoreanshallow-water rocky shores today (Marques 1983; Morton *et al.* 1998). *P. lividus* has been reported fossil from the Pleistocene of the Moroccan Atlantic coast (Néraudeau & Masrour 2008), Northern Italy (Airaghi 1898 as "*Strongylocentrotus draebachiensis* [sic!]", Borghi 1995), Morocco (Pomel 1887), Sicily (Checchia-Rispoli 1907), and the Portugal mainland (Callapez 2000), as well as from the Late Pliocene ("Astian") of Greece (Marcopoulou-diacantoni 1967). There is also a tentative record (*Paracentrotus* aff. *lividus*) from the Messinian of north-west France (Néraudeau *et al*. 2003).

Superfamily Odontophora Kroh & Smith, 2010
Family Toxopneustidae Troschel, 1872
Genus *Sphaerechinus* Desor, 1856

Sphaerechinus granularis (Lamarck, 1816)

(Figs. 2.5B, 2.6B)

2000. *Sphaerechinus granularis* (Lamarck 1822); Callapez & Soares, pp. 314.

Material: Pleistocene of Prainha: one corona fragment (DBUA-F 482–3); Pleistocene of Lagoinhas: numerous primary spine fragments (DBUA-F 149–7).

Description: corona - the coronal material is represented solely by one heavily eroded ambulacral fragment of *c*. 15 mm size. The ambulacral plates are polygeminate, with four pores belonging to the P1 type (*sensu* Smith 1978), forming a more or less regular arc. Each plate bears a primary tubercle and one to two secondary tubercles. The tubercles are apparently non-crenulate and imperforate. Primary spines - although heavily eroded, traces of an irregular rugose microstructure can be seen on the surface ridges of the primary spines (Fig. 2.5B). The cross section (Fig. 2.6c) shows pronounced, beaded wedges, followed by a dense meshwork, and at the centre a small irregular cavity.

Remarks: despite the highly fragmentary nature of the material, comparison with extant specimens enables confident assignment of the fossil material from Santa Maria to *Sphaerechinus granularis*.

Occurrence: on Santa Maria Island it was known only from the Pleistocene outcrop of Lagoinhas (Callapez & Soares 2000). At present, this species is known to occur on rocky shores (0-100 m) of the Mediterranean and in the Northeast Atlantic southwards to the Gulf of Guinea (including the archipelagos of the Azores, Madeira, Canaries and Cape Verde) and to the Channel Islands (Schultz 2005). *S. granularis* is common on the Azorean rocky sublittoral. Though preferring deeper waters (Marques 1983), it is not uncommon to spot them in the first few metres in sheltered areas (Azevedo *et al.* 1994). *S. granularis* appears to be a relatively recently evolved species, its fossil record being restricted to a few occurences reported from the Pleistocene of Calabria, southern Italy (Seguenza 1880; Airaghi 1900), Morocco (Pomel, 1887) and Sicily (Checchia-Rispoli 1907).

Irregularia Latreille, 1825
Order Echinoneoida Clark, 1925
Family Echinoneidae Agassiz & Desor, 1847
Genus *Echinoneus* Leske, 1778

***Echinoneus* cf. *cyclostomus* Leske, 1778**

(Figs. 2.8A–F, 2.9A–C)

Material: Late Miocene-Early Pliocene of ‘Pedra-que- Pica’: two complete coronas (DBUA-F 439 and 440) and seven fragments (DBUA-F 108-7, 441); Late Miocene-Early Pliocene of Ponta da Malbusca: two fragments (DBUA-F 193-33, 343-2); Late Miocene-Early Pliocene of Ponta do Castelo: one specimen (DBUA-F 438).

Description: Most specimens are fragmentary and/or crushed. The complete coronas available range from 7.5 to 30.8 mm test length. The shape of the corona is ovoid, with

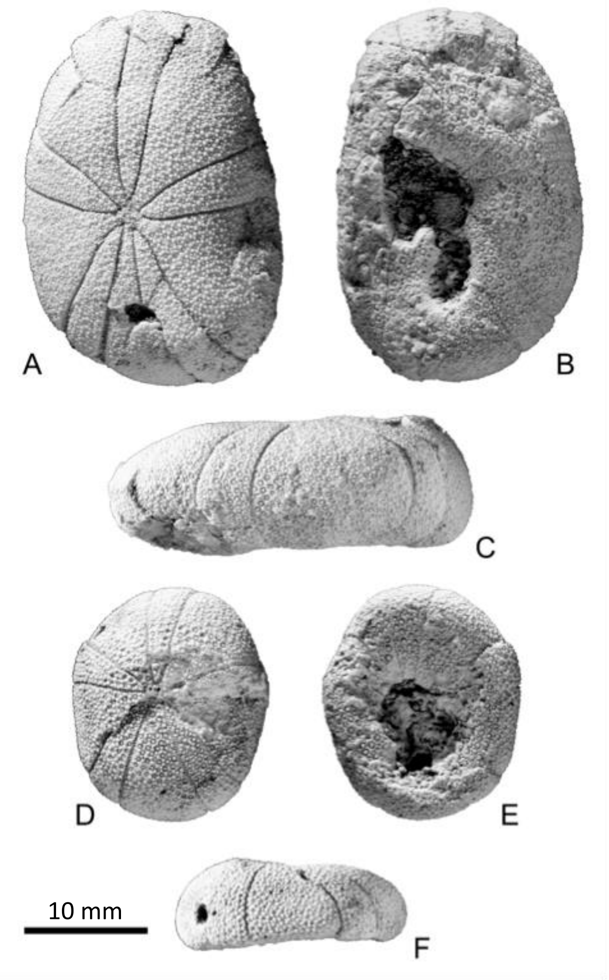


Figure 2.8. *Echinoneus* cf. *cyclostomus* Leske, 1778; A-C - aboral, oral and lateral view of DBUA-F 439; D-F - aboral, oral and lateral view of DBUA-F 440 (both from Pedra-que-Pica).

the maximum width lying posteriorly. (small specimens) to centrally (larger specimens). In profile the corona is flattened, the maximum height lying subcentrally. The apical disc (varying between 42 and 51% TL from the anterior margin) is tetrabasal and bears four circular genital pores; only the smallest of the complete specimens (DBUA-F 438) lacks them. Surprisingly, the gonopores in the largest specimen (DBUA-F 439, TL 30.8 mm) are very small. The ambulacra are non-petaloid with small, closely spaced partitioned isopores adapically. Adorally the pores are strongly oblique, less closely spaced and arranged in weak arches of three. The poriferous zones are distinctly depressed and very narrow, being clearly visible also in worn specimens. Both the aboral and oral sides are densely covered by small imperforate, noncrenulate primary tubercles. In between the primary tubercles large nodulae (“glassy tubercles” *sensu* Westergren 1911) are present on the aboral surface. Miliary and secondary tubercles are interspersed between these nodulae and the primaries, filling the

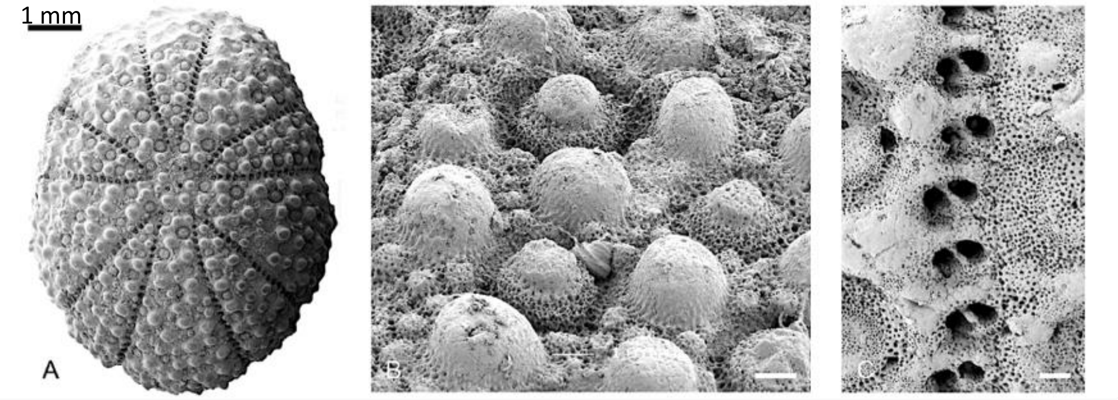


Figure 2.9. *Echinoneus* cf. *cyclostomus* Leske, 1778; A - aboral view of DBUA-F 438 (Ponta Malbusca); B-C - aboral tuberculation (B) and ambital ambulacral pores (C) DBUA-F 441 (Pedra-que-Pica). Scale bar of B and C equals 100 µm.

remaining space. On the oral side the tubercles are separated by narrow ridges with few secondary and miliary tubercles but lacking glassy tubercles. In the largest specimen (Fig. 2.9A-C; DBUA-F 439), the tubercle size varies according to the position on the corona, the oral tubercles being distinctly larger (2 times) than the aboral ones. The peristome is irregularly oval and strongly oblique (elongated along the 2-V axis). The periproct lies fully on the oral side, in between the peristome and the posterior margin and is elongated antero-posteriorly. Both peristome and periproct show distinct allometric growth, being comparatively larger in juveniles than in adult specimens (periproct: 30 vs. 21 % of TL)

Remarks: remains of members of the genus *Echinoneus* are commonly reported from Oligocene to Pleistocene deposits of the Caribbean (Donovan 1993, p. 382; Donovan & Veale 1996, pp. 633-635; Dixon & Donovan 1998, p. 104; Donovan 2001, p. 183; Simpson 2001, p. 34; Donovan *et al.* 2005, pp. 106-107). Most occurrences, however, consist of single finds of comparatively poorly preserved specimens. On Santa Maria, however, *Echinoneus* is rather common. Despite the fragmentary nature of the test, three nearly complete, albeit crushed coronas could be recovered from 'Pedra-que-Pica' and Ponta da Malbusca. When compared to extant *Echinoneus cyclostomus*, a large number of similarities are apparent. Differences observed concern the size of the gonopores in the largest of the fossil specimens (DBUA-F 439) and the apparent high variability of the aboral tubercle size. Despite the monograph of Westergren (1911) the intraspecific variability and possible ontogenetic effects on tubercle size are still poorly understood in *Echinoneus*. Thus we prefer to name the fossil material of Santa

Maria in open nomenclature until it can be compared with the wide size range of extant *E. cyclostomus*.

Occurrence: on Santa Maria, *E.* cf. *cyclostomus* was found in the outcrops of Ponta da Malbusca, 'Pedra-que-Pica' and Ponta do Castelo. Elsewhere, *E. cyclostomus* is known from the Jamaican Pleistocene (see references above) and from the early Pliocene of Egypt (Ali 1985). *E. cyclostomus* Leske, 1778 has been reported to live cryptically under rocks, boulders or in burrows in the warm tropical coastal waters of the West Indies, from the Bahamas to Tobago, on Ascension Island, but not in Western Africa. It is also found in the Indo-Pacific, along the eastern African coast from Zanzibar to Natal, from Madagascar to Hawaii and Easter Islands, and from Japan to Northern Australia and Lord Howe Island (it is not known from the west coast of America) (Schultz 2005). *E. cyclostomus* does not occur in the Azores today.

Neognathostomata Smith, 1984
Order Clypeasteroida L: Agassiz, 1835
Suborder Clypeasterina L. Agassiz, 1835
Family Clypeasteridae L. Agassiz, 1835
Genus *Clypeaster* Lamarck, 1801

***Clypeaster altus* (Leske, 1778)**

(Figs. 2.10A–L)

1862. *Clypeaster* ?*altus* Lmk.; Bronn, *in* Reiss, pp. 46–47.
1864. *Clypeaster altus* Linné. (Echinus); Mayer, p. 12.
1892. *Clypeaster altus* Lamarck; Cotter, p. 259.
1955. *Clypeaster altus* Lamarck; Ferreira, p. 16, pl. 9, figs. 66, 69; pl. 10, figs. 70, 73; pl. 11, fig. 76.
1961. *Clypeaster altus* Lamarck; Ferreira, pp. 539–540; pl. 4, figs. 22, 23, 28, 29.
1961a. *Clypeaster altus* Lam.; Zbyszewski, Ferreira & Assunção, p. 14.
1962a. *Clypeaster altus* Lam.; Zbyszewski & Ferreira, pp. 219, 231.
1962b. *Clypeaster altus* Lam.; Zbyszewski & Ferreira, p. 251, pl. 2, fig. 21.
1976. *Clypeaster altus* Klein; Mitchell-Thomé, p. 88.
1976. *Clypeaster altus* Lamarck; Mitchell-Thomé, p. 89.

Material: Late Miocene-Early Pliocene of 'Pedra-que-Pica': two specimens (DBUA-F 214, 223); Late Miocene-Early Pliocene of Ponta da Malbusca – two specimens (DBUA-F 155, 431). Additionally, two fragments from Ponta da Malbusca (DBUA-F 355, 457) are tentatively attributed to *C. altus*.

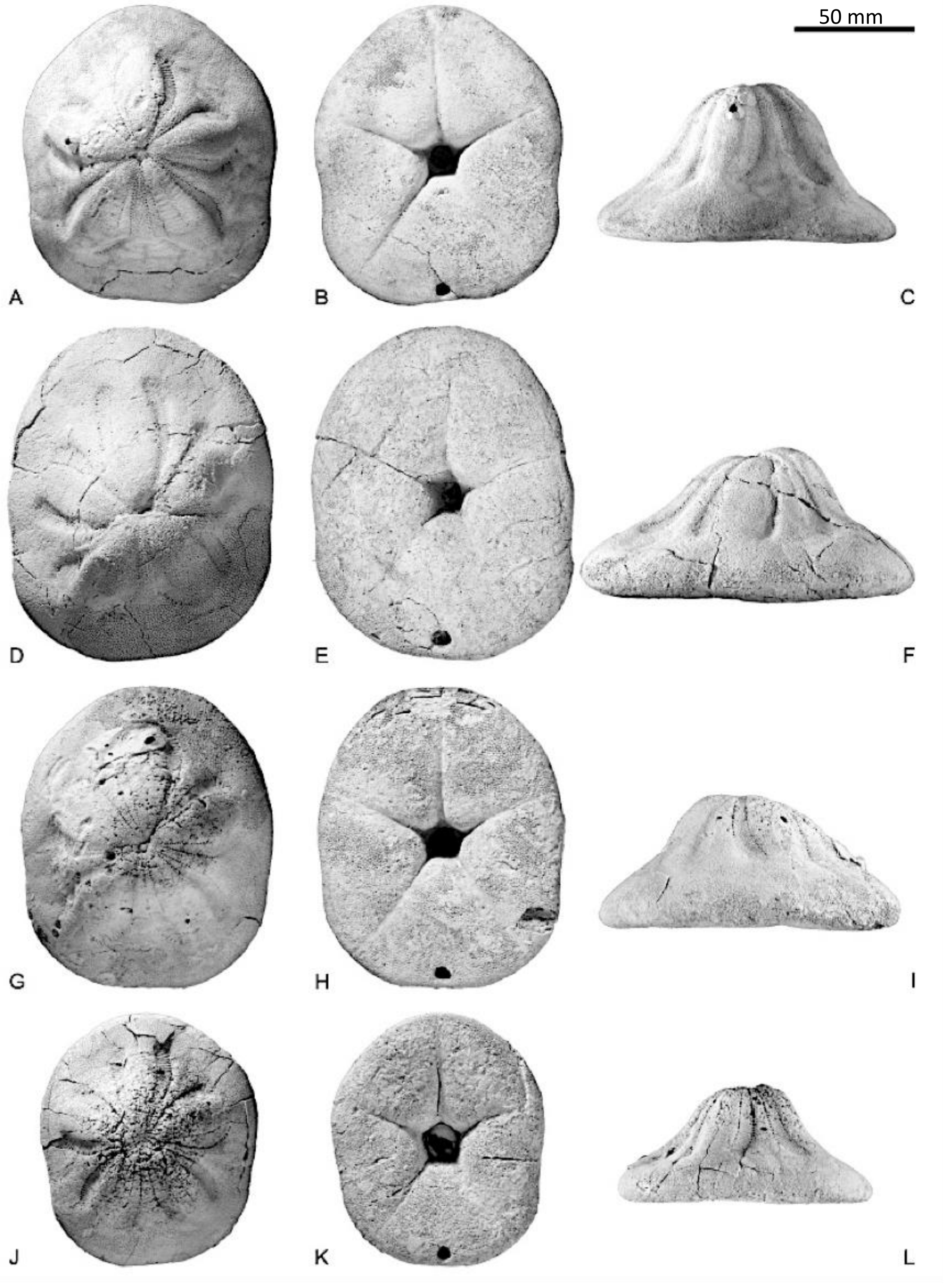


Figure 2.10. *Clypeaster altus* (Leske, 1778); A-C - aboral (A), oral (B), and left lateral (C) view of DBUA-F 155 (Ponta Malbusca); D-F - aboral (D), oral (E), and left lateral (F) view of DBUA-F 214 (Pedra-que-Pica); G-I - aboral (g), oral (h), and right lateral (I) view of DBUA-F 223 (Pedra-que-Pica); J-L - aboral (J), oral (K), and left lateral (L) view of DBUA-F 431 (Ponta Malbusca).

Description: the corona is large (commonly > 110 mm TL), antero-posteriorly elongated and has a subpentagonal to angular outline. The margin is slightly indented in interambulacra 1 and 4 and straight or slightly convex in the other interambulacra. The maximum width lies anterior of the apical disc, where ambulacral columns IIa and IVb reach the ambitus. Posteriorly ambulacral columns Ib and Va are nearly as wide. In profile the corona is high (usually between 45 and 55 % TL), trapezoid, with a (usually) thick, tumid ambitus and a domed petaloid area. The maximum height usually coincides with the adapical parts of the interporiferous zones of petals I and V. The oral surface is flattened, only the most adoral parts being steeply inclined towards the peristome, thus forming a narrow, deep infundibulum.

The apical disc is monobasal, with a large central madreporite of stellate shape and five gonopores varying from circular to oval (radially elongate). In some specimens the gonopores lie directly at the edge of the madreporite, in others they occupy a more distal position. A similar variation in gonopore position is observed in the extant *C. rosaceous* (A. Kroh, unpublished data).

The petals are straight and bear large elongate isopores. Adjacent pore pairs are separated by narrow ridges with a single row of up to nine primary tubercles. The distal parts of the poriferous zones curve towards the midline of the petals, but do not reach the perradial suture, the petals thus being widely open distally. The interporiferous zones are strongly inflated, the poriferous zones slightly depressed. Trailing podia *sensu* Mooi (1989, *e.g.,* fig. 28a) are not observed.

The tuberculation consists of closely spaced primary tubercles in sunken areoles and dense miliary tuberculation on the remaining surface. Tubercle density is highest on the interporiferous zones of the petals and the ambitus, lowest adapically in between the petals. Tubercle size is largest on the oral surface, leaving only narrow ridges in between.

The peristome is large, subcircular and lies deeply sunken in a narrow infundibulum with steep, almost vertical walls. The subcircular periproct lies inframarginally in interambulacrum 5, close to the posterior margin (usually 2.5 to 3 mm away from it in specimens > 100 mm TL).

Apart from the general double-walled nature of the clypeasteroid corona, the internal support system in the Santa Maria specimens consists of few massive pillars, leaving a large body cavity in between the walls of the infundibulum and the ambitus. Additionally, the small fragments (DBUA-F 355; DBUA-F 457) show a similar double-walled construction and similar tubercle morphology and distribution.

Remarks: *Clypeaster* fragments observed in some of the outcrops are tentatively attributed to this species due to the fact that they show consistent morphological features. There is no evidence for the occurrence of a second species of *Clypeaster* on Santa Maria.

Occurrence: this species was reported from the late Miocene-early Pliocene of Santa Maria, from the fossiliferous outcrops of Pinheiros (Bronn *in* reiss 1862; Mayer 1864; Ferreira 1961; Zbyszewski & Ferreira 1962a), Ponta da Malbusca (Ferreira 1961; Zbyszewski & Ferreira 1962a, p. 231; Zbyszewski & Ferreira 1962b), Figueiral (Ferreira 1961; Zbyszewski & Ferreira 1962b) and Ponta do Norte (Ferreira 1961; Zbyszewski & Ferreira 1962b). This species is only known from the fossil record, ranging from the Middle Miocene (Serravallian) to Early Pliocene. It is widely distributed in circum-Mediterranean countries, occurring in Algeria, France, Crete, Corsica, Italy, Sardinia and Spain (see Rose & Wood 1999; Néraudeau *et al*. 2001 and references therein).

No species of this genus are known to occur presently in the Northeastern Atlantic and on the Mediterranean coasts. Clypeasterids are confined to the tropical and subtropical coasts of all continents (Mortensen 1948). In general, they prefer sandy bottoms, feeding on the interstitial fauna, *e.g.,* foraminifera and small molluscs (Mortensen 1948).

Suborder Scutellina Haeckel, 1896

Infraorder Laganiformes Desor, 1847

Family Fibulariidae Gray, 1855

Genus *Echinocyamus* van Phelsum, 1774

Echinocyamus pusillus **(Müller, 1776)**

(Figs. 2.11A-L)

1862. *Echinocyamus minimus* Girard; Bronn, *in* Reiss, p. 46.

1864. *Echinocyamus pusillus* Müller (Spatangus); Mayer, p. 12.

1955. *Echinocyamus pusillus* Mull.; Ferreira, p. 14.

1961. *Echinocyamus pusillus* Muller; Ferreira: 535, pl. 4, fig. 25.

1961a. *Echinocyamus pusillus* Mull.; Zbyszewski, Ferreira & Assunção, pp. 14.

1962a. *Echinocyamus pusillus* Müll; Zbyszewski & Ferreira, p. 226.

1962b. *Echinocyamus pusillus* Muller; Zbyszewski & Ferreira, p. 251.

1976. *Echinocyamus pusillus* Müller; Mitchell-Thomé, p. 89.

[Remark: only references relating to fossil Azorean specimens have been included in the synonymy list above. For a full synonymy of extant *E. pusillus* the reader is referred to Mortensen (1948).]

Material: Late Miocene-Early Pliocene of Cré: 10 specimens (DBUA-F 432); Late Miocene-Early Pliocene of 'Pedra-que-Pica': four specimens (DBUA-F 434); Late Miocene-Early Pliocene of Ponta da Malbusca: 67 specimens (DBUAF 372); Late Miocene-Early Pliocene of Ponta do Castelo: one specimen (DBUA-F 433).

Description: Test very small, usually less than 8 mm. Outline oval (anterior-posteriorly elongated) to egg-shaped. Maximum width lying slightly posteriorly, ranging from 69 to 100 % TL (mean 83.6 %). In profile the test is low arched, the maximum height coinciding with the apical disc.

The apical disc lies slightly anterior of the centre (34- 43 % TL, from the anterior margin). Four genital pores are present; the distance between the posterior genital pores are 0.4 mm, on average. The ocular pores are small, being indistinct in most specimens (due to the poor preservation). A single circular hydropore is present, lying roughly at the centre of the apical disc.

The ambulacra are petaloid, consisting of 4 to 7 strongly oblique pore pairs in each column. The frontal petal is the longest; the paired petals are subequal in length. The poriferous zones diverge. Outside the petals only accessory pores (micro-unipores) are present, which form distinct arcs along the adoral plate sutures. The tuberculation is homogeneous and consists of primary tubercles in sunken areoles, with a dense miliary tuberculation occupying the remaining surface. The peristome is located subcentrally on the oral surface and varies considerably in size (from 9 to 21 % of TL in diameter). It is slightly sunken, subcircular and its posterior margin is distinctly depressed in most specimens. The periproct is usually about half as wide as the peristome, and generally less than 10% of TL in width. It is transversally elongated and lies approximately halfway between the peristome and the posterior margin.

Remarks: Two other similar *Echinocyamus* taxa are known to occur in the deeper waters of the Azores, *E. scaber macrostomus* Mortensen, 1907 and *E. grandiporus* Mortensen, 1907. In contrast to these species, however, *E. pusillus* has relatively well developed petals. This is also true for the specimens studied here, which show

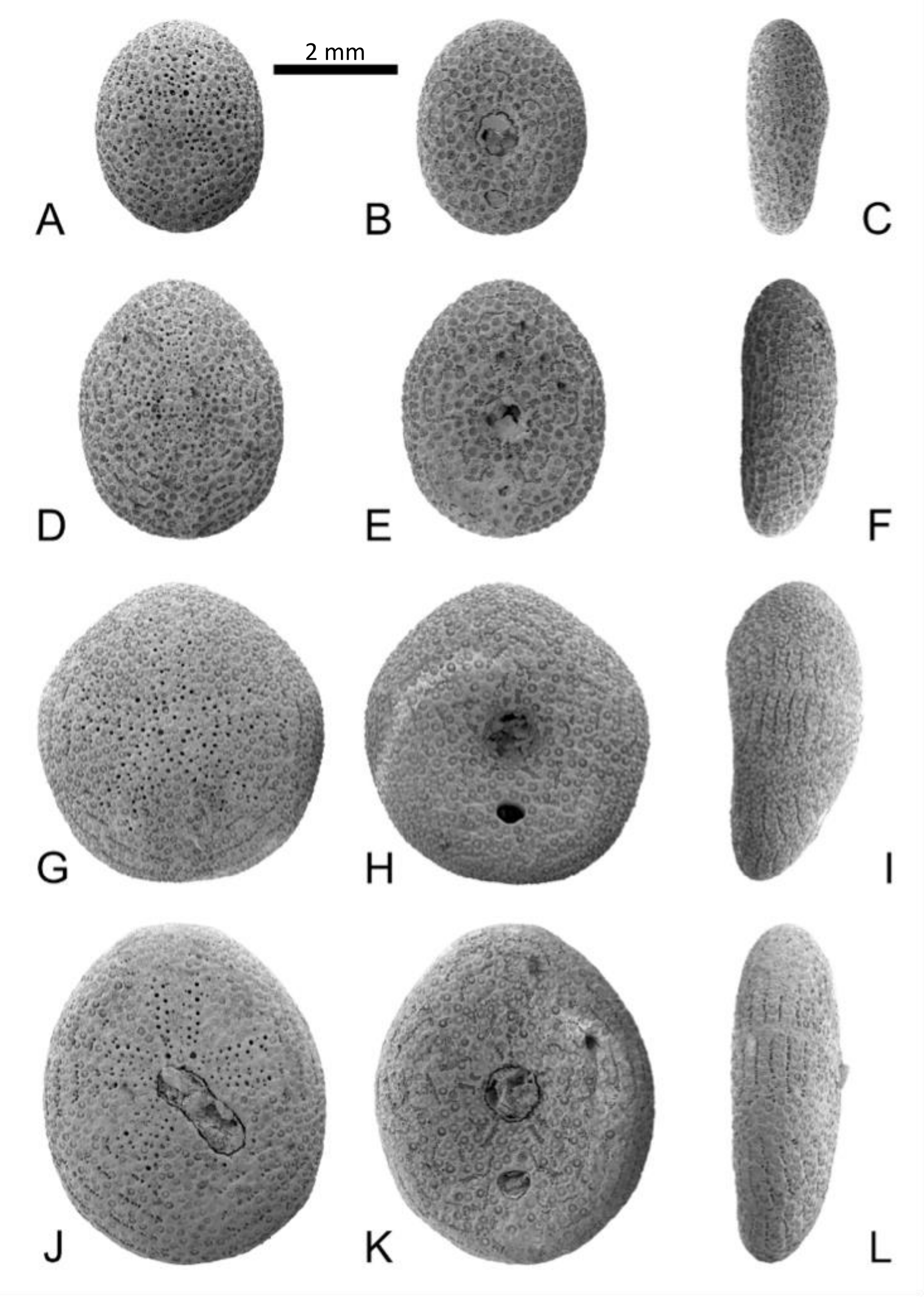


Figure 2.11. *Echinocyamus pusillus* (Müller, 1776); A-C - aboral (A), oral (B), and left lateral (C) view of DBUA-F 432-2 (cré); D-F - aboral (D), oral (E), and left lateral (F) view of DBUA-F 343-3-2 (Ponta Malbusca); G-I - aboral (G), oral (H), and left lateral (I) view of DBUA-F 343-3-1 (Ponta Malbusca); J-L - aboral (J), oral (K), and left lateral (L) view of DBUA-F 432-5 (Cré).

consistently larger pore numbers than the ones presented by Mortensen (1907, pp 28-39) for *E. scaber? grandiporus* and *E. macrostomus* of similar sizes. Another diagnostic feature in which *E. pusillus* differs significantly from the deep-water species is the smaller distance between the posterior genital pores (Mironov & Sagaidachny 1984;

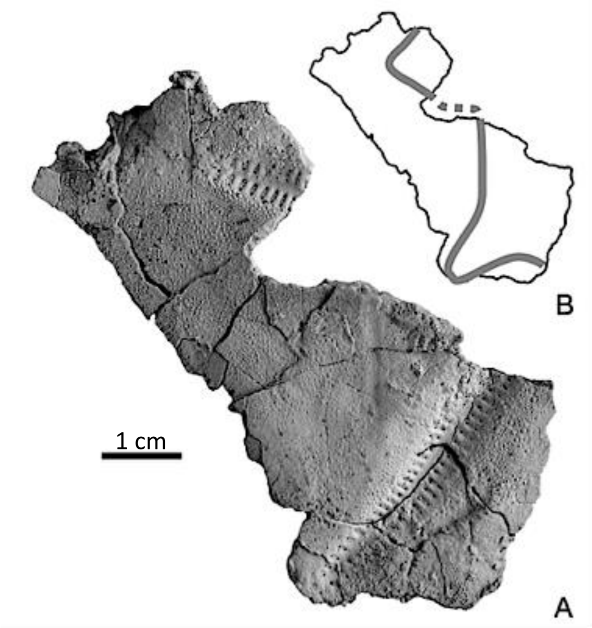


Figure 2.12. *Schizobrissus* sp.; A - aboral test fragment; B - outline and peripetalous fasciole pathway; DBUA-F 381 (Pedra-que-Pica).

Mironov 2006).In the Santa Maria specimens, the distance between the posterior genital pores never exceeds 0.6 mm, well inside the range given by Mironov (2006) for this species.

Occurrence: on Santa Maria Island *E. pusillus* was reported from Figueiral (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski & Ferreira 1962a; Zbyszewski & Ferreira 1962b). This species is a common element of the fauna of soft bottom (coarse sands/fine gravels) marine environments (0-1,250 m depth) in the Northeastern Atlantic and the Mediterranean, from Iceland, Norway, the North Sea and the western Baltic Sea to West Africa. It is known to occur presently in Azorean waters. *E. pusillus* has been commonly reported fossil from European and North African deposits of early to Middle Miocene age onwards, but the oldest records may be based on misidentifications (see discussion in Kroh 2005, p. 77, 81-82). Confirmed records of *Echinocyamus pusillus* are known from the Pliocene (*e.g.,* Borghi 1993; Néraudeau *et al*. 2003) and Pleistocene from the Mediterranean and the North Sea Basin.

Atelostomata von Zittel, 1879

Order Spatangoida Agassiz, 1840

Suborder Brissidina Stockley *et al.*, 2005

Family Brissidae Gray, 1855

Genus *Schizobrissus* Pomel, 1869

***Schizobrissus* sp.**

(Figs. 2.12A–B)

Material: a single aboral corona fragment collected from Upper Miocene to Lower Pliocene deposits at 'Pedra-que-Pica' (DBUA-F 381).

Description: The only available specimen is a large aboral fragment (length 77 mm, test thickness 1.3 to 2 mm) preserving the distal parts of petals IV and V and part of interambulacra 4 and 5. The petals are moderately sunken and feature large, elongate isopores (interporiferous area approx. 1.5 to 2 times pore diameter). The imporiferous zone is nearly as wide as a single poriferous zone. The ends of the petals are blunt and flexed anteriorly. The poriferous zones converge slightly, but do not form a lanceolate shape. Petal V is bent twice within 15 mm from its distal tip. As far as preserved, the aboral tuberculation seems homogenous outside the peripetalous fasciole. Within it, small groups of larger tubercles situated at the interradial/adapical half of the plates occur in interambulacrum 5. The course of the peripetalous fasciole is shown in Fig. 2.12B.

Remarks: although highly fragmentary, only a limited number of spatangoids come into consideration for the present specimen. Its considerable size, as well as the shape and structure of the petals combined with the tuberculation and presence of a peripetalous fasciole, rule out many groups. Most likely candidates are found within the family Brissidae, namely the genera *Brissus*, *Meoma* and *Schizobrissus*. Based on direct comparison with extant material, we rule out *Brissus* because of its tendency to form lanceolate petal tips in large specimens (at least in *B. unicolor* Leske, 1778), its deeply indented peripetalous fasciole in interambulacra 1 and 4 and its narrow imporiferous zones. Additionally, the kink observed in distal petal V is very similar to the kinks/bends found frequently in the posterior petals of *Meoma ventricosa* (Lamarck, 1816) and in various species of *Schizobrissus*. While *Meoma* and *Schizobrissus* are closely similar, and have been considered as synonyms at times (Chesher 1970), it is possible to differentiate between the two genera (Lachkhem & Roman 1995). In species of *Meoma* there is only a weak frontal notch and the petals extend almost to the ambitus, whereas *Schizobrissus* has a deep frontal notch and much shorter petals. The fragment studied here clearly shows that the petals were comparatively short, terminating in the flattened aboral portion of the test above the ambitus. In fragments of extant *Meoma ventricosa* they terminate close to the ambitus, where the test is already distinctly curved. We thus conclude that our specimen is more correctly assigned to S*chizobrissus* than to *Meoma*. Owing to the nature of the specimen, a specific identification is impossible at this time without additional material.

Occurrence: ‘Pedra-que-Pica’, Santa Maria Island, Azores. At present, no representatives of either the genus *Meoma* or the genus *Schizobrissus* (extinct) are known from Azorean waters.

Superfamily Spatangidea Fischer, 1966
Family Loveniidae Lambert, 1905
Genus *Echinocardium* Gray, 1825

Echinocardium spec. 2

(Figs. 2.13D–G)

Material: two partially preserved coronas collected from Upper Miocene to lower Pliocene deposits at Ponta dos Frades (DBUA-F 980).

Description: The specimens available are small, with a test length of about only 21 mm. The corona is very thin and fragile. The outline is distinctly heartshaped and slightly wider than long. The frontal notch is narrow and quite shallow. In profile, the test is high (*c*. 70 % of TL) and rectangular, with a vertically truncated posterior end.

The apical disc is ethmolytic with four gonopores. The petals are confluent, slightly sunken and widen towards the apex. The frontal ambulacrum is distinctly, but not deeply sunken adapically and bears a single row of moderately widely spaced partitioned isopores in each column. The periproct lies high on the posterior face and is oval, vertically elongated.

Remarks: The two specimens from Ponta dos Frades are much smaller than the Ponta da Malbusca specimen and lack the pronounced subanal projection present in that specimen. It thus appears that at least two species of *Echinocardium* were present in the Late Miocene/Early Pliocene of the Azores. In terms of shape and outline they are

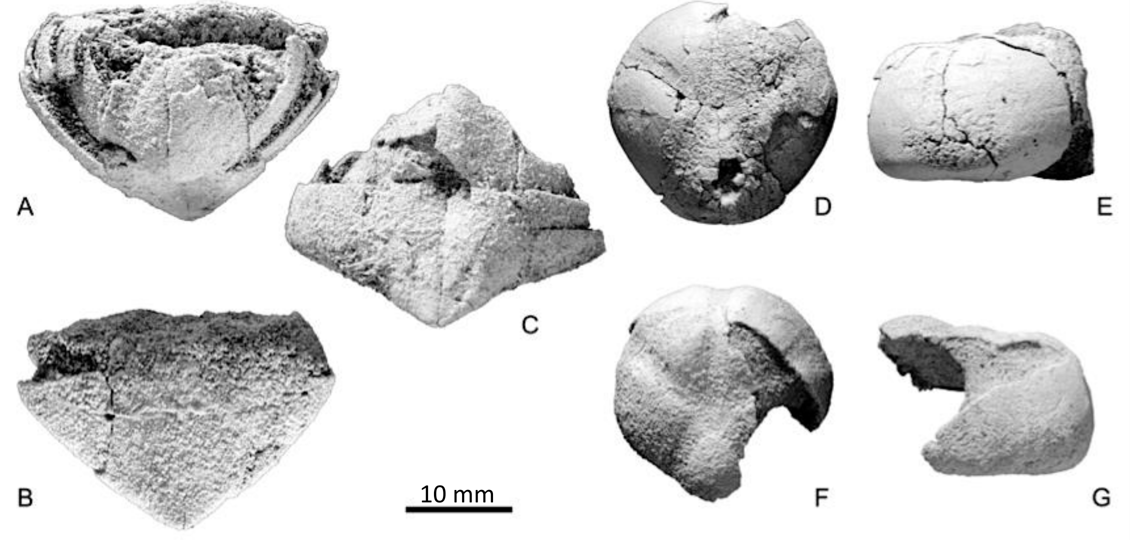


Figure 2.13. *Echinocardium* sp. 1 (A-C) and *Echinocardium* sp. 2 (D-G); A-C - aboral (A), oral (B), and posterior view of DBUA-F 370 (Ponta Malbusca); D-E - aboral (D) and left lateral (E) view of DBUA-F 980-1 (Ponta dos Frades); F-G - aboral (F) and right lateral (G) view of DBUA-F 980-2 (Ponta dos Frades).

very similar to *E. flavescens*, but do exhibit a sunken frontal ambulacrum adapically. They differ from *E. cordatum* in their small and rather widely spaced pores of adapical ambulacrum III.

Occurrence: on Santa Maria Island, known only from the late Miocene–early Pliocene of the Ponta dos Frades outcrop.

Echinocardium spec. 1

(Figs. 2.13A–C)

Material: fragmentary corona collected from Upper Miocene to lower Pliocene deposits at Ponta da Malbusca (DBUA-F 370).

Description: the single available specimen is a crushed fragment preserving the posterior end of the corona. The corona is very thin (≈0.7 mm thick) and fragile. The posterior paired petals are slightly sunken, widen towards the apex, and bear conjugate isopores. The posterior part of the plastron ends in a pointed process bearing a diamond-shaped subanal fasciole. The periproct lies high on the posterior face, is oval (vertically elongated) and appears to have been overhung by a small ‘hood’ (post-mortem distortion makes it difficult to confirm this). Aboral tuberculation, as far as preserved, appears to have been uniform at least in the posterior half of the corona.

Remarks: although highly fragmentary, the specimen from Ponta da Malbusca can clearly be assigned to the genus *Echinocardium* based on the characteristic shape of the posterior face and the structure of the posterior petals. A specific identification, however, is impossible without additional material. Today, *E. cordatum* (Pennant, 1777) and *E. flavescens* (Müller, 1776) occur in the area.

Occurrence: on Santa Maria Island, only known from the Upper Miocene/Lower Pliocene of the Ponta da Malbusca outcrop.

Spatangoida indet.

Material: Upper Miocene to Lower Pliocene of Ponta da Malbusca (two fragments; DBUA-F 188–18, 343–4) and Upper Miocene to Lower Pliocene of 'Pedra-que-Pica' (six fragments; DBUA-F 458, 459).

Description: the material is composed of heavily eroded small interambulacral fragments (less than 18.2 mm TL). They are relatively thick and bear perforated and crenulated tubercles arranged in a dense uniform pattern. A small fragment of about 9 mm TL (DBUA-F 458) bears two rows of large, elongate symmetrical isopores.

Remarks: the highly fragmentary nature of the material, largely lacking diagnostic characters, renders a more refined identification futile. It is not clear whether the fragments represented one or more spatangoid species. Based on the thickness of most fragments, it is unlikely that they derive from one of the *Echinocardium* species described above, instead they could be fragments of *Schizobrissus*, but this cannot be substantiated.

2.5. Discussion

Systematics and Biogeography

The material collected from the fossiliferous outcrops of Santa Maria Island comprises a total of 11 different taxa. The Upper Miocene to Lower Pliocene fauna includes one species of regular echinoid (*Eucidaris tribuloides*) and several irregular taxa, such as *Echinoneus* cf. *cyclostomus*, clypeasteroids (*Clypeaster altus* and *Echinocyamus pusillus*) and corona fragments of spatangoids (*Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids). *E.* cf. *cyclostomus* and the spatangoids are new records from the Miocene/Pliocene of Santa Maria, thus significantly increasing the echinoid diversity reported from that time slice on the island. The material collected from the Pleistocene outcrops (Lagoinhas and Prainha) includes three regular echinoid species, *Arbacia lixula*, *Paracentrotus lividus*, and *Sphaerechinus granularis*; the two former species are new records for the Pleistocene deposits of the island.

The extant shallow-water fauna reported from the Azores archipelago comprises a total of 14 echinoid species (Pereira 1997). Only two species of echinoids are common to both the Mio-Pliocene fauna of Santa Maria Island and the recent fauna of the Azores, *i.e., Eucidaris tribuloides* and *Echinocyamus pusillus*. However, the presence of *E. tribuloides* in the extant fauna of the Azores, based on a single report by Koehler (1898, pp. 7-9), is questionable. *E. tribuloides* typically occurs in the tropical parts of the Atlantic. As shown by Lares & Mcclintock (1991), when exposed to temperatures of 18°C this species shows a low growth rate and delayed gametic development, thus it is unlikely that it could maintain viable populations in the colder waters of the Azores, where the sea surface temperatures show an annual average of 19°C, ranging from 14°C to 24°C (Santos *et al.* 1995). Together with *E. tribuloides*, other typically tropical taxa found in the Santa Maria Mio-Pliocene but absent from the extant Azorean fauna (*E. cyclostomus*, *Clypeaster altus* and *Schizobrissus* sp.), may represent examples of local disappearance of thermophilic species due to a series of cooling events starting in the mid-Pliocene and continuing in the Pleistocene (Raffi & Monegatti 1993; Landau *et al.* 2007). The echinoids are yet another group of animals that increases the number of taxa which are believed to have disappeared from the Azores during the Pleistocene climatic deterioration: molluscs (Ávila 2005; Ávila *et al.* 2008b, 2009; Janssen *et al.* 2008), brachiopods (Kroh *et al.* 2008) and crustaceans (Winkelmann *et al.* 2010). This is consistent with the disappearance of these taxa from the North Atlantic and the Mediterranean, in which the absence of representatives of these genera on the present European and Northwest African coasts clearly contrasts with the rich Miocene fauna for the same regions (see Mortensen 1948; Chesher, 1970; Lessios *et al*. 1999; Kroh 2007). On the other hand, the presence in the Azorean Upper Miocene to Lower Pliocene of *E. pusillus*, typically a temperate species, tells us that the environmental conditions of the Azorean islands at the Miocene/Pliocene boundary did not restrict the presence of temperate species.

All the echinoid species present in the Pleistocene of Santa Maria represent relatively modern taxa (Mortensen 1943a, b; Smith 1988). The oldest of the genera, *Arbacia*, dates back to the Late Oligocene (Cooke 1941), and it is believed that *A. lixula* diverged from the American *A. punctulata* only about 3–5 million years ago (Metz *et al*. 1998). The fossil record of *A. lixula* from Santa Maria is in fact the oldest record of this common extant species. The fossil record of *Paracentrotus* extends to the Late Miocene (Mortensen 1943b), and no records of *Sphaerechinus* are known prior to the Pliocene (Mortensen 1943a). It is clear that, in terms of faunal affinities, the Pleistocene fauna shows no apparent differences regarding what is generally accepted for the Azorean extant fauna, *i.e*. a close relationship to the faunas of the Northeastern Atlantic and Mediterranean coasts (*e.g.,* Wirtz and Martins 1993; Santos *et al*. 1995; Ávila 2000, 2005).

Ecology

The Miocene echinoid fauna found on Santa Maria Island is dominated by irregular echinoids that typically live in soft bottom environments (spatangoids, clypeasteroids and *Echinoneus*), with the exception of *Eucidaris tribuloides*, which preferentially lives epifaunally on hard substrates. The presence of ecologically incompatible faunal elements may be explained by transport, as illustrated by Nebelsick (1992). Moreover, the detected dominance of irregular taxa may be explained by their preferred palaeoenvironments for, as noted by Smith (1984), irregular echinoids are potentially more prone to be preserved in the fossil record, because they live in environments of active sedimentation, in contrast to many regular euechinoids which live in areas of active erosion. Additionally, the fragmentary nature of the echinoid remains in the Santa Maria Miocene/Pliocene fossil record may testify as well that they may have spent some time decomposing on the ocean floor, before being incorporated in the sediment. Very few complete coronas were found, and most of these belong to the clypeasteroids, a group of irregular echinoids with a robust skeleton and thus a high preservation potential (Seilacher 1979; Smith 1984; Donovan & Portell 1996). Their tests are a frequent presence in the fossil record of high energy palaeoenvironments (see Nebelsick & Kroh 2002) and are the main reason why they are often preserved accumulated in coquinas (Smith 1984).

The diversity of echinoids and environments preserved in the Miocene/Pliocene deposits of Santa Maria differs markedly from that shown by the Pleistocene fossil record of the island. As pointed out by Donovan (2003), Pleistocene faunas tend to be closely related to the living biota of any area, and the Azorean Pleistocene is no exception (a similar conclusion was reached for the Pleistocene Azorean marine molluscs by Ávila *et al.* 2009). This is particularly the case, since the Pleistocene fossil record is usually highly selective in terms of palaeoenvironments exposed (only deposits from the uppermost subtidal and intertidal are currently accessible – environments which are prone to erosion and not usually preserved from older periods).

The three echinoid species identified from the Pleistocene outcrops of Santa Maria are the most conspicuous echinoids of the extant Azorean shallow waters (Marques 1983; Azevedo *et al.* 1994). They are typically found in the first few metres of the rocky shores of the archipelago, similar to the palaeoenvironmental settings preserved in the Pleistocene fossil record (see Ávila *et al.* 2009), thus making these echinoids the most likely species to occur in the Pleistocene fossil record of the islands. On the other hand, this may also be the reason for the apparent low echinoid diversity (*e.g.,* deeper Pleistocene sediments are currently unknown to occur onshore), making it difficult to find taxa living in slightly deeper settings such as brissids and diadematoids.

Dispersal and Colonization

As truly oceanic islands, the Azores were never connected to continental land masses. The great distances from nearest the continental shores (2,000 km from the Portuguese mainland) may represent a problem to many benthic species. However, all echinoid species present in the Pleistocene outcrops are known to have long planktotrophic larval stages, and thus can be considered to have had a great dispersal potential (Pedrotti & Fenaux 1992; Emlet 1995). The colonization of these islands is believed to have been made through chance-event dispersal for the majority of species, albeit for some at least this probably occurred during glacial terminations (short periods of time when sea-surface currents and favourable winds may have provided ‘windows of opportunity’; see Ávila 2005; Carine 2005; Ávila *et al.* 2009). Additionally, the abundant seamounts present between the Azores and the European and African mainland may have acted as ‘stepping stones’ particularly at times of low sea level, promoting the dispersal of benthic taxa with planktotrophic larvae.

In his review of the faunal history of the Atlantic islands, Briggs (1975) postulated that the lack of endemism in the Azores was due to the Pleistocene glacial episodes, which had wiped out the older Azorean fauna. Recent palaeontological studies do not support this idea, showing that several species of molluscs endemic to the Azores persisted in the archipelago (see Ávila *et al.* 2008a, b). Species solely restricted to shallow sand bottoms, however, were indeed heavily affected by low stands during glacial episodes when sea level dropped below the shelf break of the islands (Ávila *et al.* 2008b). Our limited data also show that, so far as echinoids are concerned, the fauna of the Azorean rocky shores in the Pleistocene was identical to the modern rocky shore fauna in the area. However, the echinoid taxa reported here from the Pleistocene outcrops of Santa Maria all have long-lived planktotrophic larval stages today and are thus unlikely to develop endemic offshoots. Modern examples of shallow-water echinoids investigated genetically (*e.g., Arbacia* – Metz *et al.* 1998, *Diadema* – Lessios *et al*. 2001) do show active gene flow over considerable distances.

2.6. Conclusions

In terms of general patterns, the fossil echinoid faunas from the Santa Maria Island outcrops reflect the overall Neogene faunal history of the North Atlantic. The conspicuous presence of species with tropical affinities in the Upper Miocene to Lower Pliocene fossil record, contrasts with a more temperate fauna present in the Pleistocene, which in turn is similar to the extant fauna in the Azores. Moreover, and similarly to what happens nowadays, the fossil echinoids from Santa Maria Island also support biogeographical relationships with the Northeastern Atlantic and the Mediterranean, in both the Miocene/Pliocene-boundary interval and the Pleistocene.

The low diversity of palaeoenvironments preserved in the sedimentary record of Santa Maria, particularly in the Pleistocene deposits, explains the low diversity of the echinoid fauna these in these time slices. This is particularly true if we consider that, in spite of the sampling effort (including bulk sampling) made since 1998, no other classes of echinoderms were collected. This is possibly related to diagenetic dissolution, which is prone to affect smaller-sized disarticulated elements of asterozoans, crinoids and holothurians more strongly than larger-sized echinoid remains. Nonetheless, the seven new records show that the specific richness of the echinoid fauna of Santa Maria Island was largely underestimated and should prove a valuable aid to future biogeographic studies in the Northeastern Atlantic.

ACKNOWLEDGEMENTS

Critical reviews and constructive comments from Alexander Mironov and a second, anonymous reviewer are gratefully acknowledged. We are grateful to the organizers and participants of the International Workshops "*Palaeontology in Atlantic Islands*" who helped in the fieldwork. We also thank the direcção regional da ciência e Tecnologia (regional government of the Azores), direcção regional do Ambiente e do Mar (Regional Government of the Azores), FCT (Fundação para a ciência e Tecnologia) of the Portuguese government for financial support, and we thank the Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto for field assistance. Fabrizio Lirer (Instituto Ambiente Marino costiero, Napoli) kindly provided information on Italian Pleistocene stratigraphy.

P. Madeira was supported by grant SFRH/BD/61146/2009 (FCT - Fundação para a Ciência e Tecnologia) of the Portuguese government, and by the SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Infrastructure Action under the FP6 and FP7 programmes.

2.7. References

Abdel-Monem, A.A., Fernandez, L.A. & Boone, G.M. (1975) K-Ar ages from the eastern Azores group (Santa Maria, São Miguel and the Formigas Islands). *Lithos*, 8, 247–254.

Agassiz, L. 1835. Prodrome d'une monographie des radiaires ou échinodermes. *Mémoires de la Société des Sciences Naturelles de Neuchâtel*, **1**, 168-199.

Agassiz, L. (1840) Catalogus systematicus ectyporum echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. *Sequuntur characteres diagnostici generum novorum vel minus cognitorum*. Oliv. Petitpierre, Neuchâtel, pp. 1–20.

Agassiz, L. & Desor, P.J.E. (1847) Catalogue raisonné des espèces, des genres, et des familles d'échinides. *Annales des Sciences Naturelles, troisième Série, Zoologie*, 8, 5–35, 355–380.

Agostinho, J. (1937) Sobre a tectónica da ilha de Santa Maria. *Açoreana*, 1, 281–286.

Airaghi, C. (1898) Echinidi del Pliocene Lombardo. *Atti della Società Italiana di Scienze naturali e del Museo Civico di Storia naturale in Milano*, 37, 357–377.

Airaghi, C. (1900) echinidi Postpliocenici di Monteleone calabro. *Atti della Società Italiana di Scienze Naturali*, 39, 65–74.

Ali, M.S.M. (1985) On some Pliocene echinoids from the area north of Mersa Alam, red Sea coast, egypt. *Paläontologische Zeitschrift*, 59(3–4), 277–300.

Ávila, S.P. (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago*, Supplement 2(A), 99–131.

Ávila, S.P. (2005) *Processos e padrões de dispersão e colonização nos Rissoidae (Mollusca: Gastropoda) dos Açores*. Phd Thesis, Universidade dos Açores, Ponta delgada, x+329 pp.

Ávila, S.P., Amen, R., Azevedo, J.M.N., Cachão, M. & García-Talavera, F. (2002) Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). *Açoreana*, 9, 343–370.

Ávila, S.P., Madeira, P., Mendes, N., Rebelo, A., Medeiros, A., Gomes, C., García-Talavera, F., Marques Da Silva, C., Cachão, M., Hillaire-Marcel, C. & de Frias Martins, A.M. (2008a) Mass extinctions in the Azores during the last glaciation: fact or myth? *Journal of Biogeography*, 35, 1123–1129.

Ávila, S.P., Madeira, P., Marques Da Silva, C., Cachão, M., Landau, B., Quartau, R. & De Frias Martins, A.M. (2008b) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science*, 23, 777–785.

Ávila, S.P., Madeira, P., Zazo, C., Kroh, A., Kirby, M., Da Silva, C.M., Cachão, M. & De Frias Martins, A.M. (2009) Palaeocology of the Pleistocene (MIS 5.5) outcrops of Santa Maria Island (Azores) in a complex oceanic tectonic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274, 18–31.

Ávila, S.P., Rebelo, A., Medeiros, A., Melo, C., Gomes, C., Bagaço, L., Madeira, P., Borges, P.A., Monteiro, P., Cordeiro, R., Meireles, R. & Ramalho, R. (2010) *Os fósseis de Santa Maria (Açores). 1. A jazida da Prainha*. OVGA – Observatório Vulcanológico e geotérmico dos Açores, Lagoa, 103 pp.

Azevedo, J.M.N., Rego, M.O. & Ávila, S.P. (1994) Ensaio de quantificação dos macro-invertebrados bênticos marinhos das caldeirinhas (Monte da guia). *Relatórios e Comunicações do Departamento de Biologia*, 22, 23–28.

Borghi, E. (1993) *Echinocyamus pusillus* (Müller, 1876) nel Pliocene e nel Pleistocene dell'emilia. echinodermi fossili emiliani IV. *Bollettino de la Società Reggiana Scienze Naturali*, 13, 1–18.

Borghi, E. (1995) *Paracentrotus lividus* (lamarck, 1816) nel Pleistocene dell'emilia. echinodermi fossili emiliani. *Bollettino de la Società Reggiana Scienze Naturali*, 15, 1–21.

Borghi E. (1999) Echinodermi fossili dell'emilia: i cidaridi del Plio-Pleistocene. *Parva Naturalia*, 1999, 105–125.

Briggs, J.C. (1975) *Marine ZooGeography*. Mcgraw-Hill, New York, xi+475 pp.

Bronn, H.G. (1860a). Die fossilen reste von Santa Maria, der südlichsten der Azorischen Inseln. In: G. Hartung, *Die Azoren in ihrer äusseren Erscheinung und nach ihrer geognostischen Natur*. Verlag von Wilhelm Engelmann, Leipzig, pp. 116–129.

Bronn, H.G. (1860b). Die Klassen und Ordnungen des Their reichs, wissenschaftlich dargestellt in Wort und Bild. *Zweiter Band. Actinozoen*. C.F. Winter'sche Verlagshandlung, Leipzig & Heidelberg, 434 pp.

Callapez, P.M. (2000) Upper Pleistocene marine invertebrates from Gruta da Figueira Brava (Arrábida, Portugal). *In*: M.T. Antunes (Ed.), last Neanderthals in Portugal. Odontologic and other evidence. *Memórias da Academia de Ciências de Lisboa, Classe de Ciências*, 38, 79–99

Callapez, P. & Soares, A.F. (2000) Late Quaternary warm marine mollusks from Santa Maria (Azores): paleoecology and paleobiogeographic considerations. *Ciências da terra* (UNL), 14, 313–322.

Carine, M.A. (2005) Spatio-temporal relationships of the Macaronesian endemic flora: a relictual series or window of opportunity? *Taxon*, 54, 895–903.

Checchia-Rispoli, G. (1907) Gli echinidi viventi e fossili sella Sicilia. Parte seconda: gli echinidi del Piano Siciliano dei ditorni di Palermo. *Palaeontographia Italica*, 13, 199–232.

Chesher, R.H. (1970) Evolution in the genus *Meoma* (Echinoidea: Spatangoida) and a description of a new species from Panama. *Bulletin of Marine Science*, 20, 731–761.

Clark, H.L. (1925a). *A catalogue of the recent Sea-Urchins (Echinoidea) in the collection of the British Museum (Natural History)*. Oxford University Press, London, 250 pp.

Claus, C.F.W. (1876) *Grundzüge der Zoologie.* N.G. Elwert'sche Universitätsbuchhandlung, Marburg & Leipzig, 3rd Ed, ixii+1254 pp.

Claus, C.F.W. (1880) *Grundzüge der Zoologie*. N.G. elwert'sche Universitätsbuchhandlung; Marburg & Leipzig, 4th Ed, vol. 1:,vii+821 pp., vol. 2, iv+522 pp.

Cooke, W.C. (1941) Cenozoic regular echinoids of eastern United States. *Journal of Paleontology*, 15, 1–20.

Cotter, J.C.B. (1892) Notícia de alguns fósseis terciários da ilha de Santa Maria no Arquipélago dos Açores. *Comunicações da Comissão de trabalhos Geológicos de Portugal*, 2, 255–287.

des Moulins, C. (1837) Troisième Mémoire sur les échinides. Synonymie générale. *Actes de la Société Linnéenne de Bordeaux*, 9, 45–364.

Desor, E. (1847) Sur quelques oursins fossiles de la Patagonie. *Bulletin de la Société Géologique de France*, Série 2, 4, 287–288.

Desor, E. (1855–1858) *Synopsis des échinides fossils*. Reinwald, Paris, ilxviii+ 490 pp.

Dixon, H.L. & Donovan, S.K. (1998) Oligocene echinoids of Jamaica. *Tertiary Research*, 18, 95–124.

Donovan, S.K. (1993) Jamaican Cenozoic Echinoidea. *In*: R.M. Wright & E. Robinson (Eds.), Biostratigraphy of Jamaica. *Geological Society of America Memoir*, 182, 371–412.

Donovan, S.K. (2001) Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 177–192

Donovan, S.K. (2003) Completeness of a fossil record: the Pleistocene echinoids of the Antilles, *Lethaia*, 36, 1–7.

Donovan, S.K. & Portell, R.W. (1996) *Clypeaster lamprus* H.L. Clark (Echinodermata, Echinoidea) in the Manchioneal Formation (early Pleistocene) of Jamaica. *Caribbean Journal of Science*, 32, 83–88.

Donovan, S.K. & Veale, C. (1996) The irregular echinoids *Echinoneus* Leske and *Brissus* Gray in the Cenozoic of the Antillean region. *Journal of Paleontology*, 70, 632–640.

Donovan, S.K., Portell, R.W. & Veltkamp, C.J. (2005) Lower Miocene echinoderms of Jamaica, West Indies. *Scripta Geologica*, 129, 91–135.

Emlet, R.B. (1995) Developmental mode and species geographic range in regular sea urchins (echinodermata: echinoidea). *Evolution*, 49, 476–489.

Ferreira, O.V. (1955) A fauna Miocénica da ilha de Santa Maria. *Comunicações dos Serviços Geológicos de Portugal*, 36, 9–44.

Ferreira, O.V. (1961) Equinídeos do Miocénico de Portugal continental e Ilhas Adjacentes. *Comunicações dos Serviços Geológicos de Portugal*, 45, 529–564.

Fischer, A.G. (1966) Spatangoids. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, U. echinodermata*. GSA & Univ. Kansas Press, Boulder, CO & Lawrence, KS, 3 (2), U543–U628.

França, Z., Cruz, J.V., Nunes, J.C. & Forjaz, V.H. (2003) Geologia dos Açores: uma perspectiva actual. *Açoreana*, 10, 11–140.

García-Talavera, F. (1990) Fauna tropical en el Neotirreniense de Santa Maria (I. Azores). *Lavori S.I.M.*, 23, 439–443.

Gray, J.E. (1825) An attempt to divide the echinida, or Sea eggs, into natural families. *Annals of Philosophy*, *new series*, 10, 423–431.

Gray, J.E. (1835) [On the genera distinguishable in *Echinus* Lamarck]. *Proceedings of the Zoological Society London*, 3, 57–59.

Gray, J.E. (1855) An arrangement of the families of Echinida, with descriptions of some new genera and species. *Proceedings of the Zoological Society London*, 23, 35–39.

Gregory, J.W. (1900) The echinoidea. *In*: Lankester, E.R. (Ed.), *A Treatise on Zoology. Part III. The Echinodermata*. A.&C. Black, London, pp. 282–332

Haeckel, E. (1896) *Systematische Phylogenie der wirbellosen Thiere (Invertebrata)*. *Vol. 2*, Georgreimer Verlag, Berlin, xviii+720.

Jackson, R.T. (1912) Phylogeny of the echini with a revision of Palaeozoic species. *Memoirs of the Boston Society of Natural History*, 7, 1–491.

Janssen, A.W., Kroh, A. & Ávila, S.P. (2008) Early Pliocene heteropods and pteropods (Mollusca, Gastropoda) from Santa Maria (Azores, Portugal): systematics and biostratigraphic implications. *Acta Geologica Polonica*, 58, 355–369.

Kirby, M.X., Jones, D.S. & Ávila, S.P. (2007) Neogene shallow-marine palaeoenvironments and preliminary Strontium isotope chronostratigraphy of Santa Maria Island, Azores. *In*: S.P. Ávila & de Frias Martins, A.M. (Eds.), Proceedings of the 1st "Atlantic IslandsNeogene" International Congress, Ponta delgada, 12–14 June (2006) *Açoreana*, Suplemento, 5, 112–115.

Koehler, R. (1898) Echinides et Ophiures provenant des campagnes du yacht l'Hirondelle. *Résultats des campagnes Scientifiques du Monaco*, 12, 1–78.

Kroh, A. (2005) *Catalogus Fossilium Austriae, Band 2, Echinoidea neogenica*. Verlag der Österreichischen Akademie der Wissenschaften, Wien, lvi+210

Kroh, A. (2007) Climate changes in the early to Middle Miocene of the central Paratethys and the origin of its echinoderm fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253, 169–207.

Kroh, A., Bitner, M.A. & Ávila, S.P. (2008) *Novocrania turbinata* (Brachiopoda) from the early Pliocene of the Azores (Portugal). *Acta Geologica Polonica*, 58, 473–478.

Kroh, A. & Mooi, R. (2018) World Echinoidea database. Available from http://www.marinespecies.org/echinoidea/ [online since 2010-08-26].

Kroh, A. & Nebelsick, J. (2003) Echinoid assemblages as a tool for palaeoenvironmental reconstruction – an example from the early Miocene of Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 201, 157–177.

Kroh, A. & Smith, A.B. (2010) The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8, 147–212.

Lackhem, H. & Roman, J. (1995) Les échinoïdes irréguliers (Néognathostomes et Spatangoïdes) du Messinien de Melilla (Maroc septentrional). *Annales de Paléontologie*, 81, 247–278.

Lamarck, J.B.P.M. de (1801) *Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux* [...]. Deterville, Paris, viii+432.

Lamarck, J.B.P.M. de (1816) *Histoire Naturelle des Animaux sans Vertèbres, présentant les caractères géneraux et particuliers de ces animaux, leur distribution, leur classes, leurs familles, leurs generes, et le citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la détermination des caractères essentiells de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des Principes fondamentaux de la Zoologie. Tome Troisième*. Verdière, Paris, 586 pp.

Lambert, J. (1905) Échinides. *In*: L. Doncieux, catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Première Partie. Montagne Noire et Minervois. *Annales de l'Université de lyon, Nouvelle Série, I. Sciences,Médecine*, 1, 10–14 (52–56).

Landau, B., Capelo, J.C. & Silva, C.M. (2007) Patterns of extinction and local disappearance of tropical marine gastropods; contrasting examples from across the North Atlantic. *In*: S.P. Ávila & de Frias Martins, A.M. (Eds.), Proceedings of the 1st "Atlantic Islands Neogene" International Congress, Ponta Delgada, 12–14 June 2006. *Açoreana*, Suplemento, 5, 50–58.

Lares, M.T. & Mcclintock, J.B. (1991) The effects of temperature on the survival, organismal activity, nutrition, growth and reproduction of the carnivorous tropical sea urchin *Eucidaris tribuloides*. *Marine Behavior and Physiology*, 19, 75–96.

Latreille, P.A. (1825) *Familles naturelles du régne animal*. Baillière, Paris, 570 pp.

Leske, N.G. (1778) Jacobi Theodori Klein naturalis dispositio echinodermatum, edita et descriptionibus novisque inventis et synonomis auctorem aucta. Addimenta ad I. T. *Klein naturalem dispositionem echinodermatum.* G.E. Beer, Leipzig, xxii+278 pp.

Lessios, H.A., Kessing, B.D., Robertson, D.R. & Paulay, G. (1999) Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution*, 53, 806–817.

Lessios, H.A., Kessing, B.D. & Pearse, J.S. (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55, 955–975.

Linnaeus, C. (1758) *Systema Naturæ per regna tria Naturae secundum classes, Ordines, genera, Species, cum characteribus, differentiis, synonymis, locis. edito decima, reformata. Tomus I. Impensis direct*. Laurentii Salvii, Holmiae, 824 pp

Madeira, P., Kroh, A., de Frias Martins, A.M. & Ávila, S.P. (2007) The marine fossils from Santa Maria Island (Azores, Portugal): a historical overview. *In*: S.P. Ávila & de Frias Martins, A.M. (Eds.), Proceedings of the 1st “Atlantic Islands Neogene” International congress, Ponta delgada, 12–14 June 2006. *Açoreana*, Suplemento, 5, 59–73.

Marcopoulou-Diacantoni, A. (1967) La faune des échinides néogènes des Pays Helléniques. *Annales Géologiques des Pays Helléniques*, 18, 331–406.

Marques, V.M. (1983) Peuplemnts benthiques des Açores. 1. Echinodermes. *Arquivos do Museu Bocage*, 2,1–7.

Mayer, K. (1864) SystematischesVerzeichniss der fossilen reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. *In*: G. Hartung, *Geologische Beschreibung der Inseln Madeira und Porto Santo*. W. Engelmann, Leipzig, pp. 183–298.

Metz, E.C., Gomez-Gutierez, G. & Vacquier, V.D. (1998) Mitochondrial DNA and bindin gene sequence evolution among allopatric species of the sea urchin genus *Arbacia*. *Molecular Biology and Evolution*, 15, 185–195.

Mironov, A.N. (2006) Echinoids from seamounts of the northeastern Atlantic; onshore/offshore gradients in species distribution. *In*: A.N. Mironov, A.V. Gebruk & A.J. Southward (Eds.), *Biogeography of the North Atlantic Seamounts*, KMK Scientific Press, Russian Academy of Sciences. P.P. Shirshov Institute of Oceanology, Moscow, pp. 96–133.

Mironov, A.N. & Sagaidachny, A.Y. (1984) Morphology and distribution of the recent echinoids of the genus *Echinocyamus* (echinoidea: Fibulariidae). *Transactions of the P.P. Shirshov Institute of Oceanology*, 119, 179–204.

Mitchell-Thomé, R.C. (1974) The Sedimentary rocks of Macaronesia. *International Journal of Earth Sciences*, 63, 1179–1216.

Mitchell-Thomé, R.C. (1976) *Geology of the middle Atlantic Islands*. Gebrüder Borntraeger, Berlin, ix+382.

Mooi, R. (1989) living and fossil genera of the Clypeasteroida (echinoidea: echinodermata): An illustrated key and annotated checklist. *Smithsonian Contributions to Zoology*, 488, 1–51.

Mortensen, T. (1903) *The Danish Ingolf-expedition 1895–1896. Vol. 4, No. 2. Echinoidea, pt. 1*. Bianco Luno, Copenhagen, 198 pp.

Mortensen, T. (1907) *The Danish Ingolf-expedition 1895–1896. Vol. 4, No. 2. Echinoidea, pt. 2*. Luno, Copenhagen, 200 pp.

Mortensen, T. (1928) *A monograph of the echinoidea. I. Cidaroidea*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 551 pp.

Mortensen, T. (1935) *A monograph of the echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 647 pp.

Mortensen, T. (1943a) *A monograph of the echinoidea. III.2 Camarodonta I*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 553 pp.

Mortensen, T. (1943b) *A monograph of the echinoidea. III.3 Camarodonta II*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 446 pp.

Mortensen, T. (1948) *A monograph of the echinoidea. IV.2 Clypeasteroida*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 647 pp.

Morton, B., Britton, J.C. & de Frias Martins, A.M. (1998) *Ecologia Costeira dos Açores*. Sociedade Afonso chaves, Ponta Delgada, x+249 pp.

Müller, O.F. (1776) *Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum Characteres, Nomina, et Synonyma Imprimis Popularium*. pis Hallageriis, Havniæ, xxxii+282 pp.

Nebelsick, J.H. (1992) Echinoid distribution by Fragment identification in the Northern Bay of Safaga, Red Sea, Egypt. *Palaios*, 7, 316–328.

Nebelsick, J.H. & Kroh, A. (2002) The Stormy Path from life to death Assemblages: The Formation and Preservation of Mass Accumulations of Fossil Sand dollars. *Palaios*, 17, 378–393.

Néraudeau, D., Goubert, E., lacour, D. & Rouchy, J.M. (2001) Changing biodiversity of Mediterranean irregular echinoids from the Messinian to present-day. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 175, 43–60.

Néraudeau, D., Barbe, S., Mercier, D. & Roman, J. (2003) Signatures paléoclimatiques des échinides du Néogène final Atlantique à faciès redonien. *Annales de Paléontologie*, 89, 153–170.

Néraudeau, D. & Masrour, M. (2008) Évolution de la biodiversité et de la distribution paléobiogéographique des échinides sur les côtes Atlantiques du Maroc du Tortonien à l'Actuel. *Geodiversitas*, 30, 211–232.

Olson, S.L. & Hearty, P.J. (2009) A sustained +21 m sea-level highstand during MIS 11 (400 ka): direct fossil and sedimentary evidence from Bermuda. *Quaternary Science Reviews*, 28, 271–285.

Palumbi, S.R. & Lessios, H.A. (2005) Evolutionary animation: how do molecular phylogenies compare to Mayr's reconstruction of speciation patterns in the sea? *Proceedings of the National Academy of Sciences USA*, 102, 6566–6572.

Pedrotti, M.L. & Fenaux, L. (1992) Dispersal of echinoderm larvae in a geographical area marked by upwelling (Ligurian Sea, NW Mediterranean). *Marine Ecology Progress Series*, 86, 217–227.

Pennant, T. (1777) *British Zoology. Crustacea, Mollusca, Testacea*, 4 vols., London.

Pereira, M.O.R. (1997) Checklist of the littoral echinoderms of the Azores. *Açoreana*, 8, 331–337.

Van Phelsum, M. (1774) *Brief aan . . . c. Nozeman . . . over de gewelv-Slekken of Zee-engeln. Waar achter gevoegd zyn twee beschrijvingen, de eene van zekere Soort van Zee-Wier; die andere van Maaden, in eene vuile Verzweeringe gewonden*. Rotterdam, 145 pp.

Philippe, M. (1998) Les Échinides Miocènes du Bassin du Rhône: révision systématique. *Nouvelles Archives du Museum d'Histoire Naturelle de Lyon*, 36, 3–441.

Pomel, A. (1869) *Revue des échinodermes et de leur classification pour servir d'introduction a l'étude des fossiles*. Deyrolle, Paris, 67 pp.

Pomel, A. (1883) *Classification méthodique et genera des échinides vivantes et fossiles*. Thèses présentées à la Faculté des Sciences de Paris pour obtenir le grade de docteur ès Sciences Naturelles. Adolphe Jourdan, Alger, 131 pp.

Pomel, A. (1887) *Paléontologie ou description des animaux fossils de l'Algérie. Zoophytes. 2e fascicule. – échinodermes. 2e livraison*. Adolphe Jourdan, Alger, 344 pp.

Raffi, S. & Monegatti, P. (1993) Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climaticoceanographic and stratigraphic inference. *Ciências da terra (UNL)*, 12, 45–50.

Reiss, W. (1862) Mittheilungen über die tertiären Schichten von Santa Maria, der südlichsten der Azoren, und ihre organischen einschlüsse. *Neues Jarhrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde*, 1862, 1–48.

Rose, E.P.F. & Wood, J.L. (1999) *Clypeaster* and *Echinolampas* (Echinoidea: Irregularia) from Neogene basins of southeast Spain, and the Mediterranean Messinian „salinity crisis". *In*: M.D. Candia Carnevali & Bonasoro, F. (Eds.), *Echinoderm research 1998 – Proceedings of the 5th Europea Conference Echinoderms/Milan/Italy/7–12 Sept.1998*. A.A. Balkema, Rotterdam/Brookfield. pp. 377–382.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M. & Isidro, E.J. (1995) Marine research and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5, 311–354.

Schultz, H. (2005) *Sea urchins*. Heinke & Peter Schulz Partner Scientific Publication, Hemdingen, xii+484.

Seguenza, G. (1880) Le formazioni terziarie nella provincia di reggio (Calabria). *Memoria della Reale Accademia dei Lincei, Serie 3a Memorie della Classe di Scienze Fische, Matematiche e Naturali*, 6 (1877), 1–446.

Seilacher, A. (1979) Constructional morphology of sand dollars. *Paleobiology*, 5, 191–221.

Serralheiro, A. (2003) A geologia da ilha de Santa Maria, Açores. *Açoreana*, 10, 141–192.

Serralheiro, A. & Madeira, J. (1990) Stratigraphy and geochronology of Santa Maria island (Azores). *In*: Anonymous (Ed.) *Livro de Homenagem ao Prof. Carlos Romariz. Departamento de geologia da Faculdade de Ciências da Universidade de Lisbon*, Lisbon, pp. 357–376.

Serralheiro, A., Alves, C.A. Dem., Forjaz, V.H. & Rodrigues, B. (1987) *Carta Vulcanológica dos Açores. Ilha de Santa Maria. 1:15.000.* Centro de Vulcanologia do I.N.I.C., Ponta Delgada.

Simpson, G.A. (2001) First record of the holectypoid echinoid *Echinoneus cyclostomus* Leske from the late Pleistocene Falmouth Formation of Jamaica. *Caribbean Journal of Earth Sciences*, 35, 33–36.

Smith, A.B. (1978) A functional classification of the coronal pores of regular echinoids. *Palaeontology*, 21, 759–789.

Smith, A.B. (1984) *Echinoid Palaeobiology*. Allen & Unwin, London, x+190 pp.

Smith, A.B. (1988) Phylogenetic relationships, divergence times and rates of molecular evolution for camarodont sea urchins. *Molecular Biology and Evolution*, 5, 345–365.

Stockley, B., Smith, A.B., Littlewood, T., Lessios, H.A. & MacKenzie-dodds, J.A. (2005) Phylogenetic relationships of spatangoid sea urchins (Echinoidea): taxon sampling density and congruence between morphological and molecular estimates. *Zoologica Scripta*, 34, 447–468.

Troschel, F.H. (1872) Die Familie der echinocidariden (1). *Archiv für Naturgeschichte*, 38, 293–356.

Westergren, A.M. (1911) Echini – *Echinoneus* and *Micropetalon*. Reports on the Scientific results of the expedition “Albatross”. *Memoirs of the Museum of Comparative, Zoology*, 39, 41–68.

Winkelmann, K., Buckeridge, J.S., Costa, A.C., Dionísio, M.A.M., Medeiros, A., Cachão, M. & Ávila, S.P. (2010) *Zullobalanus santamariaensis* sp. nov., a new late Miocene barnacle species of the family Archaeobalanidae (Cirripedia: Thoracica), from the Azores. *Zootaxa*, 2680, 33–44.

Wirtz, P. & Martins, H.R. (1993) Notes on Some rare and little known Marine Invertebrates From the Azores, with a discussion of the Zoogeography of the region. *Arquipélago,* 11A, 55–63.

Zbyszewski, G. & Ferreira, O.V. (1962a) Étude géologique de l’île de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal*, 46, 209–245.

Zbyszewski, G. & Ferreira, O.V. (1962b) La faune miocène de l’île de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal*, 46, 247–289.

Zbyszewski, g., Ferreira, O.V. & Assunção, C.T. (1961a) *Carta geológica de Portugal na escala 1/50 000. Notícia explicativa da folha de Ilha de Santa Maria (Açores)*. Serviços geológicos de Portugal, Lisbon, 1–28 pp.

Zbyszewski, G., Ferreira, O.V. & Assunção, C.T. (1961b) Le géologie dês îlots de Formigas au Ne de l’île de Santa Maria. *Comunicações dos Serviços Geológicos de Portugal*, 45, 513–518.

von Zittel, K.A. (1879) Echinodermata. *Handbuch der Paläontologie: Paläozoologie*. R. Oldenbourg. München & Leipzig, 1(1), 308–560.

Chapter 3. Species distributions: virtual or real - the case of *Arbaciella elegans* (Echinoidea: Arbaciidae)

Kroh, A., **Madeira, P.** & Haring, E. (2011) Species distribution: virtual or real – the case of *Arbaciella* elegans (Echinoidea: Arbaciidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 99–105.

Abstract

The distribution of species is expressed by their occurrence in local faunal lists often compiled by non-taxonomists. In the case of rare or cryptic species, this can pose a severe limitation on the validity and thus the application of the resulting biodiversity data. Here, we show an example of a shallow-water echinoid to illustrate problematic distribution data based on misidentification. This species, *Arbaciella elegans*, was established on the basis of Central African material and later reported from various places in the Mediterranean and the Northern Atlantic. Morphological comparison with the type material casts considerable doubt on the validity of these records. Genetical characterization of material from the Azores clearly shows that the dark *Arbaciella* phenotype reported to the Mediterranean and north-east Atlantic in fact represents juveniles of another species, namely *Arbacia lixula*.

Key words: Misidentification; Echinoidea; *Arbaciella*; Mediterranean.

3.1. Introduction

Marine faunal lists are usually compiled from expedition reports, museum collections and individual taxonomic papers. Huge efforts are made by international initiatives to make biodiversity data available to a broad audience [*e.g.*, OBIS – Ocean Biogeographic Information System, WoRMS – World Register of Marine Species (Appeltans *et al.* 2011), MarBef – Marine Biodiversity and Ecosystem Functioning EU Network of Excellence, GBIF – Global Biodiversity Information Facility…). In theory, this should enable decision-makers to rapidly access information needed for conservation issues and promote biodiversity research in general.

Data quality in these databases, however, strongly relies on the quality of the data sources used and the critical evaluation by the responsible taxonomic editors. Despite this rigorous evaluation process, taxonomic editors often have to rely on the correctness of individual species records, especially so in the case of rare or cryptic species where material is scarce. In these cases, an iterative approach involving data from multiple sources could increase the accuracy of species identification and distribution patterns (Tan *et al.* 2009).

We are currently critically reviewing the shallow-water echinoid fauna of the Azores, within the scope of a PhD project focussing on understanding of the colonization of the Azores by a European-type echinoderm fauna. Being oceanic islands, the Azores are natural laboratories for the study of the processes and patterns of dispersion, colonization and ultimately of the appearance of new species (Ávila *et al.* 2009). One of the echinoids recorded from the Azores (Marques 1983; Pereira 1997) – *Arbaciella elegans* Mortensen, 1910 – proved to be problematic. This is a very small and poorly known species, which typically occurs under boulders and crevices in the shallow subtidal of rocky shores. It is generally considered a very rare species (Grubelic & Antolic 2000), but this likely is due to collection bias rather than true rarity.

According to Mortensen (1910, 1935), A. elegans may be confused with juveniles of *Arbacia lixula* (Linnaeus, 1758). Later on Tommasi (1964), based on juvenile *Arbacia* material from Brazil, questioned the validity of the genus *Arbaciella* as such, suggesting that this might be a name based upon juvenile material of *A. lixula* only. These concerns, however, were considered to be clarified by Régis (1982), who

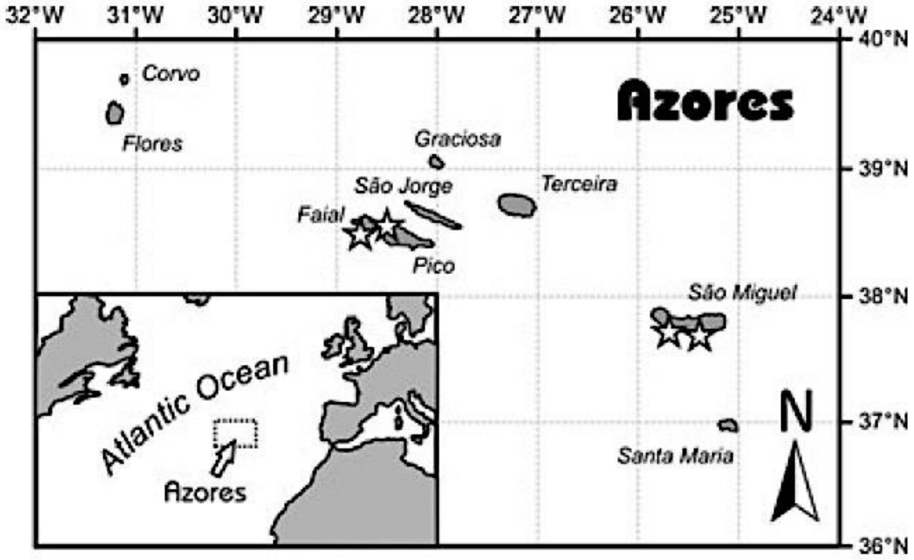


Figure 3. Study area. Stars indicate location of samples.

presented data supporting the validity of the genus based primarily on spine morphology.

To confirm the presence of A. elegans in the Azores, we located the material of Marques (1983) and collected fresh Azorean specimens and used these for the morphological and molecular investigations.

3.2. Material and methods

Specimens studied

The specimens used in this study were collected at two different islands of the Azores Archipelago (Fig. 3.1). Marina de Vila Franca do Campo, São Miguel (N37°42'48" W25°25'49"; four specimens, test diameter (D) ranging from 4.5 to 10 mm; 5 m depth; collection date: 10 July 2006) and Prainha, Madalena, Pico Island (N38°31'51" W28°32'12"; 14 specimens ranging from 1.5 to 4 mm; intertidal; collection date: 1 April 2009). This material is housed at the Natural History Museum of Vienna, 3rd Zoological Department [Lot no. 20086 (São Miguel), 20087 (Pico)].

The material of Marques (1983) is housed at Museu Nacional de História Natural (Universidade de Lisboa), Museu Bocage, Lisboa, Portugal, in the Colecções de Invertebrados [Lot no. 20743 (MB39-000367) from Ponta Delgada harbour, São Miguel Island (11 specimens, TD ranging from 4.8 to 8.1 mm; collected by V. Marques, 1982); Lot no. 20748 (MB39-000372) from Castelo Branco, Faial Island, (three specimens, TD ranging from 4.9 to 13 mm; collected by V. Marques, 1979)].

Additionally, the Azorean material was compared with specimens from the type area of *A*. *elegans* from coastal Central Africa [Museu Bocage lot no. 16723 (MB39-000193) from Baia da Costa, Angola (depth: 12 m, collected 25 August 1959; three specimens, TD ranging from 3.8 to 4.9 mm; det. G. Cherbonnier, 1963); Zoologisches Museum der Universitat Hamburg, Germany (ZMUH) specimen no. E211 from Sette Cama, Gabun (collected 17 March 1888 by C. Hupfer, holotype of *A*. *elegans* Mortensen 1910)].

Morphological analysis

SEM investigations were carried out at the Natural History Museum of Vienna, Austria (NHMW) using the JEOL 6400 electron microscope of the Department of Mineralogy and Petrology. For the examination of spine microstructure, specimens were cleaned using enzymatic digestion (Tiago *et al.* 2005). Specimens of both sampling stations were investigated and compared to adult and juvenile material of *A*. *lixula* from various Mediterranean and Atlantic localities preserved in the collections of the NHMW and the Departamento de Biologia, Universidade dos Açores, Portugal (DBUA). Morphological terminology follows Durham & Wagner (1966) and Kroh & Smith (2010).

DNA extraction and PCR amplification

Four specimens were investigated genetically: Arba1 (Vila Franca do Campo, São Miguel; from specimen no. 20086a), Arba2, Arba3 and Arba4 (all from Prainha, Madalena, Pico; from specimen nos 20087a–c; see above for locality and collection details). DNA from a small piece of lantern muscle preserved in 70% ethanol was extracted using the DNAeasy blood and tissue kit (Qiagen, Hilden, Germany). Extraction was performed according to the manufacturer’s protocol with a final elution volume of 100 µl elution buffer. A control extraction without tissue was performed to test for contaminated reagents.

PCR primers specific for *A*. *lixula* were designed on the bases of published sequences of the mitochondrial cytochrome c oxidase subunit I gene (*COI*): ArbCOI1 + 5’-GCTTGAGCAGGCATGGTAGG-3’, ArbCOI2-5’-GGTCTCCTCCACCTGCTGG-3’. The resulting PCR fragment covering 611 bp of the COI gene is slightly shorter than the sequences used by Metz *et al.* (1998). PCR (35 reaction cycles, annealing temperature:

60°C) was performed on a Master gradient thermocycler (Eppendorf) in 25 µl with 0.2 units TopTaq (Qiagen), 1 µM of each primer and 0.2 mM of each dNTP (Qiagen). Control PCRs were performed with the control extractions and with distilled water instead of template. PCR products were purified with the Qiaquick PCR Purification kit (Qiagen) and sequenced directly, both strands using the PCR primers. Sequencing was performed by AGOWA (Berlin, Germany).

Phylogenetic analysis

Editing and alignment of sequences were performed using the BioEdit software package version 5.0.9 (Hall 1999). Sequences of four species of *Arbacia* (*A. lixula*, *A. incisa*, *A. dufresnei*, *A. punctulata*) published by Metz *et al.* (1998) and of the outgroup *Strongylocentrotus purpuratus* (GenBank accession number X12631) were included for comparison.

The published sequences contain a number of Ns, and the respective positions were excluded from the alignment prior to the analysis and calculation of distances. A neighbour-joining dendrogram (NJ; Saitou & Nei 1987) using p distances was calculated with the software package Paup* (version 4.0b10; Swofford 2005). Bootstrap analysis was carried out with 1000 replicates. P distances were also calculated with Paup*. The sequences determined in the course of this study are registered under the GenBank accession numbers JN603630–JN603633. For comparison, sequences were derived from GenBank (De Giorgi *et al.* 1996; Metz *et al.* 1998).

3.3. Results

Morphology

The new specimens collected from the Azores and those of Marques (1983) are small, ranging from 1.5 to 13 mm. They are characterized by their naked aboral side (Fig. 3.2a), the spines being restricted to the ambitus and the oral side. The uppermost four plates in each interambulacral column do not bear primary spines, nor fully developed tubercles. In place of the primary tubercles, rounded nodules can be observed, which transform to spine-bearing tubercles in larger specimens (D 20 mm and above). Phyllodes are feebly developed in the smallest specimens examined.

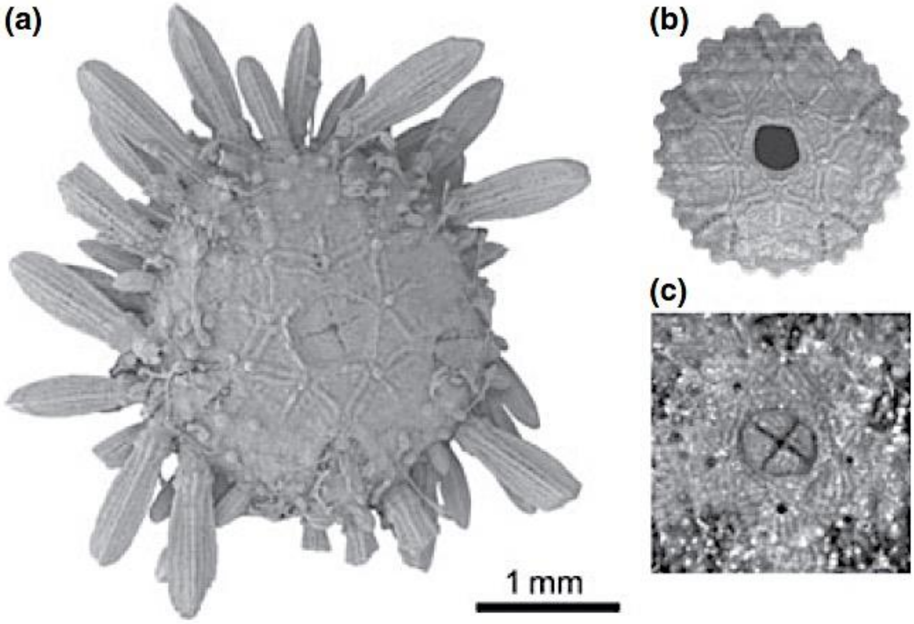


Figure 3.2. General shape and apical disc development in juvenile *Arbacia lixula* collected from the Azores: corona with spines and pedicellariae attached (a), cleaned corona (b) and the apical disc with early gonopore formation (c). Corona diameters: A: 2.43 mm [Natural History Museum of Vienna, Austria (NHMW 20087a)], B: 1.77 mm (NHMW 20087b), C: 6.1 mm (MB 20743).

With growth, the number of tube feet around the peristome increases.

The apical disc is about half of TD in small specimens (Fig. 3.2b) and becomes proportionally smaller with growth. It is of dicyclic type and has four valve-like plates covering the periproct.In the Azorean specimens, gonopores were observed in individuals of 6.1 mm TD (Fig. 3.2c) or larger. However, there appears to be a considerable variation in the onset of sexual maturity, some of the specimens between 7 and 10 mm not showing any open gonopores yet. The genital plates, like the adapical ambulacral plates, are ornamented with epistromal ridges.

In small specimens, only a single ring of short, lanceolate spines is present (Figs. 3.2a and 3.3a–e). With increasing corona size, spines become more numerous and more elongate. In cross-section, the spines are dorsoventrally flattened and show a reticulate microstructure. Hyaline wedges are just starting to form in the In small specimens, only a single ring of short, lanceolate spines is present (Figs. 3.2a and 3.3a–e). With increasing corona size, spines become more numerous and more elongate. In cross-section, the spines are dorsoventrally flattened and show a reticulate

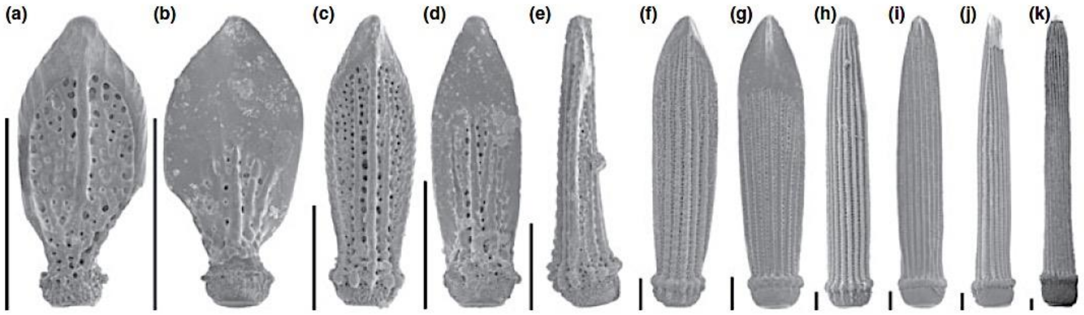


Figure 3.3. Changing spine morphology during the growth of *Arbacia lixula* (SEM images of ambital spines from a 1.77 mm test diameter specimen (a–c) to a fully grown individual (k). Scale bars equal 250 mm. a, c, f and h show aboral faces, b, d, g, i and k oral faces and e and j lateral faces.

microstructure. Hyaline wedges are just starting to form in the outer part of the spine. The spine surface microstructure differs between the oral and aboral sides of each spine. On the oral face, ridges are smooth, whereas on the aboral face, the ridges are densely coveredby micro-thorns. In specimens of *c.* 10 mm TD and above, spines start to become more rounded in cross-section and lose their lanceolate outline. They closely resemble small primary spines in adult *A. lixula*.

The colour of the specimens ranges from dark olive brown to black (Fig. 3.4a). Smaller specimens tend to be lighter in colour, because of their thinner, almost translucid skin cover. The colour of the spines too varies from purplish brown to dark olive green. Again, they tend to become darker to almost black in larger specimens. Colour perception of the specimens strongly depends on lighting and specimen preservation (alcohol versus dry specimens). If illuminated from below, a violet hue and diffuse banding can be seen in the spines.

Comparison with the type material

Morphologically, the Azorean specimens are very similar to the type material of *A. elegans* from Gabon (formerly French Congo). As described in detail by Mortensen (1910), this form is characterized by its naked aboral side, flattened and lanceolate spines, and epistromal ornament. Additionally, the early opening of the gonopores (at 7 mm TD) was considered characteristic by Mortensen, a trait that can be observed in our material as well.

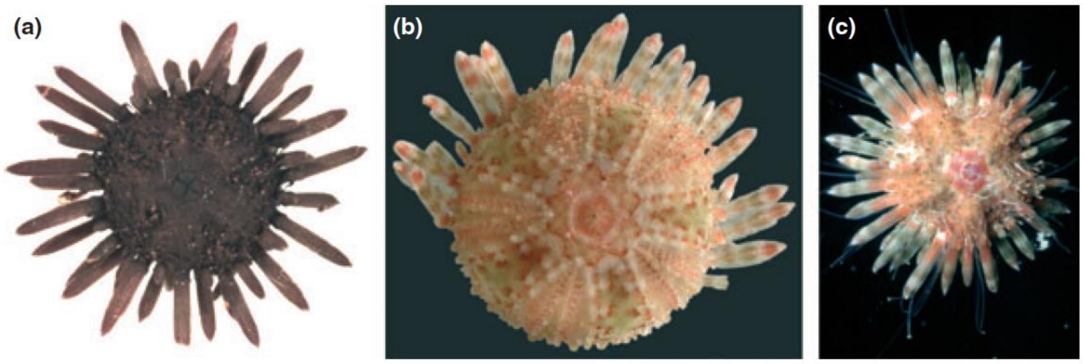


Figure 3.4. Comparison of a specimen from the Azorean population (a) with the holotype of *Arbaciella elegans* Mortensen 1910 (b) and a juvenile *Arbacia lixula* (Linnaeus, 1758) from Brazil (c). Corona diameters: a: 4.5 mm, B: 7 mm, c: *c.* 5 mm. Image b courtesy of H. Schultz, image c by A. Migotto.

The only apparent difference between the Central African specimens and the Azorean material lies in the colouration. Specimens from the Azores are of dark brown to black colour (Fig. 3.4a), like virtually all of the Mediterranean records (Tortonese 1965; Riedl 1983; Giacobbe & Rinelli 1992; Salas & Hergueta 1994; Baumeister & Koch 1998). Thus, they strikingly differ from Mortensen's (1910) bright-coloured type specimen, which is light green with pink patterns (Fig. 3.4b). Later records from Angola [Koehler 1914 and material in the ZMUH and Museu Bocage, Lisboa, Portugal (MB) collections] of A. *elegans* confirmed the colour pattern described by Mortensen.

A similarly bright colouration was observed in juveniles of the Brazilian population of *A. lixula* by Tommasi (1964; see Fig. 3.4c), who consequently questioned the validity of the genus *Arbaciella* as such.

The re-description of *A*. *elegans* by Régis (1982) was based on Mediterranean material rather than specimens from the type region. Based on that material, Régis (1982) suggested that *Arbaciella* was a valid genus and easily distinguished from *A. lixula*. Growth series of *Arbacia*, however, show that the features considered as diagnostic by Régis (1982) are in fact different ontogenetic stages (Harvey 1956; Emlet 2010).

Mitochondrial DNA phylogeny

A partial COI sequence was determined from four individuals from the Azores (Arba-1, Arba-2, Arba-3, Arba-4) collected at two sites. For comparison, the sequences were aligned with corresponding published sequences of *A. lixula*, *A. incisa*, *A. dufresnei* and *A. punctulata*. A NJ tree calculated from these sequences is shown in (Fig. 3.5). The four species are monophyletic groups in the tree and are supported by 100% bootstrap values. The relationships between species are less well supported. However, the tree was not intended to elucidate the phylogenetic relationships between species, but to illustrate intra- and interspecific variation (as reflected in p distances) of these sequences.

The sequences determined in this study are located in the *A. lixula* clade. Within this clade, there is a differentiation into two subclades representing individuals from Brazil on the one hand and from the Mediterranean (Naples, Palermo) and the Atlantic (Azores) on the other. The sequences Arba1-4 are found in the latter subclade.

P distances of the sequences Arba1-4 from the Azores range between 0.2% and 1.1%. These distances fall within the range found in the European subclade of *A. lixula* (0.2–2.9%; mean 1.0%). Between the two subclades (Mediterranean and Atlantic versus Brazil), the distances range from 1.4% to 3.4% (mean 2.4%). Mean genetic distances between the four species *A. lixula*, *A. punctulata*, *A. dufresnei* and *A. incisa* range from 8.0% to 11.6% (Table 3.1).

3.4. Discussion

Based on the morphological and molecular data presented above, the Azorean A. *elegans* first reported by Marques (1983) turned out to be actually misidentified juvenile specimens of *A. lixula*. The COI sequences determined in this study cluster within the *A. lixula* clade scattered within the Mediterranean-Atlantic subclade.

The genetic distances fall within the genetic intraspecific variation in *A. lixula* as determined from individuals from Mediterranean and Atlantic occurrences. The same is true for coronal and appendage morphology, which fully falls within the range observed in the growth series of *A. lixula*. In many taxa, newly metamorphosed and juvenile echinoids look strikingly different in comparison with conspecific adults (Emlet 2010). This is especially true for the genus *Arbacia*, where the first spines to be formed are distinctly lanceolate or paddle shaped and very unlike those of the adults.

Arbacia lixula is a common inhabitant of shallow-water hardgrounds throughout the Mediterranean, the Atlantic coast of Spain, Portugal and north-western Africa. Additionally, it occurs in the Azores, Cape Verde Islands, the Canaries,

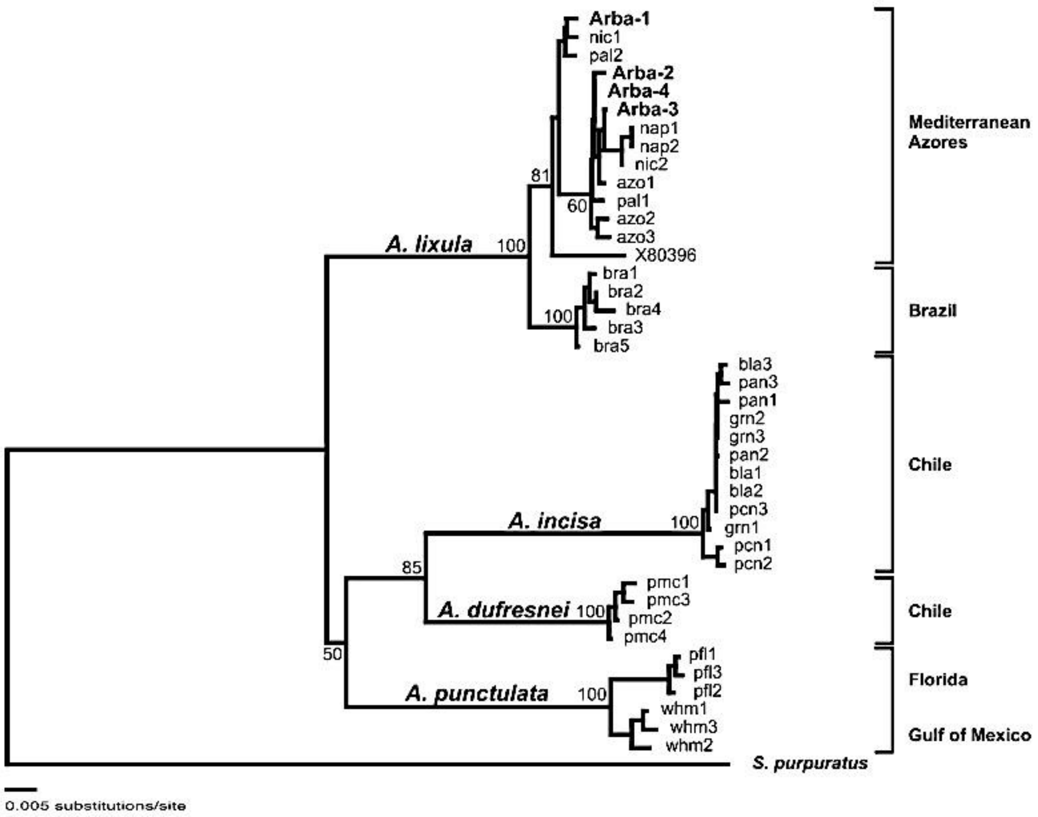


Figure 3.5. NJ tree of cytochrome c oxidase subunit I gene sequences to show the positions of the specimens analysed in this study (bold) with respect to the published sequences of Metz *et al.* 1998 (abbreviations of sequences are taken from Metz *et al.* 1998) and of De Giorgi *et al.* (1996; accession number X80396; no geographic origin available). Bootstrap values are shown at the nodes. Outgroup: *Strongylocentrotus purpuratus* (accession number X12631).

Madeira and Brazil, the latter population of *A. lixula* being a genetically distinct population (Palumbi & Lessios 2005). Specimens from Central Africa have been regarded as separate subspecies *A. lixula africana* (Troschel 1873, Mortensen 1935).Despite being highly abundant locally, juvenile individuals of *A. lixula* are rarely reported in the literature. The reason for this may lie in habitat partitioning between juveniles and adults of *A. lixula*. Like Ernst (1973), we found the juveniles of *A. lixula* mainly on the undersides of boulders, whereas the adults typically occur in more exposed habitats. Furthermore, Sala *et al.* (1998) suggest that *A. lixula* juveniles may occur in 'nursery areas' in the shallow-water that support the adult stock via migration. The reason for the habitat partitioning may lie in the different morphology of juvenile versus adult individuals. Adult *A. lixula* individuals have strongly developed phyllodes facilitating numerous suckered tube feet and are thus able to withstand considerable drag by turbulence and wave action. In juveniles, the phyllodes are not yet fully developed forcing the animals to live in sheltered microhabitats. The naked aboral side and flattened spines may represent adaptations to reduce lift and drag in juveniles.

Mortensen (1910) found *Arbacia* to be passing through an '*Arbaciella* stage' in ontogeny and thus considered the early sexual maturity of *A. elegans* as a key character for the recognition of the species. According to the same author (Mortensen 1935), *A. lixula* reaches sexual maturity only between 15 and 18 mm corona diameter. In a study of morphological disparity of several Adriatic echinoids, however, Ernst (1973) found sexually mature individuals of *A. lixula* in the smallest size classes sampled, between 9.2 and 14 mm TD (only one specimen smaller than 9 mm was sampled in that study). In the Brazilian population of *A. lixula*, Tommasi (1964) reported open gonopores in specimens as small as 6 mm. Likewise, data on *Arbacia punctulata* suggest early maturity in these animals, with fully mature specimens of only 7 mm TD reported by Harvey (1956). According to that author, maturity is typically reached at 10 mm TD in *A. punctulata*. The onset of sexual maturity, as expressed by the opening of the gonopores, thus seems to vary considerably within and between populations of *Arbacia* and is therefore poorly suited as species-specific character.

In the light of the aforementioned data, it appears that the holotype of *A. elegans* is subadult rather than fully grown. This may imply that Tommasi (1964) was correct in suggesting that this was a name given to juvenile stages, but further research on the African populations is needed to test this.

Table 3.1. Mean genetic p distances (%) between *A. lixula* (A.lix), *A. punctulata* (A.pun), *A. dufresnei* (A.duf), *A. incisa* (A.inc) and *Strongylocentrotus purpuratus* (OG). Bra = Brazilian subclade, Med = Mediterranean and NE Atlantic subclade.

	A.lix-Bra	A.inc	A.pun	A.duf	OG
A.lix-Med	2.4	11.6	10.4	10.1	22.6
A.lix-Bra		11.3	10.2	9.3	22.4
A.inc			10.7	8.0	23.7
A.pun				10.5	23.7
A.duf					23.7

Fresh material from the type area of A. *elegans* was not available for genetic comparison with the Azorean samples. Nevertheless, the data presented herein convincingly show that the latter belong to *A. lixula*, falling in the same subclade as adult specimens of *A. lixula* analysed in earlier studies (Metz *et al.* 1998).

3.5. Conclusions

The results of this study imply that *A. elegans* is not present in the Azores. The Mediterranean and Northwest African specimens of *A*. *elegans* recorded in the literature (Table 3.2) are closely similar to the Azorean material. Like the Azorean specimens, these range from brown to black instead of showing the colourful appearance of Mortensen's type material. Although most of these records lack detailed descriptions, we could not find convincing evidence that any of these specimens are anything else than juvenile *A. lixula*. If correct, this would imply that *A. elegans* does not occur in either the Mediterranean or the north-eastern Atlantic at all.

Table 3.2. Reported distribution of *Arbaciella elegans* Mortensen, 1910.

Localities	Regions	Authors
Ambrizette (Angola)	Central Africa	Koehler (1914)
Setté Cama (French Congo)	Central Africa	Mortensen (1910), Koehler (1914)
Cape Blanc (Mauritania)	Northwest Africa	Mortensen (1925)
Azores	North-eastern Atlantic	Marques (1983)
Canary Islands	North-eastern Atlantic	Hernández *et al.* (2005)
Almeria and Malaga (southern Spain)	Western Mediterranean	Salas & Hergueta (1994)
Castiglione (Algeria)	Western Mediterranean	Gautier-Michaz (1958)
Corsica Channel	Western Mediterranean	Aliani & Meloni (1999)
Elba and Ischia Islands (Thyrrenian Sea)	Western Mediterranean	Tortonese (1977)
Giglio Island (Thyrrenian Sea)	Western Mediterranean	Baumeister & Koch (1998)
Gulf of Marseille?	Western Mediterranean	Régis (1982)
Isola di Spargi, NE Sardinia	Western Mediterranean	Solinas (1989), Solinas *et al.* (1990)
Latium Coast (Italy)	Western Mediterranean	Franceschini & ChimenzGusso (1996)
Ligurian Sea (Italy)	Western Mediterranean	Signorelli & Zamboni (1998)
Off western Corsica	Western Mediterranean	Merella *et al.* (1994)
San Telmo (Baleares)	Western Mediterranean	Molinier & Picard (1957), Pérès & Picard (1964)
Tipasa (Algeria)	Western Mediterranean	Gautier-Michaz (1955), Tortonese (1965)
Adriatic Sea	Central Mediterranean	Zavodnik (2003), Grubelic &Antolic (2000)
Maltese Islands	Central Mediterranean	Schembri (1978), Tanti &Schembri (2006)
SE Sicily (Italy)	Central Mediterranean	Catalano & Scuderi (2002)
Strait of Messina	Central Mediterranean	Giacobbe & Rinelli (1992)
Talbot Ridge (between Sicily and Tunisia)	Central Mediterranean	Gautier-Michaz (1955), Pérès & Picard (1956)
Taranto Bay and Castro Marina (Adriatic Sea)	Central Mediterranean	Parenzan (1983)
Chania, Crete Island (Greece)	Eastern Mediterranean	Pancucci-Papadopoulou (1996)
Aegaean Sea	Eastern Mediterranean	Koukouras *et al.* (2007)

Regarding the status of the genus *Arbaciella* as such, the evidence available to date allows two hypotheses: (1) that all *Arbaciella* are juveniles of *Arbacia*; or (2) that *Arbaciella* is valid, but less widely distributed than reported. Juveniles of *A. lixula* do differ from the type material of *Arbaciella* only in colour, but not by structural features.

This indicates that the former hypothesis is correct, but material from the type region will be necessary to remove lingering doubts.

ACKNOWLEDGEMENTS

We gratefully acknowledge the improving comments by two anonymous reviewers and the invaluable support received by Barbara Däubl, Luise Kruckenhauser (NHM Vienna), António de Frias Martins (Univ. Açores), Alvaro Migotto (Univ. São Paulo) and Heinke Schultz (Zool. Mus. Hamburg). Patrícia Madeira was supported by the Fundação para a Ciência e a Tecnologia grant SFRH⁄BD⁄ 61146 ⁄ 2009. This research received support from the SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Research Infrastructure Action under the FP6 'Structuring the European Research Area' Programme (AT-TAF-2733), and from the SYNTHESYS 2 Project http://www.synthesys. info/, which is financed by European Community Research Infrastructure Action under the FP7 'Capacities' Programme (AT-TAF-260).

3.6. References

Aliani, S. & Meloni, R. (1999) Dispersal stratigies of benthic species and water current variability in the Corsica Channel (Western Mediterranean). *Scientia Marina*, 63, 137–145.

Appeltans, W., Bouchet, P., Boxshall, G.A., Fauchald, K., Gordon, D.P., Hoeksema, B.W., Poore, G.C.B., van Soest, R.W.M., Stöhr, S., Walter, T.C. & Costello, M.J. (Eds.) (2011) *World Register of Marine Species*. Available online at http://www.marinespecies.org.

Ávila, S.P., Marques da Silva, C., Schiebel, R., Cecca, F., Backeljau, T. & de Frias Martins, A.M. (2009) How did they get here? The biogeography of the marine molluscs of the Azores. *Bulletin de la Société Géologique de France,* 180, 295–307.

Baumeister, J.G. & Koch, I. (1998) *Arbaciella elegans* (Echinoidea: Arbaciidae) aus dem Tyrrhenischen Meer. *Stuttgarter Beitrage zur Naturkunde. Serie A (Biologie)*, 568, 1–6.

Catalano D. & Scuderi, D. (2002) Prima segnalazione di *Arbaciella elegans* Mortensen, 1910 (Echinoidea: Arbaciidae) per le acque della Sicilia Sud-Orientale, con note biogeografiche sulla specie. *Bollettino dell'Accademia Gioenia di Scienze Naturali*, 35, 643–648.

De Giorgi, C., Martiradonna, A., Lanave, C. & Saccone, C. (1996) Complete sequence of the mitochondrial DNA in the sea urchin *Arbacia lixula*: conserved features of the echinoid mitochondrial genome. *Molecular phylogenetics and evolution*, 5, 323–332.

Durham, J.W. & Wagner, C.D. (1966) Glossary of morphological terms applied to echinoids. *In*: Moore RC (Ed.), *Treatise on Invertebrate Paleontology, U. Echinodermata*. GSA and Univ. Kansas Press, Boulder, CO and Lawrence, KS, 3(1), U251–U256.

Emlet, R.B. (2010) Morphological Evolution of Newly Metamorphosed Sea Urchins – A Phylogenetic and Functional Analysis. *Integrative and comparative biology*, 50, 571–588.

Ernst, G. (1973) Aktuopaläontologie und Merkmalsvariabilität bei mediterranen Echiniden und Rückschlüsse auf die Ökologie und Artumgrenzung fossiler Formen. *Paläontologische Zeitschrift*, 47, 188–216.

Franceschini, G. & Chimenz Gusso, C. (1996) Echinodermi delle coste Laziali. *Bollettino dei Musei e Degli Istituti Biologici dell'Università di Genova*, 60–61, 191–200.

Gautier-Michaz, M. (1955) Sur la présence de l'échinide *Arbaciella elegans* Mortensen en Méditerranée occidentale. *Bulletin de la Station d'Aquiculture et de Pêche de Castiglione*, 1955:293–295.

Gautier-Michaz, M. (1958) Resultats scientifiques des campagnes de la Calypso. VII. Etudes sur le seuil Siculo-Tunisien. 5. Echinodermes. *Annales Institut Océanographique*, Monaco, 34, 145–155.

Giacobbe, S. & Rinelli, P. (1992) Ecological notes on *Arbaciella elegans* (Mortensen) from populations of Pinna in the Straits of Messina. *In*: Scalera-Liaci, L. & Canicatti, C. (Eds.) Echinoderm Research 1991, A.A. Balkema, Rotterdam, pp. 185–190.

Grubelic, I. & Antolic, B. (2000) *Arbaciella elegans* Mortensen, 1910 (Arbaciidae, Echinoidea) a new species of the Adriatic Sea fauna. *Periodicum biologorum*, 102, 217–220.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95 ⁄ 98 ⁄ NT. *Nucleic acids symposium series*, London, 41, 95–98.

Harvey, E.B. (1956) The American *Arbacia* and other sea urchins. Princeton University Press, Princeton, NJ, xvi+298 pp.

Hernández, J.C., Toledo, K., Girard, D., Clemente, S., Cubero, E. & Brito, A. (2005) Descripcion de la post-larva y primeras fases juveniles de tres equinoideos presentes en las islas Canarias: *Diadema antillarum* Philippi, 1845, *Paracentrotus lividus* (Lamarck, 1816) y *Arbaciella elegans* Mortensen, 1910. *Vieraea* 33, 385–397.

Koehler, R. (1914) Echinoderma I: Asteroidea, Ophiuroidea et Echinoidea. *In*: Michaelsen, W. (Hrsg.), *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. L. Friedrichsen & Co, Hamburg, pp. 127–303.

Koukouras, A., Sinis, A.I., Bobori, D., Kazantzidis, S. & Kitsos, M.-S. (2007) The echinoderm (Deuterostomia) fauna of the Aegean Sea, and comparison with those of the neighbouring seas. *Journal of Biological Research*, 7, 67–92.

Kroh, A. & Smith, A.B. (2010) The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8, 147–212.

Marques, V.M. (1983) Peuplements benthiques des Açores I – Echinodermes. *Arquivo do Museu Bocage* (*A*) 2:1–12.

Merella, P., Porcheddu, A. & Solinas, P.L. (1994) Première signalisation sur les côtes françaises et contribution à la connaissance de l'écologie de *Arbaciella elegans* Mortensen, 1910 (Echinoidea, Arbaciidae). *Travaux scientifiques du Parc naturel régional et des réserves naturelles de Corse*, 46, 93–102.

Metz, E. C., Gómez-Gutiérrez, G. & Vacquier, V.D. (1998) Mitochondrial DNA and Bindin Gene Sequence Evolution Among Allopatric Species of the Sea Urchin Genus *Arbacia*. *Molecular biology and evolution*, 15, 185–195.

Molinier, R. & Picard, J. (1957) Aperçu bionomique sur les peuplements marins littoraux des côtes rocheuses méditerranéennes de l'Espagne. *Bulletin de la Station d'Aquiculture et de Pêche de Castiglione, NS*, 8, 253–268.

Mortensen, T. (1910) *Arbaciella elegans*. Eine neue Echiniden-Gattung aus der Familie Arbaciidae. *Mitteilungen des Naturhistorischen Museum Hamburg*, 27(1909), 327–334.

Mortensen, T. (1925) Échinodermes du Maroc et de Mauritanie. I. Sur une petite collection d'Échinodermes du Cap Blanc (Mauritanie) récoltés par D. le Dr Th. Monod. *Bulletin de la Société des sciences naturelles du Maroc*, 5(4–5), 178–187.

Mortensen, T. (1935) *A Monograph of the Echinoidea. II Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta*. C.A. Reitzel & Oxford University Press, Copenhagen & London, 647 pp.

Palumbi, S.R. & Lessios, H.A. (2005) Evolutionary animation: how do molecular phylogenies compare to Mayr's reconstruction of speciation patterns in the sea? *Proceedings of the National Academy of Sciences, USA*, 102, 6566–6572.

Pancucci-Papadopoulou, M.A (1996) The Echinodermata of Greece. *Fauna Graeciae* 6, 1–162.

Parenzan, P. (1983) *Puglia Marittima: Aspetti geologici e biologia marina (20 anni di ricerche naturalistiche nei mari pugliesi)*. Congedo Editore, Galatina (Leche), I: pp 1–406, II: pp 415–688.

Pereira, M.O.R. (1997) Checklist of the littoral echinoderms of the Azores. Açoreana, 8,331–337.

Pérès, J.M. & Picard, J. (1956) Recherches sur les peuplementes benthiques du Seuil Siculo-Tunisien, *Annales de l'Institut océanographique*, 32:233–264.

Pérès, J.M. & Picard, J. (1964) Nouveau manuel de bionomie benthique de la mer Méditerranée, Edition revue et augmentée. Recueil des travaux de la Station Marine d'Endoume, 31, 5–137.

Régis, M.-B (1982) Données microstructurales et validité du genre *Arbaciella* Mrtsn (Echinodermata – Echinoidea). *Memoires sur le Biologie Marine et Oceanographique*, 12, 5–26.

Riedl, R. (Ed.) (1983) *Fauna und Flora des Mittelmeeres*. 3. Aufl. Paul Parey Verlag, Hamburg, 836 pp.

Saitou, N. & Nei, M. (1987) The neighbor-joining method: a new method for reconstruction of phylogenetic trees. *Molecular biology and evolution*, 4, 406–425.

Sala, E., Ribes, M., Hereu, B., Zabala, M., Alva, V., Coma, R. & Garrabou, J. (1998) Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern

Mediterranean: comparison between a marine reserve and an unprotected area. *Marine Ecology Progress Series*, 168, 135–145.

Salas, C. & Hergueta, E. (1994) Early Growth Stages and Ecology of *Arbaciella elegans* Mortensen (Echinodermata, Echinoidea) in Southern Spain. *Marine Ecology Progress Series*, 15, 255–265.

Schembri, P.J. (1978) Recent echinoids (Echinodermata: Echinoidea) from the Maltese Islands and surrounding waters. *Animalia*, 5, 123–132.

Signorelli, M. & Zamboni, A. (1998) Segnalazione di *Arbaciella elegans* Mortensen, 1910 (Echinoidea, Arbaciidae) in Mar Ligure. *Biologia Marina Mediterranea*, 5, 644–645.

Solinas, P.L. (1989) Sul ritrovamento di *Arbaciella elegans* Mortensen, 1910 (Echinoidea Arbaciidae) nelle acque italiane. *Vie marine*, 10, 73–75.

Solinas, P.L., Régis, M.-B & Tola, S. (1990) Nuova segnalazione di *Arbaciella elegans* Mortensen, 1910 (Echinoidea, Arbaciidae) nelle acque italiane. *In*: Cossu, A., Gazale, V. & Milella, I. (Eds.) *Parchi Marini del Mediterraneo. Aspetti naturalistici e gestionali*. Istituto delle Civiltà del Mare, San Teodoro, Sassari, pp 231–233.

Swofford, D.L. (2005) PAUP* – Phylogenetic Analysis Using Parsimony (*and Other Methods) Vers. 4.0b10 [Computer software and manual]. Sinauer Associates, Sunderland, MA.

Tan, D.S.H., Ang, Y., Lim, G.S., Ismail, M.R.B. & Meier, R. (2009) From ‘cryptic species’ to integrative taxonomy: an iterative process involving DNA sequences, morphology, and behaviour leads to the resurrection of *Sepsis pyrrhosoma* (Sepsidae: Diptera). *Zoologica Scripta*, 39, 51–61.

Tanti, C.M. & Schembri, P.J. (2006) A synthesis of the echinoderm fauna of the Maltese islands. *Journal of the Marine Biological Association of the United Kingdom*, 86, 163–165.

Tiago, C.G., Brites, A.D. & Kawauchi, G.Y. (2005) A simple enzymatic method for examining calcite ossicles of Echinodermata. *Journal of Microscopy*, 218, 240–246.

Tommasi, L.R. (1964) Observacões sôbre Equinóides do Brasil. *Revista Brasileira* de *Biologia*, 24, 93–93.

Tortonese, E. (1965) *Fauna d'Italia*. Vol. VI. Echinodermata. Calderini, Bologna, xiii+422 pp.

Tortonese, E. (1977) Recenti acquisizioni e rettifici intorno a Crinoidi, Oloturioidi, Ofiuroidied Echinoidi del mare Mediterraneo. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 118, 333–352.

Troschel, F.H. (1873) Die Familie der Echinocidariden (2) *Archiv für Naturgeschichte*, 39, 308–356.

Zavodnik, D. (2003) Marine fauna of Mljet National Park (Adriatic Sea, Croatia) 2. Echinodermata. *Acta Adriata*, 44, 105–160.

Chapter 4. First report of a Mediterranean species in the Azores: *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) (Asteroidea: Echinodermata)

Madeira, P., Frias Martins, A.M. & Ávila, S.P. (2017) First record of the Mediterranean asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) in the Azores Archipelago (NE Atlantic Ocean). *Arquipelago*. Life and Marine Sciences 35: 11–18.

Abstract

The first occurrence of the Mediterranean fissiparous asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) is reported from the Azores based upon dredged material off the south coast of São Miguel Island at 135 m depth. This record represents a considerable expansion of the species' geographic range, otherwise reported with certainty only from the Mediterranean Sea. *S. richardi* is capable of producing long-lived planktotrophic larvae with high dispersal potential to reach remote areas such as the Azores. Alternatively, this species is also capable of reproducing asexually through fission, which could insure the maintenance of viable numbers in a stranded population. The presence of *S. richardi* in Azorean waters and its rarity in an otherwise thoroughly investigated area does not necessarily imply a recent arrival nor a human-mediated introduction, as the depths in consideration (80-700 m) are also the least studied in the archipelago.

Key words: Asteroidea; Forcipulatida; fissiparous; Azores.

4.1. Introduction

Asexual reproduction through fission is a rare phenomenon among sea stars, documented only in 21 (Mladenov 1996) of the 1,900 species known worldwide (Mah & Blake 2012). *Coscinasterias tenuispina* (Lamarck, 1816) was the only fissiparous asteroid previously known to occur in the Azores (Pereira 1997), a volcanic archipelago located in the NE-Atlantic, half way between the North American and European shores. This study documents a second species, *Sclerasterias richardi*, a small asteroid (30 mm maximum documented diameter) known primarily from the Mediterranean Sea (Fig. 4.1.), where it lives between 80-710 m on a variety of substrates from sandy, detritic to hard bottoms (Marenzeller 1895; Pruvot 1897; Baldelli 1914; Gallo 1933; Gautier-Michaz 1958; Santarelli 1964; Tortonese 1965; Falconetti *et al.* 1976; Munar 1984; Borri *et al*. 1990; Mastrototaro & Mifsud 2008; Mifsud *et al*. 2009).

Sclerasterias richardi was first described as *Asterias richardi* based on animals collected by the R/V *Travailleur* in Corsican waters (France). Perrier (*in* Milne- Edwards, 1882) soon observed that this six-rayed asteroid was capable of self- division. In a later report, Perrier (1894) further completed his initial description and transferred this species to the genus *Hydrasterias* (family Pedicellasteridae Perrier, 1884). The author also included in the re-description of the type material two other specimens collected by the R/V *Talisman* off the Cabo Verde Islands. Fisher (1925, 1928) argued that Perrier's hexamerous forms were representatives of a young fissiparous stage of a pentamerous adult species, probably belonging to the genus *Sclerasterias* (family Asteriidae Gray, 1840), such as the much larger *S. neglecta* (Perrier, 1891) from the Bay of Biscay and the Mediterranean Sea. Tortonese (1965) agreed with Fisher's generic assignment, but considered that further research was needed.

In their revision of the Asteroidea from the Atlantic, Downey (*in* Clark & Downey 1992) reignited Fisher's concerns by pointing out that the original description of *S. richardi* was inaccurate and based upon immature specimens, thus it should be suppressed. She was possibly unaware of the studies on the sexual reproduction of this species by Falconetti *et al*. (1976, 1977) and Febvre *et al*. (1981), which presented *S. richardi* as gonochoristic with a well-marked annual reproductive cycle, from mid-September to mid-October. More recently, Mastrototaro & Mifsud (2008) argued that the unequal number and size of the arms, the presence of multiple madreporites and the documented sexual reproduction suffice to prove that it is a valid species and not a juvenile of *S. neglecta*, a species only known from historical material (Mastrototaro & Mifsud 2008). The debate on the systematic position of this species is still far from being resolved.

4.2. Material and methods

During the 3rd International Workshop of Malacology and Marine Biology, three specimens of *Sclerasterias richardi* were collected by dredging, south of the marina of Vila Franca do Campo, São Miguel Island, Azores (37°41'42"N, 25°25'22"W, 135 m depth, 17 July 2006) (Fig. 4.1.).

The specimens were placed in 100% ethanol and included in the echinoderm collection from the Department of Biology of the University of the Azores (DBUA-ECH 357). During the revision of this material, it was noticed that the specimens had become completely desiccated and the arms were partially or totally detached from the disc.The terminology used for the morphological structures is adapted after Clark & Downey (1992).

Abbreviations

Rmax: major radius from centre of disc to tip of longest arm; r: minor radius from centre of the disc to interradial edge.

4.3. Results

Systematics

Class ASTEROIDEA de Blainville, 1830
Order Forcipulatida Perrier, 1884
Family Asteriidae Gray, 1840
Genus ?*Sclerasterias* Perrier, 1891

***Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) (Fig. 4.2).**

Description of the specimens: two animals with six arms of unequal size, three larger and three smaller. One specimen with three arms of similar dimensions to the larger arms of the six-rayed specimens (Table 4.1). Arms broad, pentagonal in cross-section, narrowing gradually into a round arm tip wholly covered by the terminal plate. Arms weakly attached to the disc.

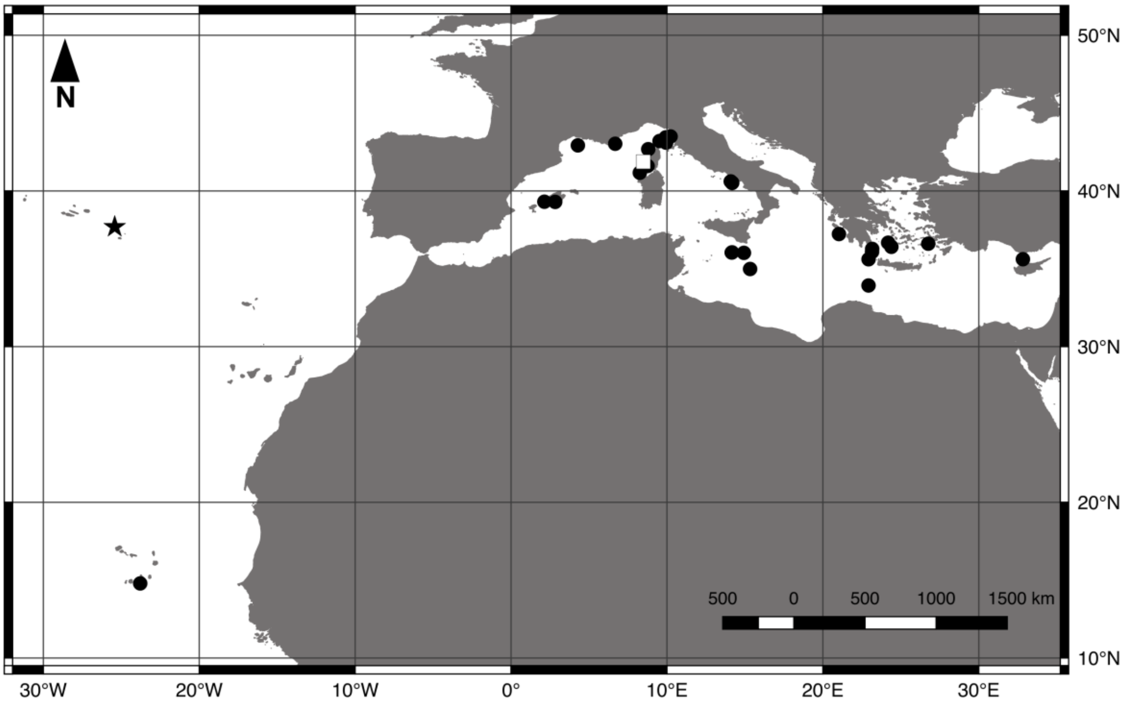


Figure 4.1. Geographical distribution of *Sclerasterias richardi* in the Mediterranean Sea and NE Atlantic. The square indicates the type locality (Perrier 1882, *in* Milne-Edwards 1882), circles the historical records (Marenzeller 1893, 1895; Perrier 1894; Ludwig 1897; Pruvot 1897; Baldelli 1914; Fisher 1928; Gallo 1933; Gautier-Michaz 1958; Santarelli 1964; Tortonese 1965; Falconetti *et al*. 1976, 1977; Febvre *et al*. 1981; Munar 1984; Borri *et al*. 1990; Mastrototaro & Mifsud 2008; Mifsud *et al*. 2009) and the star the new record from the Azores (DBUA-ECH 357).

Reticular plating on the arms arranged in fairly regular longitudinal plate series (carinal, dorsolateral, superomarginal, inferomarginal, adambulacral); arm plates have a round four-lobbed shape with the lateral arms extending towards the corresponding lobe of the adjacent plates series with exception of the small bridge-like dorsolateral plates that serve as an intermediary link between superomarginal and carinal plates. Papulae occupying the interstices between plates, forming two longitudinal rows on each side of the arm: one between the carinal and the superomarginal plates and one between the superomarginal and the inferomarginal plates; oral papillae absent. Arm spines forming fairly regular longitudinal series. Carinal plates carrying up to three short and round spines bearing small spinelets at their tips. Dorsolateral plates also bearing one small spine proximally but naked distally. Superomarginal plates armed with two spines similar in size and shape to the carinal and dorsolateral ones. Spine number and size gradually reduced to one small spine near the arm tip in both carinal

Table 4.1. Size (Rmax, r) of the specimens from the Azores and corresponding arm length, number of arms and madreporites.

Rmax (mm)	R (mm)	Arm length (mm)	Number of arms	Number of madreporites
6	1.1	3-5	6	2+?
5	0.95	2.5-4	6	2
5	0.96	4	3	2

and superomarginal plates. Inferomarginal plates with one or two flattened, spatulate to clavate enlarged spines, arranged obliquely and slightly enlarged towards the tip. Adambulacral plates diplacanthid bearing two spines arranged obliquely with the internal slightly smaller than the external one. These spines are slightly flattened and somewhat enlarged towards a round tip. All specimens with at least two madreporites (S-shaped) near the interradial edges; disc also densely covered with small spines, identical in size and shape to those found on the aboral surface of the arms. Spines of the oral armature arranged in pairs along the lateral sides of the mouth plates and of similar sizes and morphology to the adambulacral ones; adoral carina present. Numerous crossed pedicellariae almost as large as the aboral spines dispersed through the body surface, not forming a wreath around the spines; presence of a slightly enlarged unpaired tooth on the outer face of each valve of the crossed pedicellariae. Straight pedicellariae felipedal, slightly larger than the crossed-pedicellariae and restricted to the interradial area. Valves terminated at their upper extremity by a large recurved tooth. Tube feet biserial (quadraserial at the base of larger arms).

4.4. Discussion

In spite of the poor state of preservation of the animals, their identification was possible since agreeing for the most part with Perrier (*in* Milne-Edwards 1882, 1894) as well as with the exhaustive descriptions by Ludwig (1897) and Marenzeller (1893). The observations herein also agree with Falconetti *et al*. (1976), particularly on the distribution of straight and crossed pedicellaria. In addition, DBUA-ECH animals showed multiple madreporites, as documented by Mastrototaro & Mifsud (2008).

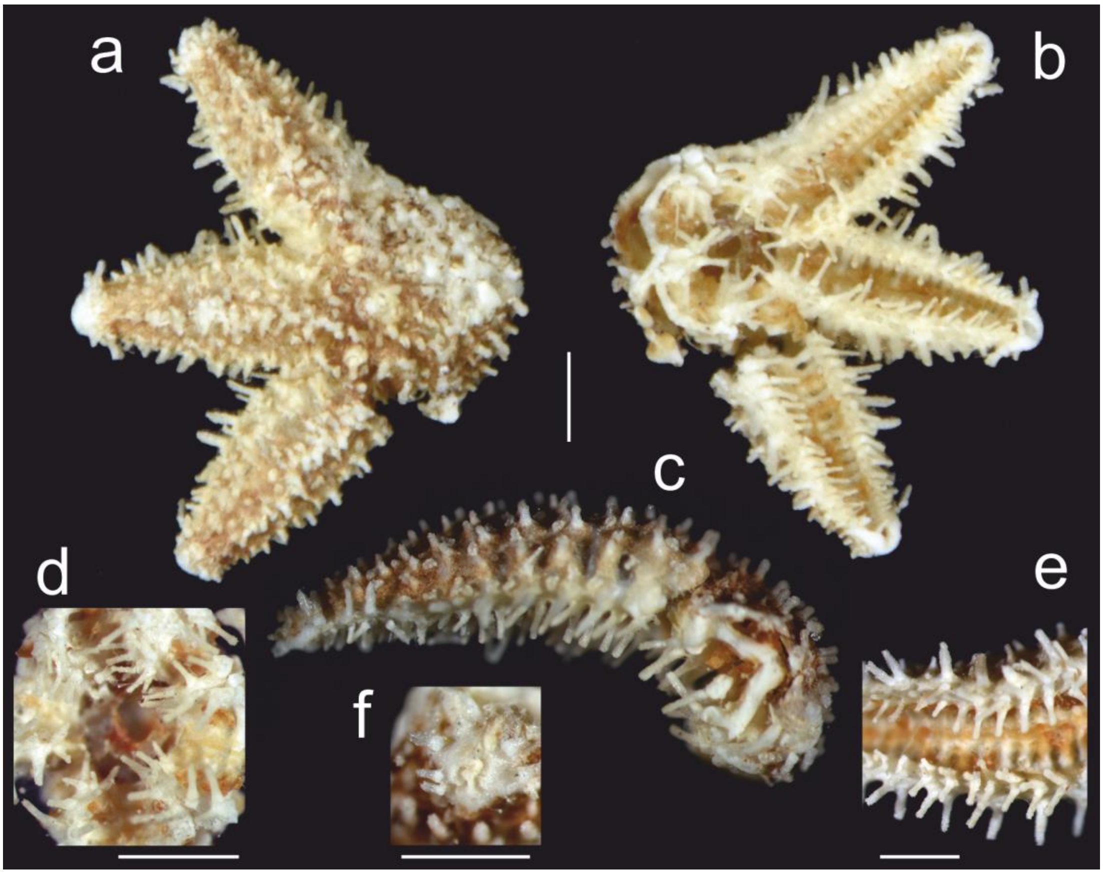


Figure 4.2. *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) (DBUA-ECH 357): (a) aboral view; (b) oral view; (c) lateral view; (d) detail of the oral region; (e) oral view of the arm; (f) S-shaped madreporite. All white scale bars are 1 mm.

Fissiparous asteroid species can be identified by the following features: non-pentamerous symmetry, different (asymmetrical) arm sizes and/or more than a madreporite (Mladenov *et al*. 1986). Among the known asteroid species from the Azores (Pereira 1997), *S. richardi* closely resembles the fissiparous *Coscinasterias tenuispina*, and animals belonging to the former species could be potentially overlooked and confused with juveniles of the latter species. However, their habitats differ sensibly since *C. tenuispina* is a common inhabitant of much shallower waters of the archipelago (≤12 m). Both species can be quickly diagnosed under binocular microscope by the distribution of the crossed pedicellariae (in wreaths around the spines of *C. tenuispina*; dispersed through the body surface of *Sclerasterias richardi*) and number of adambulacral spines (one in *C. tenuispina* and two in *S. richardi*), even at size classes as small as 5 mm maximum radius. *S. richardi* is further distinguished from *C. tenuispina* by the aboral armament, *i.e.* in the *Coscinasterias* species it is represented by isolated spines, whereas in the genus *Sclerasterias* it can be decorated by multiple spines.

The diplacanthid condition of the adambulacral plates is characteristic *Sclerasterias* (as opposed to the monocanthid of *Coscinasterias*), but not the disperse distribution of crossed-pedicellaria on the surface of the body. In this genus, similar to *Coscinasterias*, the crossed-pedicellaria is normally arranged in wreaths around the spines. However, small animals (R >22 mm) of the Pacific *S. heteropaes*, *S. alexandri* and *S. euplecta*, may present the pedicellaria distributed in a similar fashion of what was observed in Azorean specimens (Fisher 1925, 1928). In contrast, small animals of European *S. neglecta* and *S. guernei* (R=15 mm and R=17 mm, respectively) were described by Perrier (1891, 1896a) as having pedicellaria organized in the typical way, *i.e.* in wraiths around the spines. Furthermore, no Atlantic *Sclerasterias* but *S. richardi* are known to reproduce asexually through fission, including *S. neglecta* and *S. guernei*, which are known only by pentamerous specimens (Downey *in* Clark & Downey 1992). In sum, present knowledge on *Sclerasterias* in the Atlantic indicates *S. richardi* should not be suppressed contrary to the opinion of either Fisher (1925, 1928) or Downey (*in* Clark & Downey 1992). From the available data (*e.g.,* Ludwig 1897; Falconetti *et al*. 1976; Mastrototaro & Mifsud 2008), there is no evidence that the small *S. richardi* becomes identical to other NE Atlantic *Sclerasterias* (*e.g.,* crossed-pedicellariae arranged in wreath around the spines) in larger size classes. Furthermore, Falconetti *et al*. (1976, 1977) and Febvre *et al*. (1981) showed that asexual reproduction in *S. richardi* is not necessarily lost in animals capable of reproducing sexually. However, further comparisons between *S. richardi* and other *Sclerasterias* in the Atlantic Ocean and Mediterranean Sea are needed, particularly with material of *S. neglecta* and *S. guernei* of similar size classes.

The specimens herein documented were collected offshore Vila Franca do Campo, where both a marina and a port have been implanted. However, it is unlikely that these specimens represent a human-mediated introduction, considering the depth range reported for *S. richardi* (≥80 m, Falconetti *et al*. 1976). On the other hand, it is not possible to ascertain if this species represents a recent arrival, as the species depth range coincides with the least studied waters in the Azores, *i.e*. between the usual maximum SCUBA diving depth (<40 m) and the minimum depth normally targeted by international oceanographic missions (>200 m). The paucity of specimens collected, notwithstanding the considerable research effort in the frame of international workshops organized by the Sociedade Afonso Chaves and the Department of Biology of the University of the Azores (Martins 2009; Martins & Xavier 2014), clearly indicates that further sampling is needed to answer the open questions on dispersion and colonization herein posited.

The archipelago is under the influence of the Azores Current, part of the North Atlantic subtropical gyre (Santos *et al*. 1995), which generates a West to East sea-surface current pattern (*i.e.* from the American to the European coasts). Periodical anomalies temporarily reversing the usual circulation patterns, could function as “windows of opportunity” (*sensu* Ávila *et al*. 2015) for European or North-African shallow-water taxa to reach the Azores (whether by larval dispersal or rafting). Alternatively, Mediterranean species could potentially use the counter-current system to reach the islands, such as the Mediterranean water outflow that reaches the south-southeast Azorean waters around 800-1,200 m depth, though the influence of meddies (*i.e.* eddies of Mediterranean provenance) can be detected outside this depth range (Pingree & Le Cann 1993; Tychensky & Carton 1998; Bashmachnikov *et al*. 2015).

Long-lived planktotrophic larvae (>42 days, 14.5ºC, Falconetti *et al*. 1977) are adapted for long-distance dispersal and may have facilitated the arrival of colonizers of this species to the Azores from the Mediterranean Sea. Moreover, clone propagation through asexual reproduction could help to maintain effective numbers in a fringe population stranded in a remote island/archipelago. The presence of more than one madreporite and the unequal size and number of arms clearly indicate that these animals were reproducing asexually through fission. However, the sexual status of the specimens could not be ascertained, due to the desiccated and partially disarticulated state of the material. Falconetti *et al*. (1976) data showed that among the smallest sampled size classes (Rmax=7 mm) some of the animals presented no gonads. However the minimum size at the first maturity is almost unknown. Thus, the possibility that the Azorean material represents immature animals cannot be completely discarded leaving open the option that they represent vagrants or elements of an already established population in the Azorean islands.

ACKNOWLEDGEMENTS

We are grateful to the organizers and participants of the 3rd International Workshop of Malacology and Marine Biology and for their assistance in the field work. We also gratefully acknowledge the improving comments by three anonymous reviewers. Patrícia Madeira was supported by Grant SFRH/BD/61146/2009 (FCT -Fundação para a Ciência e Tecnologia) of the Portuguese government. Sérgio P. Ávila acknowledges his IF/00465/2015 research contract funded by FCT. This work was also funded by FEDER funds through the Operational Programme for Competitiveness Factors –COMPETE and by National Funds through FCT - Foundation for Science and Technology under the UID/BIA/50027/2013 and POCI-01-0145-FEDER-006821.

4.5. References

Ávila, S.P., Melo, C. Silva, L., Ramalho, R., Quartau, R., Hipólito, A., Cordeiro, R., Rebelo, A.C., Madeira, P., Rovere, A., Hearty, P.J., Henriques, D., Silva, C.M. da, Martins, A.M.F. & Zazo, C. (2015) A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews*, 114, 126–148.

Baldelli, C. (1914) Asteroidi, ofiuroidi, crinoidi, oloturoidi raccolti nel Mediterraneo dalla RN Washington (1881–1882). *Archivio Zoologico Italiano*, 7, 81–113.

Bashmachnikov, I., Nascimento, Â., Neves, F., Menezes, T. & Koldunov, N.V. (2015) Distribution of intermediate water masses in the subtropical northeast Atlantic. *Ocean Science,* 11, 803–827.

Borri, M., Righini, P. & Piras, A. (1990) Fauna echinologica dei fondi molli dell'alto Tirreno e note sulle biocenosi relative. *Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano*, 131, 377–410.

Clark, A.M. & Downey, M.E. (1992) *Starfishes of the Atlantic. Natural History Museum Publications*. Ed. Chapman & Hall, London, 794 pp.

Falconetti, C., Fredj-Reygrobaliet, D. & Fredj, G. (1976) Sexualité et fissiparite concomitants chez l'astérie *Sclerasterias richardi*: premières données. *Marine Biology*, 34, 247–257.

Falconetti, C., Fredj-Reygrobaliet, D. & Fredj, G. (1977) Induction de l'émission des gamètes et premiers stades du développement larvaire chez l'astérie fissipare *Sclerasterias richardi*. *Marine Biology*, 39, 171–178.

Febvre, M., Fredj-Reygrobellet, D. & Fredj, G. (1981) Reproduction sexuée d'une astérie fissipare, *Sclerasterias richardi* (Perrier, 1882). *International Journal of Invertebrate Reproduction and Development*, 13, 193–208.

Fisher, W.K. (1925) Asexual reproduction in the starfish *Sclerasterias*. *The Biological Bulletin*, 48(3), 171–175.

Fisher, W.K. (1928) Asteroidea of the North Pacific and adjacent waters. Part 2: Forcipulata. *Bulletin of the United States National Museumi*, 76, 1–245.

Gallo, V.R. (1933) Un ejemplar joven de *Hydrasterias richardi* (Perrier). *Boletín de la Sociedad Española de Historia Natural*, 33, 303–305.

Gautier-Michaz, M. (1958) Resultats scientifiques des campagnes de la Calypso. VII. Etudes sur le seuil Siculo-Tunisien. 5. Echinodermes. *Annales Institut Océanographique*, Monaco, 34, 145–155.

Ludwig, H. (1897) Die Seesterne des Mittelmeeres. *Zoologischen Station zu Neapel*, 24, viii(8)+491.

Madeira, P., Frias Martins, A.M. & Ávila, S.P. (2017) First record of the Mediterranean asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) in the Azores Archipelago (NE Atlantic Ocean). *Arquipelago*. Life and Marine Sciences 35: 11–18.

Mah, C.L. & Blake, D.B. (2012) Global Diversity and Phylogeny of the Asteroidea (Echinodermata). *PLoS One*, 7(4), 1–22.

Marenzeller, E. von (1893) Contribution à l'étude des Holothuries de l'Atlantique N'ord (Golfe de Gascogne, Iles Açores). *Résultats Campagnes Scientifiques du Prince de Monaco*, 6, 32 pp.

Marenzeller E. von (1895) Zoologische Ergebnisse. V. Echinodermen, gesammelt 1893, 1894. *Denkschriften der Königlichen Akademie der Wissenschaften zu München*, 62B, 123–148.

Martins, A.M.F. (Ed.) (2009) The Marine Fauna and Flora of the Azores: Proceedings of the Third International Workshop of Malacology and Marine Biology, São Miguel, Azores, July 17–28 2006. *Açoreana*, supplement 6, 225 pp.

Martins, A.M.F. & J.R. Xavier (Eds.) (2014) Proceedings of the Fourth International Workshop of Malacology and Marine Biology – SABRINA, São Miguel, Azores, July 4–13, 2011. *Açoreana*, supplement 10, 173 pp.

Mastrototaro, F. & Mifsud, C. (2008) Some observations on the morphology of *Sclerasterias richardi* a rarely encountered Mediterranean Sea star (Echinodermata: Asteriidae). *Mediterranean Marine Science*, 9(2), 103–109.

Mifsud, C., Taviani, M. & Stöhr, S. (2009) Remarks on Echinodermata from the South Central Mediterranean Sea based upon collections made during the MARCOS cruise (10 to 20th April, 2007). *Mediterranean Marine Science*, 10(2), 63–71.

Mladenov P. V., Carson, S. F., & Walker, C. W. (1986) Reproductive ecology of an obligately fissiparous population of the sea star *Stephanasterias albula* (Stimpson). *Journal of Experimental Marine Biology and Ecology*, 96, 155–175.

Mladenov, P.V. (1996) Environmental factors influencing asexual reproductive processes in echinoderms. *Oceanologica Acta*, 19(3–4), 227–235.

Milne-Edwards, A. (1882) Rapport sur les travaux de la commission chargée par M. Le Ministre de l'Instruction Publique d'étudier la faune sous-marine dans les grandes profondeurs de la Méditerranée et de l'océan Atlantique. *Archives des Missions Scientifiques et Littéraires, troisieme serie*, 9, 1–63.

Munar, J. (1984) Faunistica de Equinodermos en las Islas Baleares. *Bolletí de la Societat d'Història Natural de les Balears*, 28, 5–22.

Perrier, M.E. (1894) Stellérides. *Expéditions Scientifiques du Travailleur et du Talisman*. Masson, Paris, 1–431.

Pereira, M. (1997) Checklist of the littoral echinoderms of the Azores. *Açoreana*, 8(3), 331–337.

Pingree, R.D. & Cann, B. Le (1993) Structure of a meddy (Bobby 92) southeast of the Azores. *Deep Sea Research Part I*, 40(10), 2077–2103.

Pruvot, G. (1897) Essai sur les fonds et la faune de la manche occidentale (cotes de Bretagne) comparés a ceux du Golf du Lion. *Archives de Zoologie Expérimentale et Générale*, 5, 511–617.

Santarelli, M. (1964) Segnalazione di raecolta di *Hydrasterias richardi* (Perrier, 1882) (Asteroidea, Echinod.) nel Golfo di Napoli. *Bolletino di Zoologia*, 31(1), 15–18.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M. & Isidro, E.J. (1995) Marine research and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5, 311–354.

Tortonese, E. (1965) *Fauna D’Italia – Echinodermata*. Edizioni Calderini, Bologna, 422 pp.

Tychensky, A. & Carton, X. (1998) Hydrological and dynamical characterization of Meddies in the Azores region: A paradigm for baroclinic vortex dynamics. *Journal of Geophysical Research*, 103(C11), 25061–25079.

Extant Fauna

Chapter 5. The Echinoderm Fauna of the Azores (NE Atlantic Ocean)

Madeira, P., Kroh, A., Martins, A.M.F., Cordeiro, R. & Ávila, S.P. (*submited*). The Echinoderm Fauna of the Azores (NE Atlantic Ocean). *Zootaxa*

Abstract

In more than 150 years of research in the waters surrounding the Azores, several publications on the fauna of echinoderms of the archipelago have been produced, in the form of papers, notes, reports, reviews, and monographs. This work attempts to summarize the present knowledge on this marine group in the Azorean exclusive economic zone (*i.e.*, waters within 200 nautical miles of the archipelago's shores). A short review of the history of the species' taxonomy is given, with key references, geographical distribution, ecology, additional notes and, when possible, figures. We herein report 172 species of echinoderms (6 crinoids, 55 ophiuroids, 45 asteroids, 36 holothurians and 30 echinoids) from the Azores Archipelago, most of them inhabiting deep waters (>200 m). Only 29 shallow-water species were recorded locally (≤50 m depth). In general, the echinoderm species present in the Azores are characterized by a wide geographical distribution in the Atlantic Ocean. Only 9 taxa (all deep-water species, >840 m) appear to be restricted to the Azorean waters. Overall, the knowledge of the echinoderm fauna of the Azores is out-dated, with many species last collected in the archipelago over 100 years ago. A recent interest in the Azorean Mid-Atlantic waters has brought oceanographic cruises back to the archipelago, thus providing new opportunities for the renewal of 150 years of echinoderm studies in the area.

Key words: Echinodermata; Biodiversity; Azores; NE Atlantic Ocean.

5.1. Introduction

The echinoderms (phylum Echinodermata) are a conspicuous presence throughout all oceans and seas, at all latitudes and depths, from coastal areas down to the abyssal plains to approximately 6,000 m (Mironov 1978), and they occur in virtually all marine habitats, including coral reefs, mangroves, and rocky, sandy, and muddy substrates. They are a diverse group of generally strictly marine animals that includes the brittle stars (class Ophiuroidea, 2,064 species), sea stars (class Asteroidea, 1,900 species), sea cucumbers (class Holothuroidea, 1,400 species), sea urchins (class Echinoidea, 1,012 species), and sea lilies and feather stars (class Crinoidea, 623 species) (Pawson 2007; Appeltans *et al*. 2012; Mah & Blake 2012; Stöhr *et al*. 2012; Kroh & Mooi 2018).

In over 150 years of echinoderm studies in the Azores, a total of 150 publications include at least one specimen collected in the archipelago (Fig. 5.1). The focus of the research on the Azorean echinoderm fauna changed through time, with the first studies in the late 1800's resulting from small expeditions, which aimed to identify the main elements of the shallow-water echinoderm fauna. Drouët (1861),

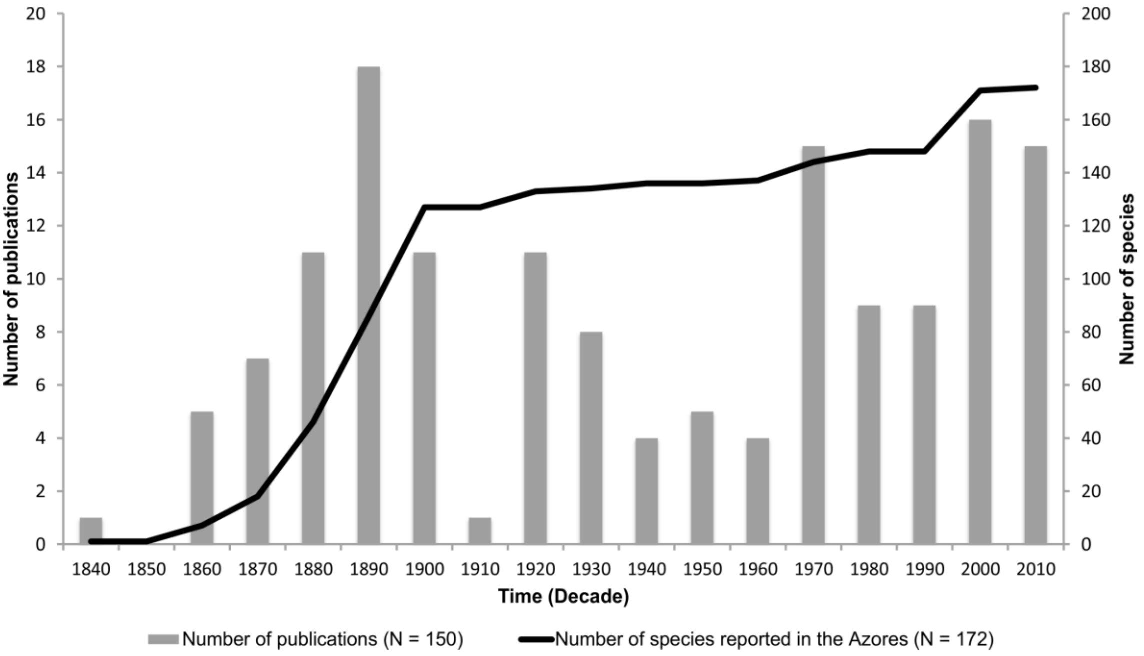


Figure 5.1. Number of echinoderm species reported for the Azores (black line; N=172) and related literature through time (grey bars; N=150).

followed by Barrois (1888), and Simroth (1888), concluded that the Azorean shallow-water echinoderm fauna seemed to be derived exclusively from European waters, particularly from the Mediterranean Sea, with no elements endemic to the area. In the late 19th century during the ‘Golden Age’ of oceanographic surveys, the ocean floor around the Azores was extensively surveyed and new material unknown to science was retrieved from deep waters. Most of what we know about the deep-water echinoderm fauna of the archipelago derives from reports based on the material collected by these cruises (Table 5.1), such as by the research vessels (RVs) H.M.S. Challenger’, ‘Princesse Alice’, and ‘Talisman’ (*e.g.,* Perrier 1898; Koehler 1909; Hérouard 1923). However, by the mid-20th century, interest in the Azorean

Table 5.1. Main oceanographic cruises in the Azores and main literature produced in each echinoderm classes.

Cruise (RV)	**References**	**Echinoderm Classes**
H.M.S. Challenger	Carpenter (1883b; 1884)	Crinoidea
	Lyman (1878a, 1979, 1882)	Ophiuroidea
	Sladen (1883, 1889)	Asteroidea
	Agassiz (1879, 1881)	Echinoidea
	Théel (1886a)	Holothuroidea
Josephine	Ljungman (1872)	Ophiuroidea
	Lovén (1871, 1874)	Echinoidea
Hirondelle	Koehler (1895a, 1896a, 1897b, 1898, 1921a)	Ophiuroidea; Echinoidea;
Hirondelle II	Perrier (1891, 1896a)	Asteroidea
	Hérouard (1923); Marenzeller (1892, 1893)	Holothuroidea
Princesse Alice Princesse Alice II	Koehler (1895b, 1896b, 1901, 1907b, 1909, 1921a)	Crinoidea; Ophiuroidea; Asteroidea; Echinoidea; Holothuroidea;
	Hérouard (1896; 1899; 1902; 1912; 1923)	Holothuroidea
Talisman	Koehler (1906a,b)	Ophiuroidea
	Perrier (1885b,c, d; 1894)	Asteroidea
	Mortensen (1903, 1927b)	Echinoidea
	Perrier (1896b, 1899, 1902)	Holothuroidea
Président Théodore-Tissier	Cadenat (1938)	Asteroidea; Echinoidea; Ophiuroidea;
Atlantis	Clark (1848)	Asteroidea; Ophiuroidea
	Clark (1949)	Asteroidea; Ophiuroidea; Crinoidea; Echinoidea
	Serafy (1974)	Echinoidea
Jean Charcot (BIAçores, Noratlante)	Cherbonnier & Guille (1972); Roux (1985); Améziane *et al.* (1999)	Crinoidea
	Cherbonnier & Sibuet (1972)	Asteroidea; Ophiuroidea
	Sibuet (1976, 1977);	Asteroidea
	Mironov (2006)	Echinoidea
Archimède (Bathyscaphe)	Sibuet (1972); Pérès (1992)	Asteroidea; Echinoidea; Crinoidea; Ophiuroidea; Echinoidea; Holothuroidea
Knorr	Roux (1980; Famous)	Crinoidea
Tydeman (CANCAP-V)	Améziane *et al.* (1999)	Crinoidea
G.O. Sars (MAR-ECO)	Dilman (2008)	Asteroidea
	Martynov & Litvinova (2008)	Ophiuroidea
	Gebruk (2008)	Holothuroidea

echinoderm fauna faded away and, from the late 1920’s onward, publications focused primarily on the re-examination of museum specimens collected during the former cruises (*e.g.,* Clark 1925; Deichmann 1930;Mortensen 1935), though some studies also dealt with shallow-water biota collected by mostly small expeditions (Nobre 1924; Cadenat 1938; Chapman 1955; Marques 1983). Three exceptions are the publications based on the material collected by the RVs ‘Atlantis’ (Clark 1948, 1949), ‘Jean Charcot’ (Cherbonnier & Guille 1972; Cherbonnier & Sibuet 1972; Sibuet 1976, 1977), and by the French bathyscaphe ‘Archimède’ (Sibuet 1972). From the 1980’s onward, the studies shifted to a more integrated analysis of the shallow-water fauna, and Marques (1984) published the first ecological study on the Azorean echinoderms. In the 21st century, the first field guides were issued that included underwater photographs of animals in the Azores (*e.g.,* Wirtz & Debelius 2003).

In more recent years, a renewed interest on the complex geological processes shaping the ocean floor led to the return of the oceanographic cruises to the Azorean deep waters, especially to areas surrounding the Mid-Atlantic Ridge (*e.g.,* RV ‘G.O. Sars’) and to the extreme environments of the deep-water chemosynthetic hydrothermal vents (*e.g.,* Lucky Strike, Menez Gwen, Rainbow). The use of modern capture techniques such as Remote Operated Vehicles (ROV) together with more traditional collecting forms (*e.g.,* dredge, trawl or sledge) added several new species to the archipelago’s deep-water echinoderm fauna, some of which proved to be new to science (*e.g.,* Stöhr & Segonzac 2005; Dilman 2008; Gebruk 2008; Martynov & Litvinova 2008). By the 2010’s, phylogeographic and taxonomic studies using genetic tools started to readdress the shallow-water echinoderm fauna of the Northeast Atlantic, including the Azores (*e.g.,* Borrero-Pérez *et al*. 2011; Kroh *et al*. 2011; Wangensteen *et al*. 2012; Micael *et al*. 2014). Also, during the last decade, local faunal lists were produced on the shallow-water echinoderm fauna that summed up the first attempts to understand the overall biodiversity of this diverse animal group in the Azores (Micael & Costa 2010; Micael *et al*. 2012). In addition, the fossil echinoderm fauna from the early Pliocene and Pleistocene of the oldest island, Santa Maria, was addressed during this decade (*e.g.,* Madeira *et al*. 2011; Ávila *et al*. 2015a,b; Santos *et al*. 2015).

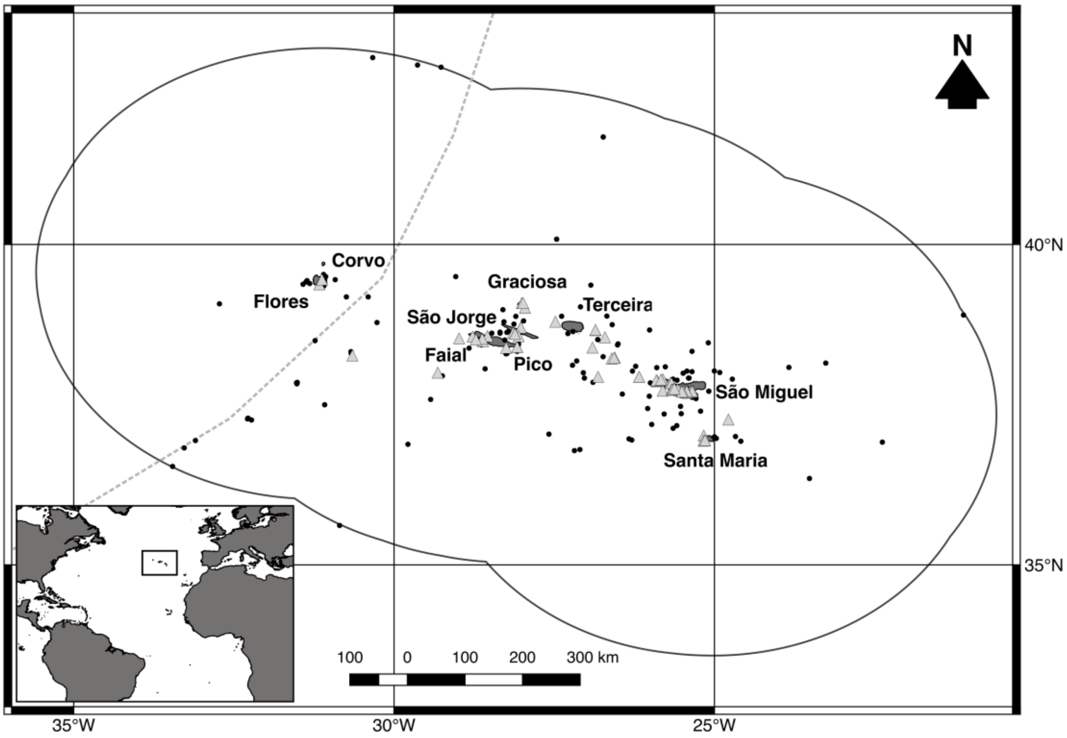


Figure 5.2. Azores Archipelago and the area defined by the 200 miles Economic Exclusive Zone (ZEE; solid line), Mid-Atlantic Ridge (hatched line), sample stations of the main historical oceanographic cruises (black circles; for references see Table 1) and the material examined herein (grey triangles).

In sum, throughout 150 years of research, the echinoderm fauna of the Azores has been the subject of several studies, which are dispersed among papers, notes, reports, reviews, and monographs. The present work attempts to summarize the present knowledge about this invertebrate group in the Azores area.

5.2. Study area

The Azores is one of the most isolated archipelagos in the Atlantic Ocean. It is composed of nine volcanic oceanic islands and several islets, spread over 600 km in a SW–NE direction, between N36°55’ and N39°43’ and W24°46’ and W31°16’ (França *et al*. 2003), almost halfway between Europe and America (Fig. 5.2), some 1,370 km from the nearest European continental shores and about 842 km from the Madeira Archipelago, the closest insular system (Morton *et al*. 1998). The islands are located nearby the Mid-Atlantic Ridge along the tectonic zone where the European, American, and Nubian plates meet (França *et al*. 2003) and are geographically clustered in three groups: the eastern group (São Miguel and Santa Maria islands), lies about 138 km distant from the central group (Faial, Graciosa, São Jorge, Pico, Terceira islands), which in turn is about 220 km away from the western group (Flores and Corvo islands). The Azorean waters are consigned by an Exclusive Economic Zone (EEZ) defined by a 200-nautical-mile radius around the islands (Fig. 5.2).

Except for Santa Maria, the oldest island (≈6 Ma; Ramalho *et al*. 2017) and the only one with a marine fossil record, the other islands are seismically active, with several historic volcanic eruptions. The nearby seafloor surrounding the islands of the Azores is irregular and composed mainly of rocky bottoms (da Silva & Pinho 2007). The insular shelf is narrow, and the marine topography is characterized by a steep slope beyond the shelf break with depths over 1,000 m just a few miles offshore (Morton *et al.* 1998; Wallenstein & Neto 2006). The Azorean EEZ encloses almost one million square kilometres, with 94–97% of its area characterized by depths exceeding 1,000 m. The abyssal plains are interrupted by several seamounts (contributing 6% of the total area of the EEZ), many of which are considered as important contributors to the biodiversity of the area (da Silva & Pinho 2007).

The Azores' extremely rugged coastline is approximately 930 km long (Instituto Hidrográfico 2000) and is exposed to medium/high levels of wave action (Wallenstein & Neto 2006; Wallenstein *et al*. 2010). The morphology of the littoral varies from island to island, though in general terms it is characterized mostly by rocky shores (Morton *et al*. 1998). Sandy beaches are rare, generally enclosed in small bays that are mostly of volcanic origin. The sand in many of the beaches is frequently seasonal, as winter storms carry the sand offshore, leaving behind the underlining basalt cobblestones (Morton *et al.* 1998). The tidal range is small (<2 m), and therefore extensive bedrock platforms that favour the occurrence of rock-pools are scarce and heterogeneous (Wallenstein & Neto 2006; Wallenstein 2010). The Azores lie at the northern edge of the North Atlantic Subtropical Gyre, with the main sea-surface currents flowing from west to the east. The Gulf Stream transports warmer waters of equatorial and tropical origin to the colder northern Atlantic (Johnson & Stevens 2000; Bashmachnikov *et al*. 2015). The average sea-surface temperatures in the archipelago range from 15–16°C in the winter to 22–24°C during summer (Bashmachnikov *et al*. 2004).

5.3. Material and methods

Compilation of the species list

The echinoderm fauna compiled and revised herein considers all the species present in the Azores as reported in the literature over the last 150 years. Table 5.1 lists the main cruises made in Azorean waters and the resulting publications. Other important bibliographic sources referring to material collected in the area include: Drouët (1861), Lyman (1865), Agassiz (1863), Selenka (1867), Agassiz (1872–1874), Lovén (1874), Barrois (1888), Nobre (1924, 1930), Grieg (1932), Chapman (1955), Tortonese (1965), Marques (1983), Wirtz & Martins (1993), Morton *et al*. (1998), Wirtz & Debelius (2003), Stöhr & Segonzac (2005), Wirtz (2009), and Wisshak *et al*. (2009a, 2010). Taxonomic reviews, in which specimens collected in the area were re-examined (many producing re-descriptions and re-identifications), are also included (*e.g.,* Mortensen 1935; Clark & Clark 1967; Hansen 1975; Paterson 1985; Clark & Downey 1992; Gebruk *et al*. 2012). Compiled faunal lists for the area were also critically reviewed and used as additional sources: Pereira (1997), García-Diez *et al*. (2005), Micael & Costa (2010), and Micael *et al*. (2012).

Species were only considered as native to the archipelago if at least one record in the Azores was documented (*i.e.,* material collected by a cruise or belonging to a zoological collection). For this purpose, a list of references was assembled referring only to publications in which the Azores are included in the geographical distribution of the species.

Synonymies of included species are not comprehensive but are restricted to works in which Azorean echinoderms were studied or mentioned by the authors. Works in which the records were based on actual specimens (collected, examined or observed) from the Azores are preceded by a superscript dollar sign ($^{\$}$) in the synonymies, whereas other studies only mentioning the Azores in faunal lists or species distributions are simply listed. All uncertain records for the area are preceded by a question mark (?). Records originally based on mixed lots are preceded by 'p.p.'. If the species' name is followed by a question mark (?) in the title, its presence in the Azores is considered questionable in this review, since its record was based either on unsound historical identifications, dubious reports (*e.g.,* possible mislabelling), or on possible vagrant animals with no evidence of an established local population (*e.g.,* shallow-water tropical species).

For a complete assessment of the Azorean echinoderm fauna, an additional list is also provided that includes all species erroneously considered as native to the Azores (*e.g.,* out-dated synonymy, misprints, mislabelling) that persist in the bibliography (*i.e.* all species we have considered that should be excluded from the Azorean checklist of echinoderms).

Locations listed in the historical reports of RVs 'Princesse Alice', 'Talisman' and 'Hirondelle' cruises, which were measured with reference to the Paris meridian were corrected to the Greenwich meridian by subtracting 2°20'14" from the longitude, except for Koehler (1909) and Hérouard (1923), which were already reported using the English meridian.

The five echinoderm classes are treated in the following order: Crinoidea, Ophiuroidea, Asteroidea, Echinoidea, and Holothuroidea. The species are ordered alphabetically, from class downwards. The World Register of Marine Species database (WoRMS Editorial Board 2017) was used as a reference for the latest taxonomic status of Azorean species, though a bibliographical confirmation was always favoured (*e.g.,* Mortensen 1928; Clark & Clark 1967; Hansen 1975; Paterson 1985; Clark & Downey 1992; Martynov 2010; O'Hara *et al*. 2017, 2018).

The type locality for each species is given whenever possible. The paragraph 'See' encloses relevant literature that references the synonymy and comprehensive descriptions of each species. Additional references used to detail each species' geographical distribution, depth range, ecology (*e.g*., type of substrate, diet), and mode of larval development are also listed in this paragraph. The geographical distribution outside of the Atlantic area is outlined only in general terms. The global depth range for each species is followed by the bathymetric distribution documented in Azorean waters (AZO). Reported habitat information together with other known ecological data are placed under the paragraph 'Habitat'. Data on the mode of larval development for the listed species is based in Mortensen (1913, 1921), Fell (1945), Schoener (1972; ophiuroids), Emlet (1995; echinoids), Kasyanov *et al*. (1998), Levitan (2000; echinoids), and McEdward & Miner (2001). Other references are also listed under the paragraph 'See'.

Santa Maria, the oldest and southernmost island of the archipelago, is the only one with documented fossiliferous outcrops, mostly marine and early Pliocene, but also late Pleistocene (MIS 5e, *i.e.* Last Interglacial) in age (see Ávila *et al*. 2018). The paragraph 'Fossil record' briefly summarizes the extant echinoid species reported from the fossil record of Santa Maria Island (see Ávila *et al.* 2009, 2010, 2015a, b; Madeira *et al*. 2011, 2017a).

Many echinoderm species (mainly holothurians and echinoids) are traditionally or commercially harvested. They are used directly for human consumption or as additives in pharmaceutical, nutraceutical, and cosmetic products. They are also used as ornamental species in aquarium trade and souvenir memorabilia (Micael *et al.* 2009). Most markets are concentrated in Asia, but several European species have been reported as being commercially harvested with potential economic importance for future fisheries. Though no echinoderm species from the archipelago have been traditionally consumed or commercially harvested in the islands, we have enclosed in the paragraph 'Commercial value' encloses information regarding if the species is harvested for food consumption, based on the following references: Lawrence (2007), Sicuro & Levine (2011), and Purcell *et al*. (2012).

The rich material collected over the years from Azorean waters is housed in zoological collections in numerous institutions throughout Europe and the USA. For instance, H.M.S. 'Challenger' specimens are currently housed in several zoological collections, such as the Natural History Museum (London) and Museum of Comparative Zoology (Harvard University). The material collected by 'Princesse Alice' is part of the zoological collections of the Muséum National d'Histoire Naturelle (Paris) and the Musée Océanographique de Monaco (Monaco). These two examples demonstrate how difficult it is to track and examine specimens reported in the literature, a task far more time-consuming and costlier than possible for this paper. Thus, to achieve a comprehensive revision of the echinoderm fauna of the Azores in a timely manner, we have relied on the published literature and local collections.

'Material examined' lists the studied specimens from the following Portuguese zoological collections: Department of Biology of the University of the Azores (DBUA-ECH, Ponta Delgada, São Miguel Island, Azores), Museu Carlos Machado (MCM, Ponta Delgada, São Miguel Island, Azores), Museu Bocage – Natural History Museum (MB–

NMHN, Lisbon, Portugal), Department of Oceanography and Fisheries (DOP, Horta, Faial Island, Azores), and 'Estrutura de Missão para a Extensão da Plataforma Continental Portuguesa' (EMEPC, Paço de Arcos, Portugal).

The material was collected using a variety of methods, including dredging, grab sampling or direct sampling by hand on the shore, SCUBA diving or by ROV ('Luso', EMEPC 2009). Additional material from the Gorringe Seamount (W of Portugal, NE Atlantic) was also included for comparison. The depths at which the specimens were collected ranged from 0 to 1,201 m. Most specimens were preserved in 70–96% ethanol or dried, though some of the oldest material may have been temporarily immersed in a solution of buffered formalin as a fixation agent. All measurements were made on preserved animals either directly with a digital calliper or by using an eyepiece reticule on a binocular microscope. Observation of calcareous ossicles (*e.g.,* pedicellaria) was made with an optical microscope after a brief immersion in common household bleach.

The paragraph 'Description' contains a brief diagnostic description based on the specimens found in the zoological collections mentioned above. The terminology used herein was mainly adapted from Clark & Rowe (1971), but also from Roux (2002; crinoids), Stöhr *et al.* (2012; ophiuroids), Clark & Downey (1992; asteroids), Kroh & Smith (2010; echinoids), and Purcell *et al*. (2012; holothurians). The paragraph 'Remarks' includes a brief review of the history of species records and taxonomy in the region. Whenever available, we included photographs or footage frames showing echinoderms *in situ* taken by the authors (shallow-water species) or by the ROV 'Luso' (EMEPC, 2009) (deep-water species).

Abbreviations and acronyms used in the text

Institutions and Zoological Collections: DBUA-ECH — Recent echinoid reference collection of the Department of Biology of the University of the Azores; DBUA-F — Reference fossil collection of the Department of Biology of the University of the Azores; DOP — Recent reference collection of the Department of Oceanography and Fisheries of the University of the Azores; EMEPC — Portuguese expeditions 'Estrutura de Missão para a Extensão da Plataforma Continental Portuguesa'; LUSO — Remotely operated underwater vehicle operated by EMEPC; MB–NMHN — Museu Bocage, Natural History Museum; Measurements: AL — Arm length

(Crinoidea); TD — Diameter; P — Pinnules (Crinoidea); R — Major radius, from the centre to the arm tip (Asteroidea); r — Minor radius, from the centre to the interradius (Asteroidea); TL — Total length (test length in echinoids and holothuroids); Localities: AZO — Azores; FAY — Faial Island; FLS — Flores Island; FRM — Formigas Islet; GRA — Graciosa Island; PIX — Pico Island; SJG — São Jorge Island; SMA — Santa Maria Island; SMG — São Miguel Island; TER — Terceira Island; Other: bt(s) — Bare test(s) (Echinoidea); RV — Research vessel; ROV = Remotely operated underwater vehicle; Sta(s) — Station(s); spm(s) — Specimen(s).

5.4. Results and discussion

The extant echinoderm fauna of the Azores encompasses a total of 172 species: 6 crinoids (distributed among 3 orders, 6 families and 6 genera), 55 ophiuroids (6 orders, 18 families and 29 genera), 45 asteroids (6 orders, 18 families and 32 genera), 36 holothurians (6 orders, 12 families and 20 genera), and 30 echinoids (9 orders, 17 families, 25 genera). The differences in the number of species between classes are similar to differences seen in other areas (see Pérez-Ruzafa *et al.* 2013), including the nearby Canary Islands (Hernández *et al*. 2013). Twenty-nine additional species might also prove native to the archipelago, but their presence needs confirmation and their status must be currently considered as dubious in the area. We have included Table S5.1 as Supplementary Material, containing a synopsis of all the species referred to the Azores, together with information about geographical and bathymetric ranges, habitat, type area, status, and first report for the archipelago.

The Canaries have one of the best-studied echinoderm faunas among the NE Atlantic archipelagos, particularly in shallow waters. Hernández *et al*. (2013) reported a total of 127 species in this archipelago and claimed that the number was higher than those reported from other archipelagos. Our results show that the Azores surpass the Canary Islands by 45 species. However, we agree with Hernández and co-authors in considering that the differences are probably a direct result of differences in sampling efforts. To our knowledge, Azorean deep waters have been more extensively sampled (see Fig. 5.2) than those of other NE Atlantic archipelagos. Moreover, from a historical point of view, between the late 19th century and early 20th century, most of the material collected in the Azores area was extensively studied by important echinoderm scholars at the time (*e.g.,* Koehler, Mortensen, and Perrier), echoing the ‘rule of thumb’ that the distribution of a species is strongly biased by the specific research effort in the same area. To illustrate, over 34 echinoderm species alone were described based on specimens collected in the Azores. Notwithstanding, the Azorean faunal lists appear old and out-dated, with many of the reported species being last collected in the area over 100 years ago.

In addition to the 172 species, another 51 species reported for the Azores in the bibliography proved to be erroneous, mostly a direct result of misidentifications, out-dated synonymy, misprints or incorrect indirect references. Nonetheless, a more recent interest in the Mid-Atlantic waters of the Azores and their echinoderm inhabitants resulted not only in the confirmation of the presence of 38 species (7 species herein) recorded in the historical bibliography, but also in the addition of 24 new taxa to the Azores (*e.g.,* Stöhr & Segonzac 2005; Dilman 2008; Gebruk 2008; Martynov & Litvinova 2008).

Our results indicate that out of 172 species only 29 echinoderm species occur at shallow depths in the Azores (≤50 m: 1 crinoid, 6 ophiuroids, 8 sea stars, 5 holothurians, and 9 echinoids). Pereira (1997), in contrast, listed 41 shallow-water echinoderm species for the Azores (<200 m); Micael & Costa (2010) 48 species and, recently, Micael *et al*. (2012) 49 species (≤50 m). The differences among these publications apparently are related to the number of accepted records in each of the bibliographic references acknowledged by the authors. In contrast, the difference between our results and the above are mostly related to the definition of shallow-water fauna. Here, we consider shallow-water species only those documented in Azorean waters ≤50 m, whereas the previous authors included any species recorded in shallow waters anywhere in their geographical range, though only in deeper water within the archipelago, even to 100 m. For example, the sea star *Luidia sarsii sarsii* Düben & Koren, *in* Düben, 1845, has a remarkable bathymetric range of 9–1,300 m (Clark & Downey 1992). However, in its southern geographical range it tends to occur only in deep waters (Picton 1993). In the Azores, this species was recorded at depths between 100–200 m and thus is not included in the shallow-water biota of the archipelago herein.

Another source of discrepancies is the uncritical acceptance of any report from the Azores. In the present study, only species with at least one documented specimen from the Azores are accepted. For example, Koehler (1909) recorded *Ophiopsila* *aranea* Forbes, 1843, from the Azores based on the material collected by RVs 'Princesse Alice' and 'Talisman', though neither ship reportedly collected any animals in the Azores, only in Madeira and Cabo Verde waters. We also do not consider species such as *Eucidaris tribuloides* (Lamarck, 1816), based on the unlikelihood that the documented specimens are representatives of an established local population. Koehler (1895a, 1898) reported this tropical species from the Azores based on a small specimen from 130 m. It was never again collected in the area, and Lares & McClintock's (1991) study on the effects of temperature on this species' physiology and biology indicated that it is very unlikely that this tropical species could maintain a viable population in the colder Azorean waters (see as well Madeira *et al.* 2011). Furthermore, it occurs predominantly in shallow waters in its native range. Thus, the individual reported by Koehler may represent a solitary vagrant or was misidentified, and does not represent a real element of the Azorean biota.

The remarkable small number of echinoderm species recorded in the shallow waters of the Azores appears to be related to five contributing factors: limited coastal area, low habitat diversity, absence of extended soft-bottom environments, isolation-by-distance, and the recent volcanic origin of the archipelago. Pérez-Ruzafa *et al.* (2013) showed that the number of echinoderm species is highly dependent of the coastal length. The Azores lack extensive margins of shallow waters; coastal areas contribute less than 1% to the total EEZ area (da Silva & Pinho 2007). Most of the Azorean shallow waters are concentrated around the islands and around a few shallow-water seamounts. The insular platforms are narrow and characterized by steep slopes, in which the sea bottom quickly drops to abyssal depths a short distance from the coast (Ávila *et al*. 2008; Quartau *et al*. 2014) thus imposing significant constraints on the distribution of shallow-water organisms (da Silva & Pinho 2007). Furthermore, most shores are exposed to strong swell (Wallenstein & Neto 2006) with very few protected bays (small and scattered throughout the islands) and even fewer marine lagoons (*e.g.,* Fajã de Santo Cristo; Morton *et al*. 1998). Thus, habitat diversity in the Azores is low, with no documented shallow-water coral reefs, mangroves, nor seagrass, and few places of high sedimentation (in waters <50 m depth), such as muddy or maerl/rumble like bottoms. In the long term, the relative high exposure of the Azorean coastline together with tropical storms that occasional reach the archipelago, could have contributed to the exclusion of rheophobic echinoderm species that might have reached the islands. The degree of isolation of the islands from potential nearby sources, about 842 km from the nearest island (Madeira Island) and 1,370 km from the European continental shores (Morton *et al*. 1998), increases if the main sea-surface currents in North Atlantic are taken in account. The islands lie in an area of relatively weak eastward flow between the North Atlantic Drift and its southern branch, the Azores Current. The flow originates far to the west off the Grand Banks (Klein & Siedler 1989), thus potentially reducing immigration of new settlers.

The Azores is one of the youngest archipelagos in the NE Atlantic, in which island ages range from *c.* 6 Ma (Santa Maria Island; Ramalho *et al*. 2017) to 0.27 Ma (Pico Island; Demand *et al*. 1982). Both active volcanism and earthquakes can cause deleterious effects on the local echinoderm communities through the destruction of habitats, abrupt increases in temperature, smothering through obrution (either by ashes or by landslides), displacement by flood waves, gas poisoning and water acidification (Lawrence 1996). Overall, the Azores Archipelago appears to be a hazardous place for the small echinoderm populations isolated on its shores.

As in any other volcanic oceanic island/seamount system, the marine shallow-water fauna of the Azores derives primarily from episodic arrival of settlers that manage to establish a viable population in the archipelago. Among the recent records, two specimens of the tropical, long-spined sea urchin *Diadema africanum* Rodríguez *et al.*, 2013, were recorded by Minderlein & Wirtz (2014) off Santa Maria, the southernmost island. This shallow-water sea urchin plays a major role in the structure of the shallow benthic environment of the eastern Atlantic and was classified as a key-herbivore species in the Canaries, where it controls single-handedly the algal assemblages in this archipelago (Tuya *et al.* 2004). This species was previously not known from waters north of the Madeira Archipelago, and we believe that it represents a recent arrival to the archipelago. Thus, the inclusion of *D. africanum* in the shallow-water fauna of the Azores should be considered with caution until further data can confirm the establishment of a population.

In contrast, the small sea star *Asterina gibbosa* (Pennant, 1777) was one of the first echinoderm species recorded from the Azores in the late 19th century. However, through the history of zoological studies in the archipelago, we can only find a total of four reports of this species: 1) Barrois (1888) claimed they were quite common on the coast of Faial Island; 2) Clark & Downey (1992) reported a batch of specimens from the Azores in the Natural History Museum (London), with no further collection data; 3) a photograph taken in 1985 by one of the authors (Frias Martins) of a specimen in the intertidal of São Miguel Island, and 4) Morton *et al*. (1998) observed this sea star in the low intertidal and subtidal of the Azores. The near absence of records for the Azores cannot be explained alone by the cryptic behaviour of this small NE Atlantic sea star. Thus, it appears that local populations of *Asterina gibbosa* could be subject to major fluctuations on Azorean rocky shores. Micael *et al*. (2012) suggested that this species has locally disappeared. Whether this 'disappearance' from the coastal areas of the archipelago is definitive, only time will tell.

The shallow-water echinoderm fauna appears to be mainly associated with rocky shores, though nine species appear to be restricted to soft bottoms. In contrast, most of the deep-water fauna is mainly composed by species found in association with sediments. However, the known habitats for the these species are based on biased data, as the majority of the deep-water fauna of the Azores is known from dredging, sometimes over large distances. Furthermore, obvious logistic problems arise when sampling rocky outcrops at depths below 100 m. Nonetheless, the increasing use of ROVs offers new information on species *in situ*, their environment, ecology, and behaviour (*e.g.,* Roux 1980; Rogacheva *et al*. 2012, 2013). For example, footage recorded by ROV systems has shown that several holothurian species rarely captured with traditional methods are active swimmers (*e.g.,* Rogacheva *et al*. 2012). A more recent study by Stöhr & Segonzac (2005) also showed that the environments inhabited by deep-water echinoderms in the Azores include chemosynthetic areas, *e.g.*, *Ophioctenella acies* Tyler *et al*., 1995, recently found in the hydrothermal vents of Menez-Gwen and Lucky Strike.

The echinoderm fauna in the Azores consists of 126 Atlantic species (including 39 species that also occur in the Mediterranean), 37 cosmopolitan taxa, and only 9 endemic deep-water species (Fig. 5.3). However, it is necessary to note that 6 of the endemic species are known only from the type material collected more than 100 years ago, and one was last recorded 80 years ago. Most of the echinoderm fauna inhabiting the archipelago's shallow waters consists of species restricted to the eastern side of

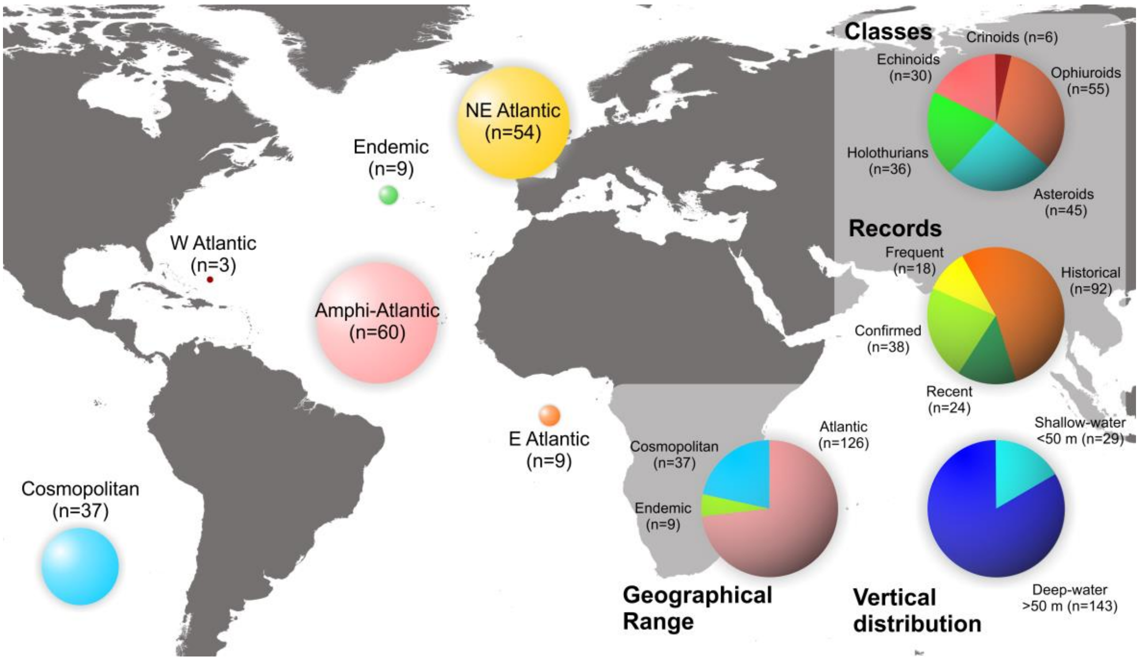


Figure 5.3. Echinoderms from the Azores per class, number of records in the literature, vertical distribution and geographical range.

the Atlantic, with 28 species also occurring in the Mediterranean Sea. Exceptionally, six species also occur in West Atlantic shallow waters, and and two have also widespread distributions outside the Atlantic, the heart urchin *Echinocardium cordatum* (Pennant, 1777) and the brittle star *Amphipholis squamata* (Delle Chiaje, 1828). However, these two species may represent cryptic species complexes. In contrast, the deep-water fauna is characterized by species with a wide geographical distribution in the Atlantic (with just 42 species restricted to the east side of the Atlantic) and 35 species also occurring in other oceans. Additionally, Azorean deep waters also support 3 species found elsewhere only in the West Atlantic. Interestingly, among the 36 holothurian species reported from the archipelago, 31 are considered deep-water species, and at least half of these are benthopelagic (14 to 17 species). Overall, the echinoderm fauna in the Azores mirrors in a ‘microcosm’ important issues surrounding this diverse invertebrate group at biogeographical, ecological, and taxonomical levels.

5.4.1. Systematics

Phylum Echinodermata Bruguière, 1791

Class Crinoidea Miller, 1821

Order Comatulida Clark, 1908

Family Antedonidae Norman, 1865

Genus *Antedon* de Fréminville, 1811

Species *Antedon bifida* (Pennant, 1777)

Antedon bifida moroccana **(Clark, 1914)**

(Fig. 5.4)

$^{\$}$1888. *Antedon rosacea* Norman; Barrois: 32, 33, 115.
$^{\$}$1888. *Antedon*; Simroth: 231.
$^{\$}$1898. *Antedon rosacea*?; Koehler: 3.
1911a. *Antedon bifida* (Pennant); Clark: 38–39.
1914. *Antedon moroccana* A. H. Clark; Clark: 307.
1927a. *Antedon moroccana* A. H. Clark; Mortensen: 27.
$^{\$}$1955. *Antedon bifida* (Pennant); Chapman: 338.
1965. *Antedon bifida* (Penn.); Tortonese: 27.
$^{\$}$1967. *Antedon bifida moroccana* (A. H. Clark); Clark & Clark: 226–234, fig. 13c.
$^{\$}$1983. *Antedon bifida moroccana* (A. H. Clark); Marques: 1.
1994. *Antedon bifida* (Pennant); Nichols: 113–134.
1997. *Antedon bifida* (Pennant, 1777); Pereira: 332.
$^{\$}$1998. *Antedon bifida*; Morton *et al.*: 150, fig. 7.5C.
2010. *Antedon bifida* (Pennant, 1777); Micael & Costa: 321.
2012. *Antedon bifida* (Pennant, 1777); Micael *et al.*: 3.

Type locality: Tangier, Morocco.

See: Clark & Clark (1967); Lahaye & Jangoux (1988); de Domenico *et al.* (2009).

Distribution: Northeast Atlantic and Mediterranean Sea, from Morocco to west of Sierra Leone and Liberia, including the Azores, Madeira and Canaries; the subspecies *A. bifida bifida* (Pennant, 1777) is distributed further north in the Northeast Atlantic, from Portugal northwards to the British Islands.

Depth: 0–200 m [AZO: 3–60(?130) m].

Habitat: present in waters with strong tidal currents and related upwelling phenomena; in shallow-waters, it lives in relatively protected areas, clinging to rocks, algae or other sessile fauna; nocturnal.

Type of Development: the females brood the eggs, which produced a doliolaria larvae (non-feeding pelagic larvae, *c.* 5 days).

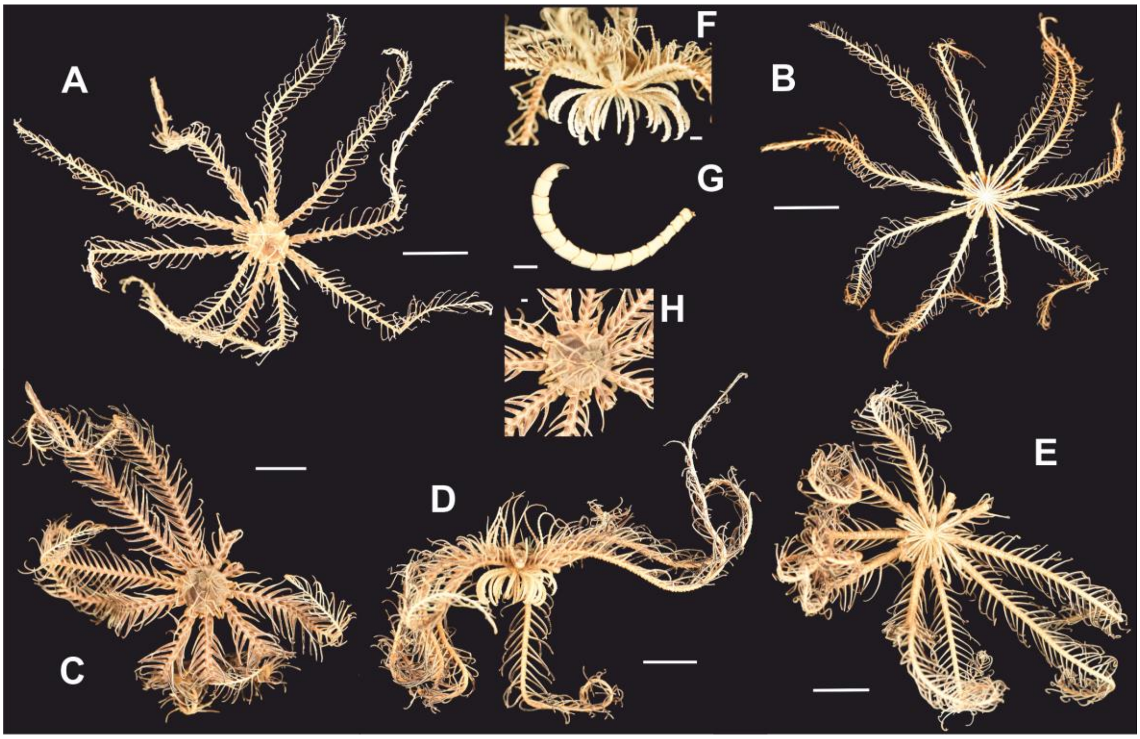


Figure 5.4. *Antedon bifida moroccana* (Clark, 1914) (DBUA-ECH 071). Dorsal view (A, C); ventral view (B, E); lateral view (D); detail of the disc, dorsal view (H), lateral view (E) and cirri (G); scale bars are 1 cm (A–F, H) and 1 mm (G).

Material examined: DBUA-ECH 071 (Piscina da Lagoa, Lagoa, SMG, AZO, *c.* N37°44'29" W25°34'27", 1996.07.25, 12 m; 9 spms, AL=46–74 mm); DBUA-ECH 072 (Baixa do Ouro, Caloura, SMG, AZO, *c.* N37°43'32" W25°32'47", 1996.12.05, 15 m; 3 spms, AL=37–64 mm).

Description: disc naked, with ten slim pinnate arms about 37–74 mm in length; centrodorsal discoidal, bearing crowded and irregular cirrus sockets in two or three more or less alternating rows; cirri XXV–XXXIV, 13–16, from 7 to 11 mm long; in lateral view the cirri are twice as broad distally as proximally with the distal half strongly recurved; the cirrals in the outer part of the cirri are almost as broad as long dorsally, becoming terminally slightly longer, about one third again as long as broad; overall cirral outline not centrally constricted or appressed but strongly compressed laterally; conspicuous group of perisomic interradials in each interradius; division series (IBr) short and well separated laterally; first pinnule (P1) composed for the most part of elongated segments, though a few of the basal segments may be shorter; P1 composed of 25–31 segments (*c.* 12 mm long) to about 19–20 segments (*c.* 6–7 mm) in smaller specimens (arm length ≤46 mm); P1 is at least twice as long as the second pinnule (P2), which is similar in size to the third pinnule (P3), the first genital pinnule;

gonads absent from the first two pinnules (P1 and P2) and confined to proximal half of the pinnule; the production of the distal ends of the segments of the proximal pinnules is marked; in ethanol, the anterior side is more or less cream colour with ambulacral grooves and pinnules dark reddish-brown or dark purple; posterior side uniformly light cream.

Remarks: the *Antedon* species present in the Atlantic show a great morphological variation resulting in somewhat overlapping interspecific diagnosing characters, which historically have puzzled taxonomists. Clark (1914) believed that the overall variation was essentially a result of different environmental settings. Later, Clark & Clark (1967) again questioned if the several forms of *Antedon*, from the west and east tropical Atlantic waters (*A. duebeni* Böhlsche, 1866 and *A. hupferi* Hartlaub, 1890, respectively) and from the temperate and boreal Northeast Atlantic waters [*A. bifida* subspecies and *A. petasus* (Düben & Koren, 1846), respectively] could be all conspecific, a matter still to be settled.

The first report of an *Antedon* to the archipelago was made by Barrois (1888) under the name *Antedon rosacea*, a known synonymy of the European *A*. *bifida*. Simroth (1888) also listed an *Antedon* among the Azorean echinoderm fauna, but failed to assign it to a particular species. Koehler (1898) examined a very small and damaged specimen collected in the archipelago by RV 'Hirondelle' at 130 m and commented that he could not ascertain if it belonged to *Antedon rosacea*. Chapman (1955) remarked that the animals from the Azores differ slightly from the typical *A*. *bifida* by having fewer segments in the first pinnule. Clark & Clark (1967) examined material from the Azores and concluded that the *Antedon bifida* present in the archipelago belonged to the subspecies *moroccana*. This subspecies differs essentially from the typical form by the overall aspect of the cirri segments. The first two pinnules (P1 and P2) seem also slightly smaller with fewer segments in *A*. *b. moroccana.* The overall cirrus shape exhibited by the Azorean material examined herein agrees with descriptions and illustrations of the *moroccana* form presented by Clark & Clark (1967) and by de Domenico *et al*. (2009). Nevertheless, smaller specimens showed slightly smaller P1 and P2, with fewer segments, similar to what was presented by Clark & Clark (1967) for *Antedon bifida moroccana*. These discrepancies were dismissed as size-related individual variations in view of the overall similarity with *A. bifida* particularly with the subspecies *moroccana*.

Genus *Leptometra* Clark, 1908

***Leptometra celtica*? (M'Andrew & Barrett, 1857)**

1909. *Antedon phalangium,* (J. Müller); Koehler: 269.
1932. *Leptometra phalangium* J. Müller; Grieg: 43.
1980. *Leptometra celtica* (Mac Andrew & Barrett, 1858); Marques: 98.
?$1992. *Leptometra;* Pérès: 252.

Type locality: Sound of Skye, Scotland.

***See*:** Clark & Clark (1967: 564–573, figs. 32c–g); Clark (1980: 193–195, fig. 2); Fonseca *et al.* (2014).

Distribution: East Atlantic, from Faeroe channel to off Sierra Leone including the archipelagos of Madeira, Canaries, and the seamounts Seine and Gorringe.

Depth: 46–1,279 m (AZO: ?700 m).

Habitat: mud, or sand, or gravel with mud (rarely on hard bottoms); can form dense beds.

Remarks: Koehler (1909) included the Azores in the geographical distribution of *Leptometra phalangium* (Müller, 1841), a species regarded as endemic to the Mediterranean Sea (Tortonese 1965). All reports of *Leptometra phalangium* from the Atlantic were a result of confusion with *L. celtica*, the only *Leptometra* species known to occur in the Atlantic (Clark & Clark 1967). Regardless, the citation for the Azores by Koehler (1909) and later reproduced by Grieg (1932) and Marques (1980) is likely erroneous, as to best of our knowledge no material belonging to either *L. celtica* or *L. phalangium* was ever collected in the archipelago.

In 1992, Pérès claimed to have observed a *Leptometra* crinoid during a dive by the bathyscaphe 'Archimède' west of Santa Maria Island at a depth of 700 m. It is possible that Pérès might be referring to *L. celtica*, considering this species' geographic and bathymetrical wide range. On the other hand, on stating a 'crinoid of *Leptometra* type', he could have been simply referring to a comatulid (an unstalked form), which in this case *Pentametrocrinus atlanticus* (Perrier, 1883a) should be also considered, a species known to occur in the Azorean deep waters (see below).

Family Pentametrocrinidae Clark, 1908

Genus *Pentametrocrinus* Clark, 1908

Pentametrocrinus atlanticus **(Perrier, 1883a)**

$^{\$}$1909. *Eudiocrinus atlanticus*, Perrier; Koehler: 271–274, pl. 32, figs. 15–18.

$^{\$}$1967. *Pentametrocrinus atlanticus* (Perrier); Clark & Clark: 790–794.

$^{\$}$1978. *Pentametrocrinus atlanticus* (Perrier); Messing: 699–708, figs. 1–18.

1980. *Pentametrocrinus atlanticus* (Perrier); Clark: 203–204.

1990. *Pentametrocrinus atlanticus* (Perrier, 1883); Messing & Dearborn: 26, fig. 6.

?$^{\$}$1992. *Leptometra;* Pérès: 252

2005. *Pentametrocrinus atlanticus* (Perrier, 1883); García-Diez *et al*.: 46.

Type locality: North of Spain (N44°01’20” W7°04’45”).

See: Perrier (1883a); Koehler (1909); Messing (1978).

Distribution: North Atlantic; in the western Atlantic reported from Florida and the Caribbean islands; in the eastern Atlantic recorded from the Porcupine Bank (SW of Ireland) and from Bay of Biscay south to Western Sahara, including the Azores and Canaries.

Depth: 374–2,115 m (AZO: 1,165 m).

Habitat: soft substrates, fine sand to mud; it can be found together with sponges, alcyonarians and azooxanthellate colonial scleractinians.

Remarks: Koehler (1909) reported a single specimen belonging to *Pentametrocrinus atlanticus* (= *Eudiocrinus atlanticus*) among the material collected in the Azores by RV ‘Princesse Alice’ (sta 578: N38°26’00” W26°30’45”, 1,165 m). Later, Clark & Clark (1967) and Messing (1978) re-examined the animal from the Azores and confirmed the historical identification by Koehler. It is possible that the crinoid observed by Pérès (1992) during a dive by the bathyscaphe ‘Archimède’ west of Santa Maria at 700 m depth, and described by the author as ‘crinoid of *Leptometra* type’ may have been this species (see remarks above under *Leptometra celtica*).

Family Bourgueticrinidae Loriol, 1882

Genus *Democrinus* Perrier, 1883b

Democrinus parfaiti **Perrier, 1883b**

$^{\$}$1883b. *Rhizocrinus rawsoni*; Carpenter: 173–175.

$^{\$}$1884. *Rhizocrinus rawsoni* Pourtalès, 1874; Carpenter: 262–269, pl. 9, figs. 3–5, pl. 10, figs. 3–20, pl. 53, figs. 7–8.

$^{\$}$1909. *Rhizocrinus Rawsoni*, Pourtalès; Koehler: 255–256.

1927a. *Democrinus Parfaiti* Perrier; Mortensen: 20, fig. 8.

$^{\$}$1977. *Democrinus parfaiti* Perrier; Clark: 172–177, fig. 3.

1980. *Democrinus parfaiti* Perrier; Clark: 205, fig. 1.

$^{\$}$1985. *Democrinus parfaiti* (Perrier, 1883); Roux: 480–481.

1988. *Democrinus parfaiti* Perrier, 1883; Harvey *et al*.: 157.

? $^{\$}$1992. *Rhizocrinus rawsoni*?; Pérès: 256.

2005. *Democrinus rawsonii* (Pourtalès, 1874); García-Diez *et al*.: 46.

2014. *Democrinus parfaiti* Perrier, 1883; Mironov *et al*.: 116.

Type locality: Cape Blanc, NW Africa.

See: Perrier (1883b); Clark (1977); Harvey *et al.* (1988).

Distribution: Northeast Atlantic, from the Azores eastwards between N24° and N50° including the archipelagos of Madeira and Canaries, as well as the Ormond Seamount.

Depth: 870(?650)–4,260 m [AZO: 1,550–1,919(?2,950) m].

Habitat: pteropod or *Globigerina* ooze, mud, gravel to rocky bottoms.

Remarks: almost as soon as it was described by Perrier (1883b) *Democrinus parfaiti* was considered by Carpenter (1883a, 1884) as conspecific with the Caribbean *Rhizocrinus rawsonii* (= *Democrinus rawsonii* Pourtalès, 1874), based on inaccurate figures exchanged by the two authors (Clark 1977). The latter species was reported for the first time to the Azores by Carpenter (1883b, 1884) based on the material collected by RV 'H.M.S. Challenger' (sta 76: N38°11' W27°09', 1,645 m). At the time, Carpenter (1883b) attributed deviations from the typical *R. rawsonii* observed in the Azorean material to water temperature differences. Following the previous author, Koehler (1909) identified RV 'Princesse Alice's material from the Azores as *R. rawsonii*, though observing that the cruise material was quite close to the specimens described by Perrier (1883b) as *D. parfaiti*. On the redescription of the later species, Clark (1977) re-examined the material from the Azores collected by RV 'H.M.S. Challenger' and placed it under *D. parfaiti* (an East Atlantic species). Without material of the Caribbean species for comparison and based on the historical bibliography, Clark concluded that *D. parfaiti* was distinguished by the conical shape of the calyx, by the indistinct or faint sutures between the ossicles in the calyx and by the presence of an abrupt constriction across the radials. Recently, Mironov *et al.* (2014) remarked that Carpenter (1884) could have been correct in considering the species conspecific, but unfortunately did not give any further details. Regardless, the reports of *D. rawsonii* to the archipelago were based on the assumption that this species was conspecific with *D. parfaiti*, thus are considered herein to be erroneous. Additionally, during two dives made by the bathyscaphe 'Archimède' north of São Miguel and West of Santa Maria, Pérès (1992) observed stalked crinoids that he believed to be *D. rawsonii* (= *Rhizocrinus rawsoni*), which were quite abundant at depths 2,630 and 2,950 m.

Family Bathycrinidae Bather, 1899

Genus *Bathycrinus* Thomson, 1872a

Bathycrinus gracilis **Thomson, 1872a**

$^{\$}$1909. *Bathycrinus gracilis*, Wyville Thomson; Koehler: 254–255.

1977. *Bathycrinus gracilis* Wyville Thomson; Clark: 164–167, figs. 1a–f.

1980. *Bathycrinus gracilis* Wyville Thomson; Clark: 206–207, fig. 5.

2014. *Bathycrinus gracilis* Thomson, 1872; Mironov *et al*.: 115.

Type locality: off West coast of France (N47°38' W12°08').

See: Carpenter (1884); Clark (1977); Mironov *et al.* (2014).

Distribution: Northeast Atlantic, from SW of Ireland to Cape Finisterre (NW Spain) and the Azores.

Depth: 2,880–5,275 m (AZO: 5,005 m).

Habitat: soft bottoms, on *Globigerina* ooze.

Remarks: *Bathycrinus gracilis* is known from relatively few specimens, none of which was recovered complete, including the immature type material (presumably lost) (Carpenter 1884; Koehler 1909; Clark 1977, 1980). Moreover, the only known record from Azorean waters is based on a single animal collected by RV 'Princesse Alice' (sta 749: N38°54'00" W21°06'45", 5,005 m), only slightly larger than the type material (Clark 1977). Nevertheless, the paucity of available specimens can be explained by the great depths at which this species lives. Additionally, the West Atlantic species *B. aldrichianus* Thomson, 1876 is closely related to *B. gracilis* and Mironov *et al*. (2014) suggested that it might prove to be conspecific.

Order Cyrtocrinida Sieverts-Doreck, *in* Moore *et al.*, 1952

Suborder Holopodina Arendt, 1974

Family Holopodidae Zittel, 1879

Genus *Cyathidium* Steenstrup, 1847

Cyathidium foresti Cherbonnier & Guille, 1972

$1972. *Cyathidium foresti* nov. sp.; Cherbonnier & Guille: 2193–2196, pl. 1, figs. A–I.

1980. *Cyathidium foresti* Cherbonnier & Guille; Clark: 209.

$1997. *Cyathidium foresti* Cherbonnier and Guille 1972; Heinzeller *et al*.: 11–21, figs. 1–7.

$1999. *Cyathidium foresti* Cherbonnier et Guille, 1972; Améziane *et al*.: 441–448, figs. 1-3.

2006. *Cyathidium foresti* Cherbonnier et Guille, 1972; Mironov & Krylova: 32.

$2009a. *Cyathidium foresti* Cherbonnier and Guille, 1972; Wisshak *et al*.: 77–83, figs. 1–4.

$2010. *Cyathidium foresti;* Wisshak *et al*.: 2382.

Type locality: Azores (N39°23’30” W31°19’00”).

See: Cherbonnier & Guille (1972); Clark (1980: 208); Heinzeller & Fechter (1995, as *Cyathidium meteorensis*); Heinzeller *et al.* (1997); Améziane *et al.* (1999); Wisshak *et al.* (2009a).

Distribution: Northeast Atlantic, known only from the Azores and the Great Meteor Seamount.

Depth: 380–900 (?1,140) m (AZO).

Habitat: attached on hard substrata (*e.g.,* basalt) or skeletal remains, such as deep-water oysters (*Neopycnodonte zibrowii* Gofas *et al*., *in* Wisshak *et al*., 2009b).

Type of Development: direct, produces a ‘cyathidula’ type of larvae.

Remarks: Cherbonnier & Guille (1972) described a new enigmatic echinoderm species found among the material collected by RV ‘Jean-Charcot’ in the Azores (N39°30’–N36°54’ W31°15’–W25°09’, 380–900 m). Overall, this species resemble more a barnacle than a crinoid, with no stalk, permanently attached to the hard substrata via an expanded aboral base of the calyx. The body is reduced to a rounded cone, with the first brachial series forming a pentagonal vault enclosing reduced arms when coiled inwards. Cherbonnier & Guille (1972) concluded that the affinity of their new species lay within *Cyathidium* Steenstrup, 1847. At the time, this genus was composed exclusively of fossil species, most thought to be extinct by the end of the Cretaceous. Since the publication by Cherbonnier & Guille (1972), three more extant species were described for the genus, although *C. meteorensis* described by Fechter (1973) from the Great Meteor Seamount was later found to be identical with *C. foresti* (Clark 1980; Heinzeller *et al*. 1997; Améziane *et al*. 1999). Additionally, *in situ* observations of *C. foresti* in the channel between Faial and Pico islands (420–500 m depth) by Wisshak *et al*. (2009a) gave further insight on this species’ ecology and associated ‘living fossil community’.

Order Hyocrinida Rasmussen, 1978

Family Hyocrinidae Carpenter, 1884

Genus *Anachalypsicrinus* Clark, 1973

Anachalypsicrinus nefertiti **Clark, 1973**

$^{\$}$1980. *Anachalypsicrinus nefertiti*; Roux: 191, pl. 1, figs. 1–3.

1985. *Anachalypsicrinus nefertiti* (A.-M. Clark, 1973); Roux: 481–482, figs. 2–3.

1992. *Anachalypsicrinus nefertiti* A.M. Clark, 1973; Tyler & Zibrowius: 222, figs. 3h, 5 b–c, g.

2014. *Anachalypsicrinus nefertiti* A.M. Clark, 1973; Mironov *et al*.: 117.

Type locality: off W Ireland (N53°11’12”–N53°11’36” W20°05’06”–W20°03’54”)

See: Clark (1973: 269–270, figs. 1a–e, 2, pl. 1, figs. a–d); Tyler & Zibrowius (1992).

Distribution: Northeast Atlantic, from off S–SW Ireland south to the Azores and east to the Bay of Biscay and off Morocco.

Depth: 2,000–2,810 m (AZO: 2,200–2,810 m).

Habitat: hard substrata.

Remarks: Roux (1980) identified *Anachalypsicrinus nefertiti* in deep sea photographs taken by the project ‘Famous’ in the south of the Azores (N36°49’36”–N36°57’30” W33°05’–W33°16’30”, 2,220–2,810 m). The abyssal depths and the type of substrata may account for the paucity of reports throughout its known geographical distribution.

Class Ophiuroidea Gray, 1840

Order Amphilepidida O'Hara *et al*. 2017

Family Amphiuridae Ljungman, 1867

Genus *Amphipholis* Ljungman, 1866

Amphipholis squamata **(Delle Chiaje, 1828)**

(Fig. 5.5)

$^{\$}$1872. *Amphipholis squamata* (Delle Chiaje); Ljungman: 633–634.

$^{\$}$1872. *Amphipholis lineata* n.; Ljungman: 634.

1888. *Amphipolis squamata* Delle Chiaje; Barrois: 32.

$^{\$}$1888. *Amphiura squamata* Lütken; Barrois: 73.

1888. *Amphipolis lineata* Ljungman; Barrois: 32, 115.

1888. *Amphiura squamata* Delle Chiaje; Barrois: 115.

$^{\$}$1898. *Amphiura squamata*, (Delle Chiaje); Koehler: 53.

$^{\$}$1898. *Amphiura tenuispina*, Ljungmann; Koehler: 53–55, pl. 6, figs. 22–23.

$^{\$}$1909. *Amphiura tenuispina*, Ljungmann; Koehler: 180.

$^{\$}$1955. *Amphipholis squamata* (Delle Chiaje); Chapman: 400.

1965. *Amphipholis squamata* (D.Ch.); Tortonese: 231–234, fig. 107.

1980. *Amphipholis squamata* (Delle Chiaje, 1828); Marques: 100.

$^{\$}$1983. *Amphipholis squamata* (Delle Chiaje, 1828); Marques: 3, fig. 2.

1997. *Amphipholis squamata* (Delle Chiaje, 1828); Pereira: 332.

2005. *Amphipholis squamata* (Delle Chiaje, 1829); García-Diez *et al*.: 48.

Type locality: Mediterranean Sea.

See: Mortensen (1927a: 221–222, fig. 125; 1936: 292–293); Tortonese (1965); Paterson (1985: 91, fig. 36); Sponer & Roy (2002); Boissin *et al*. (2008a); Hernández-Herrejon *et al.* (2008: 146–147, figs. 15.E–F).

Distribution: present in all seas, cosmopolitan (absent in the polar areas).

Depth: 0–1,962 m (AZO: 0–1,229 m).

Habitat: soft to hard substrates, common among algae and under rocks during low tide, found also on the roots of floating *Macrocystis*; in the Azores they are also a common presence among algae.

Type of Development: brooding hermaphrodite species; reproduces also through self-fertilisation.

Material examined: DBUA-ECH 241 (Baixa do Porto, Lajes, FLS, AZO, *c.* N39°22'50" W31°10'00", 1990.10.29; 1 spm, D=1 mm); DBUA-ECH 267 (São Roque, SMG, AZO, *c.* N37°44'37" W25°38'19", 2012.11.16, intertidal; 5 spms, D=2 mm); DBUA-ECH 277 (FRM, AZO, *c.* N37°16'14" W24°46'52", 1990.06.08, 6–8 m; 1 spm, D=3 mm); DBUA-ECH 284 (Gorringe Bank, NE Atlantic, *c.* N36°40' W11°12', 2006; 1 spm, D=2 mm); DBUA-ECH 308 (Baixa do Porto, Lajes, FLS, AZO, *c.* N39°22'50" W31°10'00", 1990.10.27; 4 spms, D=1–2 mm); DBUA-ECH 312 (Lajes, PIX, AZO, *c.* N38°23'22" W28°15'04", 1994.08.07, 1 m; 4 spms, D=2–3 mm); DBUA-ECH 314 (off Ribeira das Tainhas, SMG, AZO, N37°42'04" W25°25'02", 2006.07.24, 45–117 m; 1 spm, D=1 mm); DBUA-ECH 353 (Poços, SMG, AZO, *c.* N37°50'06" W25°40'10", 1996.07.08, intertidal; 5 spms, D=1–2 mm); DBUA-ECH 354 (Vila Franca do Campo, SMG, AZO, N37°41'39" W25°27'11", 2006.07.21, 95–121 m; 1 spm, D=2 mm); DBUA-ECH 417 (Mosteiros, SMG, AZO, N37°53'52" W25°48'19", 2011.07.06, 10 m; 1 spm, D=1 mm).

Description: disc round to subpentagonal, covered on both sides by coarse and imbricated scales. Centrodorsal and surrounding primary plates distinct. Radial shields small, between 1/3 and 1/2 of the disc radius (length > breadth), contiguous throughout their whole length. Sharp limit between the scales of the dorsal and ventral side near the edge of the disc. Ventral interradial plates imbricate and slightly smaller than the dorsal plates. Two oral papillae on each side of the jaw forming a continuous series with the blunt block-like to conical infradental papillae; the

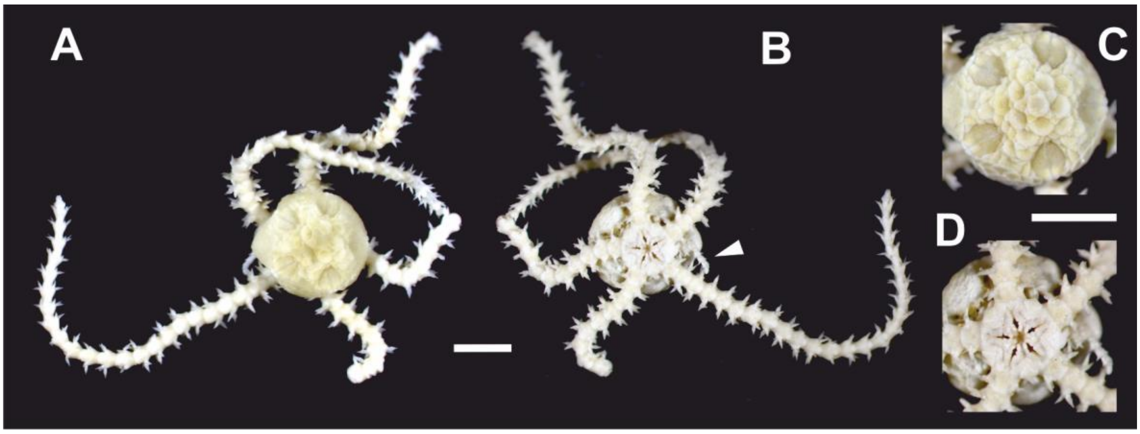


Figure 5.5. *Amphipholis squamata* (Delle Chiaje, 1828) (DBUA-ECH 354). Dorsal view (A); Ventral view (B); detail of the disc and arm, dorsal view (C) and ventral view (D); arm of a young (indicated by the white arrowhead) out of the adult bursae; scale bars are 1 mm.

distalmost oral papilla very broad. Oral shields rounded to triangular in small specimens, becoming more rhombic (produced inwards) in larger animals. Arms about three or four times the D. Tentacle pores small, with two tentacle scales proximally decreasing to one on the distal part of arms. Dorsal arm plates separated, proximally fan-shaped (length < breadth), with round distal edge, becoming more square-like on distal arm (length ≥ breadth). Ventral plates with slight indentation in the distal edge, contiguous only on the proximal part of the arm. Large lateral arm plates, meeting along the longitudinal mid-line, both dorsally and ventrally. Four, further out three, short, conical arm spines. One specimen (DBUA-ECH 354) with a juvenile's arm sticking out from a bursal slit. Colour in ethanol uniformly white.

Remarks: the specimens herein examined diverge slightly from what is described for the typical *Amphipholis squamata*, particularly regarding the shape and size of disc plates on the dorsal side. For example, the coarser plating, a well-defined central rosette and relatively larger radial shields are all features that agree with the description of *A. tenuispina* by Koehler (1898) based on animals collected by RV 'Hirondelle' in the Azores (sta 198: N38°26'25" W28°38'56", 800 m). Mortensen (1927a) remarked on the existence of transitional stages that hardly support the maintenance of 'tenuispina' as a separate variety of *A. squamata* even less as a separate species. In turn, Paterson (1985) stated that the primary plates are indistinguishable, except in smaller specimens. Future works will have to address the specific significance of *A. squamata* morphological variation throughout its geographical range. Molecular studies on *A*. *squamata* populations in New Zealand (Sponer & Roy 2002) and in French Mediterranean coast (Boissin *et al*. 2008b) indicate that *A*. *squamata* represents a cryptic species complex.

Genus *Amphiura* Forbes, 1843

Amphiura otteri **Ljungman, 1872**

$^{\$}$1882. *Amphiura otteri*, Ljn.?; Lyman: 128.

1906b. *Amphiura grandis* Koehler; Koehler: 277–278.

$^{\$}$1909. *Amphiura grandis* Kœhler; Koehler: 175–177, pl. 27, figs. 3–4.

$^{\$}$1915. *Amphiura otteri* Ljungman, 1871; Clark: 230.

1927a. *Amphiura grandis* Koehler; Mortensen: 208–209.

1927a. *Amphiura Otteri* Ljungman; Mortensen: 209.

1985. *Amphiura otteri* Ljungman, 1872; Paterson: 86–87, fig. 33.

2005. *Amphiura otteri* Ljungman, 1872; García-Diez *et al*.: 49.

2014. *Amphiura otteri* Ljungman, 1872; Smirnov *et al*.: 200.

Type locality: Portugal.

See: Ljungman (1872: 631–632); Paterson (1985); Benavides-Serrato *et al.* (2011: 291).

Distribution: North Atlantic, in the west from Labrador Basin to Caribbean Sea and in the east from Iceland to the West African coasts, including the Azores.

Depth: 198–3,200 m (AZO: 1,620–1,900 m).

Habitat: soft sediments, mud to ooze.

Remarks: in the first report of *Amphiura otteri* from the archipelago, Lyman (1882) regarded this species as doubtful. Clark (1915) re-examined Lyman's specimens, including the material collected at one of the RV 'H.M.S. Challenger' stations located inside Azorean waters (sta 76: N38°11' W27°09', 1,646 m) and confirmed his identification. Koehler (1896b, 1909) described *Amphiura grandis*, based on specimens collected by RV 'Princesse Alice' in the Bay of Biscay and in the Azores (sta 1334: N39°30' W29°02'15"), a species later synonymised with *A. otteri* by Paterson (1985). Additionally, *A. otteri* was reported also from the archipelagos of Canaries and Cabo Verde (*e.g.,* Koehler 1909; Mortensen 1927a; Paterson 1985). However, these reports seem to be based directly or indirectly on the material collected by RV 'Talisman'. At the time, Koehler (1906b, as *Amphiura grandis*) recorded the location of the stations using a system of coordinates based on the Paris Meridian. When converting the longitudes to the Greenwich Meridian, it is clear that the reported material came from waters off the coast of NW of Africa, outside the Canaries and Cabo Verde waters.

Amphiura richardi Koehler, 1896b

$^{\$}$1896b. *Amphiura Richardi* nov. sp.; Koehler: 245–246.

$^{\$}$1909. *Amphiura Richardi*, Kœhler; Koehler: 178–179, pl. 27, figs. 1–2.

1927a. *Amphiura Richardi* Koehler; Mortensen: 209.

2005. *Amphiura richardi* Koehler, 1906; García-Diez *et al*.: 49.

Type locality: Azores (N38°26’00” W26°30’45”).

See: Koehler (1909); Paterson (1985: 88).

Distribution: Northeast Atlantic; a rare species know from the Bay of Biscay to the Azores and ?Canary Islands.

Depth: 850–1,494 m (AZO: 1,165–1,494 m).

Habitat: soft to hard substrate.

Remarks: Paterson (1985) reported this species off Morocco, based on material collected by RV ‘Talisman’. In contrast, Koehler (1906b) reported this species as taken by ‘Travailleur’ in northern Spain (sta 39, 1881: N44°05’ W7°05’26”). Perrier (1894) who dealt with the sea stars from RVs ‘Travailleur’ and ‘Talisman’ reported similar values for the same dredge as Koehler. In view of this, Paterson’s account from NW Africa was dismissed in favour of the historical report by Koehler. Moreover, the original material on which Paterson (1985) based his record from the Canaries could not be traced. As this author did not include the type locality in the geographical distribution of *A. richardi*, it is possible that he confused the archipelago of the Azores for the Canaries.

Amphiura sarsi Ljungman, 1872

(Fig. 5.6)

$^{\$}$1872. *Amphiura* (*Ophiopelte*) *Sarsi* n.; Ljungman: 630.

1882. *Amphiura sarsi*, Ljn.; Lyman: 124, 144.

1888. *Amphiura Sarsi* Ljungman; Barrois: 32.

1888. *Amphiura Sarsii* Ljungm.; Simroth: 231.

$^{\$}$1915. *Amphiura sarsi* Ljungman, 1871; Clark: 231, pl. 5, figs. 8–9.

1927a. *Amphiura Sarsi* Ljungman; Mortensen: 209.

$^{\$}$1969. *Amphiura sarsi* Ljungman; Downey: 37.

$^{\$}$1970. *Amphiura sarsi* Ljungman, 1871; Clark: 13, figs. 3l–m.

1997. *Amphiura sarsi* Ljungman, 1871; Pereira: 332.

2000. *Amphiura sarsi*; Morton & Britton: 59.

Type locality: Azores.

See: Lyman (1882); Clark (1915); Cherbonnier (1970: 1272); Clark (1970).

Distribution: Northeast Atlantic, known only from the Bay of Biscay, the Azores, Madeira and Josephine Seamount.

Depth: 55–1,098 m (AZO).

Habitat: soft bottom with shells or inside crevices on large rocky boulders.

Material examined: EMEPC G3D2 Ma001 (Southeast of TER, AZO, N38°33’11” W26°42’30”, 2007.05.18, 350–744 m; 1 spm, D=3 mm).

Description: disc almost star-shaped, depressed in the interradial areas, covered dorsally by fine scales; central rosette and primary plates distinct. Radial shields almost parallel, separated proximally by a few scales, about 30% D long. Ventral side of disc partially naked. Two conical infradental oral papillae and one blunt adoral shield spine on either side of the jaw. Mouth shields rounded triangular (length < breadth). No tentacle scales. Five long arms about six times the D. Four or five short, finely serrated spines, decreasing to three distally; the second from below slightly thicker, its tip is somewhat blunt with two horizontal small thorns at each side (axe shaped). Dorsal arm plates transversally oval, separated. Ventral arm plates almost square-shaped, contiguous. Colour (alive): yellow arms with light yellowish orange bands; ventral side of disc same colour as arms; dorsal surface brown; interior of mouth red. Colour (in ethanol): white.

Remarks: the genus *Amphiura* is one of the largest ophiuroid genera (Stöhr & Segonzac 2005), comprising almost 200 valid species, 50 of them known from the Atlantic. The specimen herein documented agrees for the most part with the type description by Ljungman (1872), which is unique among the other *Amphiura* species reported from the Azores by the absence of tentacle scales. Also, it conforms well to the illustrations by Clark (1970), based on the syntypes collected in the Azores. However, specimens examined here presented 4 or 5 arm spines in the proximal part of the arms decreasing to 3 distally, a number slightly lower than the 5 or 6 reported by Ljungman. Surprisingly, Lyman (1882) in his *Amphiura* key mentioned just four

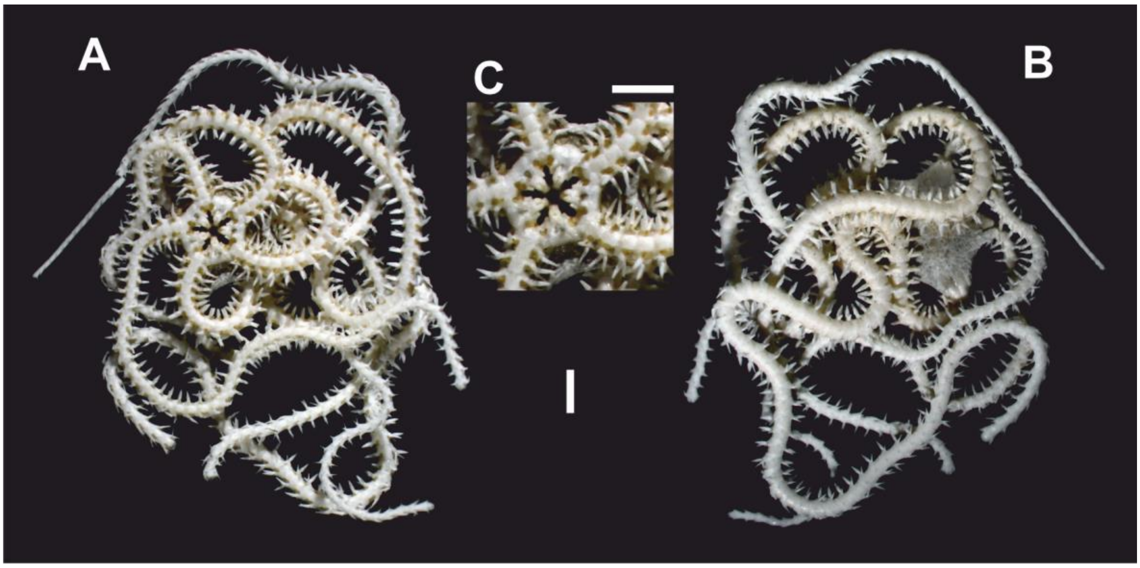


Figure 5.6. *Amphiura sarsi* Ljungman, 1872 (EMEPC G3D2 Ma001). Dorsal view (A); ventral view (B); detail of the disc, ventral view (C); scale bars are 1 mm.

spines for this species. Clark (1915) published the only known picture of *A*. *sarsi*, the Ljungman syntype. The animal appears to be slightly larger than ours, disc diameter about 4 mm. The size difference may account for the difference in the number of arm spines, as was observed in other *Amphiura* species (*e.g.,* Mortensen 1933b).

Among the *Amphiura* with no tentacle scales known from the Atlantic, the specimen herein examined also closely resembles *Amphiura filiformis* (Müller, 1776), known from the Mediterranean Sea and the Northeast Atlantic south to Angolan waters (Madsen 1970). These two species are distinguished primarily by the arrangement of the disc scales. The scales on the dorsal side of the disc are finer in *A*. *sarsi* than in *A*. *filiformis*, the central rosette is also relatively distinct in the former and indistinct in the latter. On the ventral side, *A*. *sarsi* possess few scales and in *A*. *filiformis* tends to be completely naked. In the original description of *A*. *sarsi*, Ljungman (1872) suggested that this species may be a form of *A*. *filiformis*. The subject was never revisited. Madsen (1970) also considered the possibility of his *A*. *senegalensis* being a juvenile of *A*. *sarsi* that had not yet developed axe-shaped spines. The specimen studied herein is about the same size as the type material of *A*. *senegalensis* and has already axe-shaped spines. This suggests that some of the characters used to diagnose *A*. *sarsi* (*e.g.,* arrangement of disc scales, number and shape of the arm spines) are subject to ontogenetic or individual variation in other *Amphiura* species (Mortensen 1933b; Madsen 1970).

Additionally, *Amphiura sarsi* was regarded as the only endemic species of the Azores (*e.g.,* Pereira 1997; Morton & Britton 2000). However, this seems to be a consequence of misinterpretation of the original report. Ljungman (1872) used material from the 'Josephine' expedition to describe his new species, listing specimens collected both from the Azores and from the Josephine Seamount. Historically, the record in the seamount with the same name as the expedition was overlooked, and subsequent references placed the Azores as the type locality and the only known location for this species (*e.g.,* Lyman 1882; Barrois 1888; Simroth 1888). Mortensen (1927a) is a rare example where both locations are listed. Later, this species was as well recorded from the Bay of Biscay (Cherbonnier 1970) and Madeira Archipelago (Jesus & Abreu 1998).

Subgenus *Amphiura* Forbes, 1843

***Amphiura* (*Amphiura*) *grandisquama* Lyman, 1869**

$^{\$}$1896a. *Amphiura longispina* sp. nov.; Koehler: 211—212.

$^{\$}$1898. *Amphiura longispina*, Kœhler; Koehler: 52—53, pl. 9, figs. 45—46.

$^{\$}$1907b. *Amphiura grandisquama* Lyman; Koehler: 301.

$^{\$}$1909. *Amphiura grandisquama*, Lyman; Koehler: 177—178.

1914b. *Amphiura grandisquama* Lyman; Koehler: 190—191.

1927a. *Amphiura grandisquama* Lyman; Mortensen: 209.

1970. *Amphiura grandisquama* Lyman; Madsen: 177—178, fig. 12.

1985. *Amphiura grandisquama* Lyman, 1869; Paterson: 87, fig. 33.

2005. *Amphiura grandisquama* Lyman, 1869; García-Diez *et al*.: 48.

Type locality: off Tennessee Reef (Florida Strait).

See: Lyman (1869: 334–337); Madsen (1970); Paterson (1985); Alvà & Vadon (1989: 836); Jesus & Abreu (1998: 62); Bartsch (2008: 234–235).

Distribution: cosmopolitan, in the Atlantic, Pacific, Indian Oceans and in the ?Mediterranean Sea; in the west Atlantic from South Carolina to the Caribbean, including Tristan da Cunha; in the east Atlantic from Iceland to the Gulf of Guinea, including the Azores, Madeira, Canaries, Cabo Verde, Saint Helena, Meteor and Josephine seamounts. The subspecies *A. grandisquama natalensis* Mortensen, 1933b is restricted to southern Africa.

Depth: (?2)18–2,870 m (AZO: 599–880 m).

Habitat: soft to hard substrates.

Type of Development: brooder (embryos are kept in the bursae until the juvenile stage is reached).

Remarks: Koehler (1896a, 1898) described *Amphiura longispina* based on a single specimen collected by RV ‘Hirondelle’ in the Azores (sta 242: N38°48’30” W27°58’46”, 861 m). On the re-examination of *A. grandisquama* from the Caribbean, Koehler (1907b) confirmed his initial suspicions that *A. longispina* was identical with the species described by Lyman (1869). Additionally, the species *Monamphiura apicula* (Cherbonnier, 1957) from the Mediterranean Sea (Tortonese 1965; Koukouras *et al.* 2007) has been considered conspecific with *A. grandisquama* by some authors (*e.g.,* Madsen 1970; Paterson 1985; Bartsch 2008). If this is the case, the distribution range of the latter should be extended to the Mediterranean Sea and to depths as shallow as 2 m (Koukouras *et al*. 2007).

Family Ophiactidae Matsumoto, 1915

Genus *Ophiactis* Lütken, 1856

Ophiactis abyssicola (Sars, 1861)

$^{\$}$1896a. *Ophiactis corallicola* Koehler; Koehler: 208.

$^{\$}$1896a. *Ophiactis abyssicola* (Sars); Koehler: 208.

$^{\$}$1896b. *Ophiactis abyssicola* Sars; Koehler: 243.

$^{\$}$1898. *Ophiactis corallicola*, Kœhler; Koehler: 46.

$^{\$}$1898. *Ophiactis abyssicola* (Sars); Koehler: 46–48, pl. 5, fig. 17, pl. 6, fig. 18.

$^{\$}$1898. *Ophiactis echinata*, nov. sp.; Koehler: 48–49, pl. 5, figs. 15–16.

$^{\$}$1906b. *Ophiactis corallicola* Koehler; Koehler: 272–273.

$^{\$}$1909. *Ophiactis abyssicola*, (Sars); Koehler: 169.

$^{\$}$1909. *Ophiactis corallicola*, Kœhler; Koehler: 170, pl. 1, fig. 11, pl. 7, figs. 4–5.

$^{\$}$1921a. *Ophiactis corallicola* Kœhler; Koehler: 3.

1927a. *Ophiactis echinata* Koehler; Mortensen: 199.

1927a. *Ophiactis abyssicola* (M. Sars); Mortensen: 202–203, fig. 114.

1932. *Ophiactis abyssicola* M. Sars; Grieg: 36–37.

1972. *Ophiactis echinata* Koehler; Cherbonnier & Sibuet: 402.

1980. *Ophiactis abyssicola* (M. Sars, 1861); Marques: 101.

2005. *Ophiactis abyssicola* (Sars, 1861); García-Diez *et al*.: 48.

$^{\$}$2005. *Ophiactis abyssicola* (M. Sars, 1871); Stöhr & Segonzac: 4722.4

$^{\$}$2008. *Ophiactis abyssicola* (M. Sars, 1861); Martynov & Litvinova: 102–104, figs. 17C–E.

Type locality: Norway.

See: Sars (1861: 18–20, pl. 2, figs. 7–12, as *Amphiura abyssicola*); Clark (1918: 304–305); Mortensen (1927a); Paterson (1985: 76–78, fig. 32); Martynov & Litvinova (2008).

Distribution: cosmopolitan, present in both Pacific and Atlantic Oceans; in the Atlantic from the Davis Strait, off Iceland and Scandinavian waters to Southern Africa, including the archipelagos of the Azores, Canaries and Cabo Verde; reported elsewhere off Tristan da Cunha.

Depth: 118–4,721 m (AZO: 726–1,998 m).

Habitat: soft bottoms, ooze, fine sand, gravel and shells to rock, among sponges, gorgonians and other sessile fauna.

Remarks: *Ophiactis abyssicola* is a highly variable species, an attribute that is reflected by its numerous synonyms. In the Azores alone, this species was reported under three different names. For example, Koehler (1898) erected *O. echinata* based on a single specimen collected by RV 'Hirondelle' in the Azores (sta 198: N38°26'25" W28°38'56", 800 m). Later authors such as Clark (1918) and Mortensen (1927a, 1933a) believed that this species was a juvenile of *O. abyssicola*. See also remarks under *O. canotia* Lyman, 1879 and *O. nidarosiensis* Mortensen, 1920.

Ophiactis canotia Lyman, 1879

$^{\$}$1879. *Ophiactis canotia* sp. nov.; Lyman: 40–41, pl. 13, figs. 353–355.
$^{\$}$1882. *Ophiactis canotia*, Lym.; Lyman: 119–120, pl. 19, figs. 16–18.
$^{\$}$1915. *Ophiactis canotia* Lyman, 1879; Clark: 260.
1918. *Ophiactis canotia*; Clark: 305.
1927a. *Ophiactis canotia* Lyman; Mortensen: 199.
1933a. *Ophiactis canotia* Lyman; Mortensen: 48–49, fig. 29.
$^{\$}$1969. *Ophiactis canotia* Lyman; Downey: 84.

Type locality: Azores (N38°30' W31°14').

See: Lyman (1882).

Distribution: known only from the type material collected in the Azores.

Depth: 1,830 m (AZO).

Habitat: soft bottoms (*Globigerina* ooze).

Remarks: *Ophiactis canotia* is only known from two specimens described by Lyman (1879) collected at one station in the Azores (H.M.S. *Challenger*, sta 73). This species is quite close to another deep-water species native to the Azores, *O. abyssicola* (only distinguished on the basis of dorsal plates outline) and might prove to be conspecific (Mortensen 1933a).

Ophiactis plana? Lyman, 1869

?$^{\$}$1909. *Ophiactis profundi*, Lütken et Mortensen; Koehler: 173.

1918. *Ophiactis plana;* Clark: 301–302.

1927a. *Ophiactis profundi* Lütken and Mrtsn.; Mortensen: 199, 200.

2005. *Ophiactis profundi* Lütken & Mortensen, 1829; García-Diez *et al*.: 48.

Type locality: off Carysfort Reef, Florida.

See: Lyman (1869: 330–331); Lyman i*n* Koehler (1914b: 155); Clark (1915: 264; 1918: 298); Clark (1974: 464–465); Alvà & Vadon (1989: 836); Jesus & Abreu (1998: 62, as *Ophiactis profundi*); Stöhr & Segonzac (2005: 16).

Distribution: Atlantic, in the west from North Carolina to the Caribbean waters and the Gulf of Mexico; in the east from Namibia to South Africa, including the archipelagos of the ?Azores and ?Madeira.

Depth: 18–412 m (?AZO: 650–914 m).

Habitat: soft sediments, also on sponges and on corals.

Type of Development: asexual reproduction through fission.

Remarks: Koehler (1909) reported *Ophiactis profundi* from the Azores based on two specimens collected by RV ‘Princesse Alice’ (sta 2214: N39°26’10” W31°21’30”, 650–914 m), a deep-water species believed to be restricted to the Pacific (Stöhr & Segonzac 2005). Later Koehler (1922) commented that the material collected by RV ‘Princesse Alice’ in the Atlantic was either *O. profundi* or ‘a form extremely close to it’ (see as well Lütken & Mortensen 1899). Clark (1918) synonymised *O. profundi* with *O. plana* based on a comparison of the type material of both species, and included RV ‘Princesse Alice’ records from the Azores under the geographical distribution of *O. plana*. Mortensen (1924, 1936) agreed that *O. plana* and *O. profundi* could be conspecific, but stated further studies were necessary. The matter is still unresolved pending a future revision (see Stöhr & Segonzac 2004). In spite of the great depths at which RV ‘Princesse Alice’ specimens were collected we believe they most probably belong to the Atlantic form *O. plana*. The same can be assumed for the Madeira record by Jesus & Abreu (1998).

Ophiactis nidarosiensis? Mortensen, 1920

?[$]1909. *Ophiactis hirta*, Lyman; Koehler: 171.

Type locality: Trondhjemfjord, Norway.

See: Mortensen (1920: 60–63, fig. 5; 1933a: 51; 1933b: 346–347, fig. 58a; 1936: 264).

Distribution: recorded to the Scandinavia, Iceland, southern Africa, off Gough Island (Tristan da Cunha, S Atlantic) and ?Azores.

Depth: 100–560 m (AZO: ?1,095 m).

Habitat: ?volcanic sand (AZO).

Type of Development: asexual reproduction through fission.

Remarks: Koehler (1909) described a small specimen collected by RV 'Princesse Alice' in Azorean waters (sta 1344: N38°45'30" W28°7'45", 1,095 m) as distinct from the type material of *Ophiactis hirta* collected by Lyman (1879, RV 'H.M.S. Challenger') in the Pacific, but not enough to consider it a different species. Clark (1918) suggested this specimen might represent a juvenile stage of *Ophiactis abyssicola*, a cosmopolitan deep-water species. Mortensen (1920, 1927) believed this specimen was actually *O. nidarosiensis*. Unfortunately, the specimen collected by RV 'Princesse Alice' was lost (Mortensen 1920), and until new material is retrieved, the presence of either species in the archipelago should be considered as doubtful.

Ophiactis tyleri Stöhr & Segonzac, 2005

[$]2005. *Ophiactis tyleri* sp. nov.; Stöhr & Segonzac: 4722.15–17, fig. 9.

[$]2006. *Ophiactis tyleri* Stöhr & Segonzac, 2005; Desbruyères *et al*.: 482, figs. 1–3.

Type locality: Mid-Atlantic Ridge, Azores (N38°18'58" W30°40'32").

See: Stöhr & Segonzac (2005); Desbruyères *et al.* (2006).

Distribution: known only from Azorean waters, namely the Menez Gwen hydrothermal fields.

Depth: AZO: 842–844 m.

Habitat: hard substrates; can be found at hydrothermal vents.

Type of Development: asexual reproduction through fission.

Remarks: *Ophiactis tyleri* is relatively recently described species known only from two specimens collected at two stations in the Azores deep waters by 'DIVANAUT 1' cruise. Though not restricted chemosynthetic environments, *O. tyleri* is the first *Ophiactis* species to be recorded from hydrothermal vents (Stöhr & Segonzac 2005; see remarks under *Ophioctenella acies*).

Ophiactis virens (Sars, 1859)

?$1888. *Ophiactis* sp.?; Simroth: 231.

1927a. *Ophiactis virens* M. Sars; Mortensen: 199.

1965. *Ophiactis virens* (M. Sars); Tortonese: 238–239, fig. 110.

1980. *Ophiactis virens* (M. Sars, 1857); Marques: 102.

$1983. *Ophiactis virens* (M. Sars, 1857); Castro & Viegas: 24.

$1983. *Ophiactis virens* (M. Sars, 1857); Marques: 3.

1997. *Ophiactis virens* (M. Sars, 1857); Pereira 1997: 332.

1998. *Ophiactis virens* (M. Sars, 1857); Jesus & Abreu: 65.

2010. *Ophiactis virens* (M. Sars, 1857); Micael & Costa: 322.

2012. *Ophiactis virens* (M. Sars, 1857); Micael *et al.*: 3.

Type locality: Mediterranean Sea.

See: Tortonese (1965).

Distribution: Northeast Atlantic and Mediterranean Sea; along the Western African coast and in the archipelagos of the Azores, Madeira, Canaries and ?Cabo Verde.

Depth: 0–90 m; a littoral species in the Azores.

Habitat: rocky shores, coralligenous concretions, under stones and among algae and bryozoans; can form large aggregations.

Type of Development: asexual reproduction through fission.

Remarks: Koehler (1924) listed the Azores and Cape Verde in the geographical distribution of *Ophiactis virens*. We do not know the original observation on which he based these records. In the echinoderm fauna of the Azores, Simroth (1888) reported an *Ophiactis* sp., which may represent the first record of *O. virens* to the Azorean archipelago since is the only *Ophiactis* species ever reported in Azorean shallow waters. Additionally, Koehler (1921b) commented that aside from the Mediterranean Sea (Naples), the other area where this species was known to occur was the archipelago of Madeira. Regardless, Castro & Viegas (1983) and Marques (1983) reported having collected *O. virens* throughout the archipelago, thus confirming the presence of this species in the Azores. Both studies indicate that locally *O. virens* lives among algae, but Marques added that this species was far less abundant compared to

Amphipholis squamata. We do not know where Castro & Viegas might have deposited their material and we could not find Marques' material at the Museum Bocage, Natural History Museum (Lisbon). The zoological collection of the Department of Biology of the University of the Azores houses a large number of samples derived from rocky shore algae scrapings collected over a time period of twenty years. Among those, we found numerous specimens of *A. squamata*, yet we have failed to find a single specimen of *O. virens*. The presence in the collection of numerous specimens belonging to a species does not necessarily imply a high local abundance (biased sampling), but its absence on the other hand may reflect its rare status at present. It is possible that local populations of this fissiparous six-armed species have simply declined since the publications by Castro & Viegas or Marques in the 1980s.

Family Ophiolepididae Ljungman, 1867

Genus *Ophiotypa* Koehler, 1897a

Ophiotypa simplex Koehler, 1897a

$^{\$}$1972. Ophiotypa simplex Koehler; Cherbonnier & Sibuet: 416.
1985. Ophiotypa simplex Koehler, 1897; Paterson: 144–145, fig. 55.
1999. Ophiotypa simplex Koehler, 1897; Jesus & Fonseca: 347, Fig. 4.
2008. Ophiotypa simplex Koehler, 1897; Martynov & Litvinova: 81–82, fig. 2F.
2014. Ophiotypa simplex Koehler, 1897; Smirnov *et al.*: 204.

Type locality: Gulf of Bengal, Indian Ocean.

See: Koehler (1897a: 281–283, pl. 5, figs. 1–3); Paterson (1985); Martynov & Litvinova (2008).

Distribution: cosmopolitan, present in the Atlantic, Pacific and Indian deep waters; from the Venezuelan Basin in the Caribbean eastwards to the Azores and ?Portugal, south to waters between Cabo Verde and NW Africa; recorded also from the Reykjanes Ridge (S of Iceland).

Depth: (?27 m)1,670–4,412 m (AZO: 3,665 m).

Habitat: soft substrates.

Remarks: historically, *Ophiotypa simplex* has been recorded at several locations between the Azores and Iberian waters (*e.g.,* Koehler 1906b, 1909). Cherbonnier & Sibuet (1972) published the only report of this species inside the archipelago based on the material collected by RV 'Jean Charcot' ('Noratlante' cruise, sta P63 E8: N36°48'05" W27°06', 3,665 m). The report from Portugal by Jesus & Fonseca (1999) may represent a different species since it was collected at 27 m, far too shallow for this abyssal species.

Family Ophionereididae Ljungman, 1867

Genus *Ophiochiton* Lyman, 1878

Ophiochiton ternispinus **Lyman, 1883**

$^{\$}$1906a. *Ophiochiton solutum* nov. sp.; Koehler: 16–17, pl. 2, figs. 22–23.

$^{\$}$1906b. *Ophiochiton solutum* Koehler; Koehler: 269–271, pl. 20, figs. 39–40.

1927a. *Ophiochiton solutus* Koehler; Mortensen: 224.

1985. *Ophiochiton ternispinus* Lyman, 1883; Paterson: 96–98, fig. 39.

1989. *Ophiochiton ternispinus* Lyman, 1883; Alvà & Vadon: 840.

2008. *Ophiochiton ternispinus* Lyman, 1883; Martynov & Litvinova: 104–107, fig. 17H.

2011. *Ophiochiton ternispinus* Lyman, 1883; Benavides-Serrato *et al.*: 331–332.

2014. *Ophiochiton ternispinus* Lyman, 1883; Smirnov *et al.*: 208.

Type locality: southwest of Ireland.

See: Lyman (1883: 255); Mortensen (1933a: 67–69, fig. 40, pl. 3, figs. 25–26); Paterson (1985); Alvà & Vadon (1989); Borges & Amaral (2007: 858); Benavides-Serrato *et al.* (2011).

Distribution: Atlantic Ocean, in the west from the Davis Strait south through the NE American coasts to Brazil, including the Gulf of Mexico and Caribbean Sea and in east from SE of Iceland to Namibia, including the Azores.

Depth: 256–2,220 m (AZO: 2,155–2,220 m).

Habitat: soft substrates.

Remarks: Koehler (1906a, b) described *Ophiochiton solutus* (= *O. solutum*) based on the specimens collected by RV 'Talisman' in the NW African coast (type locality) and the Azores (sta 129, 1883: N38°00' W27°02'46", 2,155–2,220 m). Mortensen (1927a, 1933a) suggested that this species was identical to *O. ternispinus*, a species described by Lyman (1883) from SW Irish waters. Later, on examining the type material of *O. solutus* and *O. ternispinus*, Paterson (1985) agreed with Mortensen and established the synonymy.

Genus *Ophionereis* Lütken, 1859

Ophionereis reticulata**? (Say, 1825)**

$^{\$}$1906b. *Ophionereis reticulata* Lütken; Koehler: 271.

$^{\$}$1909. *Ophionereis reticulata*, Lütken; Koehler: 181.

1927a. *Ophionereis reticulata* Lütken; Mortensen: 224.

1997. *Ophionereis reticulata* Lütken; Pereira: 332.

2005. *Ophionereis reticulata* (Say, 1825); García-Diez *et al*.: 50

Type locality: Florida Keys, USA.

See: Say (1825: 148, as *Ophiura reticulata*); Clark (1953); Pearse & Williams (1951: 140); Thomas (1973: 586–588, figs. 1, 5A); Yokoyama *et al.* (2008, 2011).

Distribution: tropical Western Atlantic, from North Carolina and Bermuda, through the Caribbean coast to Brazil; possibly reaching the archipelagos of ?Cabo Verde and ?Azores.

Depth: 0–200(?560) m (?AZO: 98–560 m).

Habitat: sediment-rocky shore interface.

Type of Development: lecithotrophic.

Remarks: the tropical West Atlantic shallow-water species *Ophionereis reticulata* was reported from the Azores by Koehler (1906b, 1909). Unfortunately, he fails to give any kind of description aside from the small size of the specimens (<5 mm, whereas a normal adult reaches 13 mm; Hernández-Herrejon *et al*. 2008). The presence of this species in Azorean waters might represent an occasional vagrant, a case similar to *Eucidaris tribuloides*. In Brazil, *O. reticulata* spawns in the summer when the waters can reach average temperatures as high as 27°C. Yokoyama *et al*. (2008, 2011) concluded that the rise in water temperatures plays a major factor in the reproduction of this species. Thus, like tropical *E. tribuloides*, it is hard to believe that this tropical brittle star could sustain a viable population in the significantly cooler Azorean waters, particularly if we consider the depth at which the material was recorded by RV 'Talisman' (sta 123, 1883: N38°23' W28°49'46", 560 m) and RV 'Princesse Alice' (sta 882: N38°3'40" W28°34'45", 98 m). On the other hand, Clark (1953: 65) commented that 'the chief trouble in differentiating the species of *Ophionereis* as with other genera, is to distinguish between the really characteristic features and those which are contingent upon the particular ontogenetic stage reached'. The only known material of *O. reticulata* in the east side of the Atlantic was all identified and reported by Koehler (1906b, 1909).

In addition to the Azorean records, Koehler (1906b) also reported five specimens belonging to *O. reticulata* collected by RV 'Talisman' in the Cabo Verde waters, between 103 and 225 m depth. While the specimen from 560 m deep may in reality not be a member of the shallow-water genus *Ophionereis*, the remainder of Koehler's material could prove to belong to the only *Ophionereis* species known from the East Atlantic, *O*. *sexradia* Mortensen, 1936. This brittle star was first described from the Gulf of Guinea, and later reported from the Canaries (Clark 1953) and Madeira (Jesus & Abreu 1998). Regardless, whether the reports for the Azores originated either by a misidentification or by an occasional vagrant, the presence of *Ophionereis* in the northern latitudes of the Azores should be dismissed as doubtful until new material is collected.

Family Ophiopholidae O'Hara *et al*. 2018

Genus *Ophiopholis* Müller & Troschel, 1842

***Ophiopholis aculeata*? (Linnaeus, 1767)**

?$^{\$}$1865. *Ophiopholis bellis* Lyman; Lyman: 14, 96–99, pl. 1, figs. 4–6.

?$^{\$}$1915. *Ophiopholis aculeata* (Retzius); Clark: 267.

See: Serafy (1971); Picton (1993: 44); Tyler *et al.* (2005: 185).

Distribution: circumboreal Arctic; in the Atlantic, from the arctic waters southwards to Cape Hatteras in the West Atlantic and to the English Channel in the east.

Depth: 0–300 m, exceptionally 1,000 m (AZO: ?).

Habitat: eurytopic; frequently found in crevices and borings in the rock or in association with sponges.

Type of Development: planktotrophic.

Remarks: Lyman (1865) remarked that he identified a specimen of *Ophiopholis aculeata* (= *Ophiopholis bellis*) from Faial Island in the collection of the Museum of Comparative Zoology (Harvard University). However, when he presented the specimens list (p. 99) he added a question mark after 'Fayal', as if he had some doubts about the provenance of the material or in his identification. Unfortunately, Lyman did not give any further details about its origin, omitting the depth, collector or date. Later, Clark (1915) listed the material present in the Harvard collection, including the material from the Azores previously analysed by Lyman, yet he did not express any concerns, nor gave any further details. This circumpolar cold-water species was never (re)collected in the archipelago waters, and thus the inclusion of this species in the Azorean fauna should be considered with caution.

Family Ophiothamnidae O'Hara *et al*. 2018

Genus *Histampica* Clark, 1970

Histampica duplicata **(Lyman, 1875)**

$^{\$}$1896a. *Amphiura duplicata* Lyman; Koehler: 208.

$^{\$}$1896b. *Amphiura duplicata* Lyman; Koehler: 244.

$^{\$}$1898. *Amphiura duplicata*, Lyman; Koehler: 49–50.

$^{\$}$1909. *Ophiactis duplicata*, (Lyman); Koehler: 171.

1927a. *Amphiactis duplicata* (Lym.); Mortensen: 198.

1932. *Amphiura duplicata* Lyman; Grieg: 37.

2005. *Histampica duplicata* (Lyman, 1875); García-Diez *et al*.: 48.

Type locality: Barbados, Caribbean.

See: Lyman (1875: 19–20, fig. 87, pl. 5, fig. 78, as *Amphiura duplicata*); Paterson (1985: 79, 80, fig. 32); Martynov & Litvinova (2008: 101–102, fig. 17B); Benavides-Serrato *et al.* (2011: 313–314).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian Oceans; in the west Atlantic, from Bermuda and Caribbean to Brazil; in the East Atlantic, from the Faeroe Plateau and Reykjanes Ridge (South of Iceland) to North Africa, including the Azores and Cabo Verde archipelagos.

Depth: 125–2,870 m (AZO: 1,095–2,178 m).

Habitat: hard to soft (sand or mud) substrates; can be found in association with azooxanthellate corals.

Remarks: *Histampica duplicata* was recorded in the Azores by Koehler (1896a,b, 1898, 1909) based on material collected by the RVs ‘Hirondelle’ and ‘Princesse Alice’. Lyman (1875) had placed this species originally under the genus *Amphiura*. Lütken & Mortensen (1899) did not agree with this generic position and transferred this species to *Ophiactis* Lütken, 1856, based on the number of mouth papillae, an opinion shared by Koehler (1909). Later, Clark (1918) also based on number of mouth papillae (and number of tentacle scales) placed this species under the genus *Amphiactis* Verrill, 1869. Finally, Clark (1970) based on the number and morphology of mouth papillae transferred this cosmopolitan species to her newly described genus *Histampica*, where it is still accepted today.

Family Ophiotrichidae Ljungman, 1867

Genus *Ophiothrix* Müller & Troschel, 1840a

Ophiothrix fragilis **(Abildgaard, *in* Müller, 1789)**

(Fig. 5.7)

$^{\$}$1872. *Ophiothrix rubra* n.; Ljungman: 624–625.

$^{\$}$1874. *Ophiothrix rubra* Ljn.; Lyman: 248.

1888. *Ophiothrix rubra* Ljungman; Barrois: 32.

$^{\$}$1888. *Ophiothrix lusitanica* Ljungman; Barrois: 32, 72.

$^{\$}$1898. *Ophiothrix fragilis*, Abbildgard; Koehler: 58–59.

$^{\$}$1909. *Ophiothrix fragilis*, (Abildgard); Koehler: 200.

$^{\$}$1924. *Ophiothrix fragilis* (Abildg); Nobre: 89.

$^{\$}$1927a. *Ophiothrix fragilis* (Abildgaard); Mortensen: 174–175, fig. 98.

$^{\$}$1930. *Ophiothrix fragilis* (Abildg); Nobre: 69.

$^{\$}$1938. *Ophiothrix fragilis* (Abildgaard); Nobre: 65–68, figs. 34–35.

$^{\$}$1955. *Ophiothrix fragilis* (Abildgaard); Chapman: 400.

1980. *Ophiothrix fragilis* (Abildgaard); Marques: 103.

$^{\$}$1983. *Ophiothrix fragilis* (Abildgaard); Marques: 3, fig. 3.

1997. *Ophiothrix fragilis* (Abildgaard, 1789); Pereira: 332.

$^{\$}$1998. *Ophiothrix fragilis*; Morton *et al.*: 76, 169, fig. 4.2L

$^{\$}$2003. *Ophiothrix fragilis*; Wirtz & Debelius: 271.

2005. *Ophiothrix fragilis* (Abildgard, in Müller 1789); García-Diez *et al.*: 48.

2010. *Ophiothrix fragilis* (Abildgaard, 1789); Micael & Costa: 322.

2012. *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789); Micael *et al.*: 3.

See: MacBride (1907); Koehler (1921b: 74–77, figs. 48–49); Mortensen (1927a); Nobre (1938); Pérez-Ruzafa *et al.* (2003: 112); Stöhr (2005: 269, figs. 16A-N).

Distribution: Mediterranean Sea and East Atlantic, from Iceland to South Africa, including the Azores, Madeira, Canaries and Cabo Verde.

Depth: 0–509 m (AZO: 0–150 m).

Habitat: on hard bottom, among algae, shells, serpulids, etc., also under stones on the shore, predated specially by *Luidia ciliaris*.

Type of Development: planktotrophic.

Material examined: DBUA-ECH 064 (Islet of Vila Franca do Campo, SMG, AZO, *c.* N37°42’21” W25°26’34”, 1997.03.03; 1 spm, D=8 mm); DBUA-ECH 121 (São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2012.11.16, intertidal; 9 spms, D=2–4 mm); DBUA-ECH 125 (Poços de São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.17, 8 m; 2 spms, D=3–6 mm); DBUA-ECH 126 (Poços de São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.03, 10 m; 2 spms, D=3–6 mm); DBUA-ECH 127 (Poços de São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.17, 10 m; 8 spms, D=4–8 mm); DBUA-ECH 133 (Baixa da Caloura, SMG, AZO, *c.* N37°42’20” W25°30’30”, 1996.12.05, 15 m; 3 spms, D=2–5 mm); DBUA-ECH 195 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1996–06–07; 2 spms, D=3–4 mm); DBUA-ECH 254 (PIX, AZO; 1 spm, D=5 mm); DBUA-ECH 342 (Sabrina Bank, SMG, AZO, N37°52’09” W25°54’08”, 2011.07.07, 150 m; 1 spm, D=5 mm); DBUA-ECH 395 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2011.03.10, 6 m; 1 spm, D=3 mm); DBUA 416 (Sabrina seamount, SMG, AZO, *c.* N37°52’35” W25°53’50”, 2011.07.07, 34 m; 1 spm, D=4 mm).

Description: disc subpentagonal covered more or less evenly by short stumps, terminating in a crown of very small sharp and thin spines, typical three in number but occasionally more (this is particularly true in the largest specimen, D = 8 mm, DBUA-ECH 064). Radial shields about 19–24% D, naked with a few scattered stumps (most individuals) to almost entirely covered. No spines present on the dorsal surface of the disc. Stumps also present on the ventral surface of the disc. Mouth shields somewhat triangular (length < breadth). A hole is present at the base of each jaw. No oral papilla. Numerous crowded tooth papillae. One small tentacle scale; arms about three to four times the D; the largest specimen (D = 8 mm, DBUA-ECH 064) with four of the five arms showing evidence of predation with varying degrees of regeneration. Dorsal plates of arms naked with longitudinal keel, protruding distally to form a faint elevated knob. Ventral arm plates almost rectangular with a concave outer edge. Seven thorny arm spines, increasing gradually in length from very small lowermost to the fifth or sixth arm spine, then decreasing in size again; distally lowermost arm spine hooked-shaped. Colour: disc uniform light brown, green, greyish-green to purple or pink; the disc colour was frequently lighter towards the centre to almost white or light pink; some specimens had a deep green circular spot in the centre of the disc; others presented as well small brown to dark green specks; radial shields sometimes almost totally white or having a white distal part (also the base of the arms), mid-way deep green, proximally pink as the rest of the disc arms green to greyish green with stripes (darker brown, greyish green or pink); some individuals had a conspicuous white spot on the dorsal plates; arm spines as the arms; exceptionally, oral surface of the disc orange becoming somewhat darker pinkish in the centre and arms banded yellow and

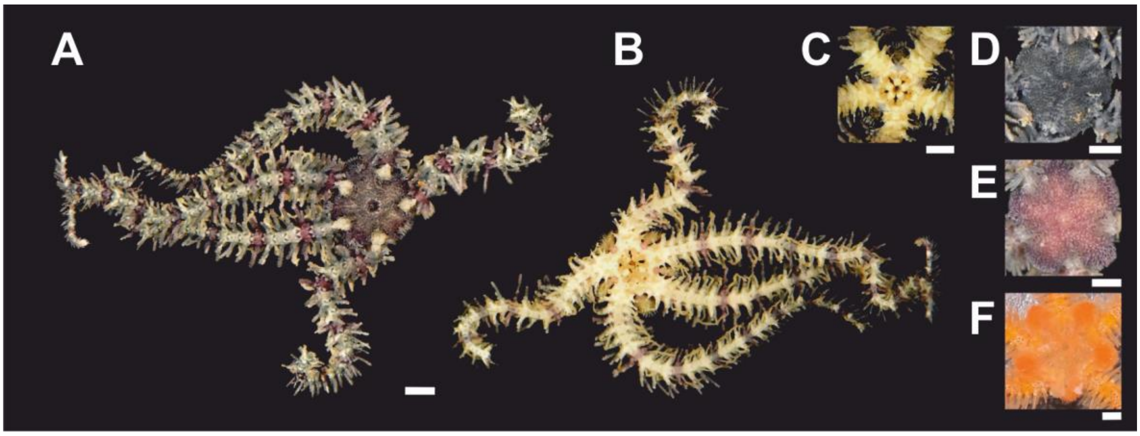


Figure 5.7. *Ophiothrix fragilis* (Abildgaard, *in* Müller, 1789) (juveniles, DBUA-ECH 121: A–C; DBUA-ECH 342: F). Dorsal view (A); ventral view (B); detail of the disc, ventral view (C); dorsal view (D–F); scale bars are 1 mm.

orange with the dorsal plates presenting dark lines forming an irregular pattern (DBUA-ECH 342). Colour (in ethanol): many individuals had lost all colour, presenting a uniform cream colour, though some showed a conspicuous white circular spot in the centre of the dorsal surface of the disc.

Remarks: *Ophiothrix fragilis* is a highly polymorphic species, a fact reflected by the numerous synonyms and varieties described (Tortonese 1965), which is mirrored by the history of this species in the Azores. Ljungman (1872) based *Ophiothrix rubra* an animal collected in the Azores. Lyman (1874) re-examined Ljungman’s type specimen and concluded that *O*. *rubra* was conspecific with *Ophiothrix lusitanica*, whereas Ljungman believed that it was closely related to the *Ophiothrix echinata*. Barrois (1888) agreed with Lyman and commented that *Ophiothrix lusitanica* seemed rather common on the shores of all Azorean islands. Conversely, Koehler (1898, 1909) identified material collected in the Azores by *Hirondelle* at 130 m depth and by *Princesse Alice* between 54 and 98 m depth as ‘*pentaphyllum*’ and ‘common’ forms, respectively. Later, Koehler (1921b) reduced the forms previously described as independent species or varieties to four basic subspecies: ‘*echinata*’, ‘*lusitanica*’, ‘*pentaphyllum*’ and ‘*abildgaardi*’. Mortensen (1927a) found Ljungman’s type material to be identical with *O. fragilis*, confirming unambiguously the synonymy (though without commenting which variety it was most closely related to). Among later authors working with material from the Azores, only Chapman (1955) ventured to identify a specimen collected in archipelago as *O. fragilis* var. *lusitanica*.

Historically, many authors commented that diagnosis of *O. fragilis* subspecies was quite difficult since they are linked by intermediary forms (*e.g.,* Mortensen 1927a; Nobre 1938; Tortonese 1965; Clark 1974). Among the littoral subspecies, '*lusitanica*' is viewed as the southern form from the Atlantic French coasts south to NW Africa, '*echinata*' is viewed as a typical Mediterranean form, the form '*triglochis*' is thought to be restricted to Southern Africa and '*nuda*' to Cabo Verde (Koehler 1921b; Cadenat 1938; Nobre 1938; Tortonese 1965; Madsen 1970; Clark 1974). Nevertheless, it is known that these subspecies can co-occur sympatrically (*e.g*., Cadenat 1938; Alvà & Vadon 1989). Comparing the description of the type specimen of *O*. *rubra* by Ljungman (1872) and Lyman (1874) with our own specimens, the most striking commonality is the presence of thorny spinelets on the radial shields. This morphological feature is normally associated with *O*. *alopecurus*, which Koehler (1921b) synonymised as a rare form of '*echinata*'. The specimens examined herein were relatively small, no larger than 8 mm in disc diameter, a feature that could also indicate that they belong to the smaller variety '*echinata*'. However, in this subspecies the disc stumps have only up to three terminal spines ('trifid stumps'). This contrasts with the occasional presence of stumps terminating in a crown with up to five thorns in our material, which is more characteristic of the subspecies '*lusitanica*'. Another typical feature of this later subspecies shared with our specimens, is the absence of disc spines, and even and regular distribution and size of disc spinelets. Interestingly, Clark (1974) observed the same intermediary characteristics between '*echinata*' and '*lusitanica*' in specimens from South Africa previously identified as *Ophiothrix triglochis* (= *Ophiothrix fragilis*).

The choice, in which subspecies the Azorean specimens should be placed is even less clear considering the colour pattern alone (see Figs. 5.7A–E). For example, some specimens had a conspicuous white or lighter coloured spot on the dorsal plates, which is characteristic of '*echinata*'. In contrast, other specimens presented a uniform green colour which places them in the range the '*lusitanica*' variety. The specimen from deeper waters (150 m; DBUA-ECH 342) presented an overall structure similar to the shallow-water material. However, the animal presented a brightly yellow/orange colour pattern typical of the deeper water variety '*pentaphyllum*' (Fig. 5.7F). Overall, the material of *O*. *fragilis* housed in the DBUA-ECH collection presented features intermediary to the varieties '*echinata*' and '*lusitanica*'. Whether these subspecies reflect environmental differences (*e.g.,* differences in temperature and depth) or underlying genetic differences between populations is not clear, but recent genetic studies on the European varieties by Muths and co-authors (2009) suggest that *O. fragilis* represents a single, but plastic, species.

Madsen (1970) synonymized *Ophiothrix indigna* Koehler, 1906a (from Madeira and Gulf of Cadiz) with *O. cotteaui* (de Loriol, 1900) as it merely represented adults of the latter species. However, Madsen erroneously placed *O. indigna*'s type locality in the Azores. *Ophiothrix fragilis* can be easily distinguished from *O. cotteaui* or even from *O. luetkeni* Thomson, 1873 (see below) by its naked dorsal arm plates with a more or less produced distal edge.

Ophiothrix luetkeni Thomson, 1873

$^{\$}$1879. *Ophiothrix Lütkeni*? Wyv. Thom.; Lyman: 54.
$^{\$}$1882. *Ophiothrix lütkeni* Wyv. Thomson; Lyman: 218.
$^{\$}$1882. *Ophiothrix lütkeni* (?) Wyv. Thomson; Lyman: 286.
1892. *Ophiothrix luetkeni;* Bell: 133.
$^{\$}$1909. *Ophiothrix Lütkeni*, Wyville Thomson; Koehler: 201–202, pl. 29, figs. 8–10.
1927a. *Ophiothrix Lütkeni* Wyv. Thomson; Mortensen: 176–177, fig. 99.
1997. *Ophiothrix luetkeni* Wyville Thomson; Pereira: 332.
2005. *Ophiothrix luetkeni* Wyville Thomson, 1873; García-Diez *et al.*: 48.
2010. *Ophiothrix luetkeni* Wyville Thomson, 1873; Micael & Costa: 322.
2012. *Ophiothrix luetkeni* Wyville Thomson, 1873; Micael *et al.*: 3.

Type locality: SW Ireland.

See: Thomson (1873: 100); Koehler (1906a: 31–33, pl. 3, figs. 43–46; 1921b: 71–72, fig. 46); Mortensen (1927a).

Distribution: Northeast Atlantic from the British Islands to Cabo Verde, including the Azores Archipelago and Josephine Seamount.

Depth: 130–838 (?932) m [AZO: ?54–165 (?823) m].

Habitat: soft bottom (rarely on hard substrates), sand, gravel and shelly substrates.

Remarks: the first report of *O. luetkeni* in the Azores was made by Lyman (1879), though he remarked that the specimen was too young and left the identification tentative. The depth of 823 m (RV 'H.M.S. Challenger', sta 75: N38°37' W28°30') reported by Lyman seems a result of mislabelling. It is likely that the station's depth might be much shallower, between 92–165 m (see remarks under *Astropecten hermatophilus*). In contrast, Koehler (1909) recorded this species in the Azores at 54 m, a surprisingly shallow depth since this species generally tends to occur below 100 m (see Koehler 1921b). In spite of the small size revealed by RV 'Princesse Alice' individuals (disc diameter between 5–8 mm), it is hard to believe that Koehler (1909), who was familiar with the morphological variability of both *O. fragilis* and *O. luetkeni*, could possibly have misidentified the specimens. Thus, we believe that a possible mislabelling occurred in the depth values of the stations.

Order Euryalida Lamarck, 1816
Family Asteronychidae Verrill, 1899
Genus *Astrodia* Verrill, 1899

Astrodia tenuispina **(Verrill, 1884)**

?$^{\$}$1888. Euryalide; Simroth: 231
$^{\$}$1972. *Astrodia tenuispina* Verril, 1884; Sibuet: 121–122.
1992. *Astrodia tenuispina*; Pérès: 254.

Type locality: off Nantucket Shoals.

See: Verrill (1884: 219, as *Asteronyx tenuispina*); Gage *et al*. (1983: 287–288); Ventura *et al.* (2007: 246); Okanishi & Fujita (2014: 198–200, figs. 10–11).

Distribution: cosmopolitan, in the Pacific and Atlantic oceans; in the Atlantic, from off Nantucket Island to Brazil including the Caribbean and Gulf of Mexico deep-waters, eastwards from Rockall Trough south to the Iberian Peninsula, including the Canary Islands and the Azores.

Depth: 512–3,548 m (AZO: 2,480 m)

Habitat: epizooic on other sedentary marine species, such as the pennatulid *Scleroptilum grandiflorum* Kölliker, 1880 on which the Azorean specimen was found; probably planktivorous.

Type of Development: produces large yolky eggs, possibly indicative of a direct or lecithotrophic development.

Remarks: the record of the cosmopolitan *Astrodia tenuispina* in the archipelago was based on a single specimen collected by bathyscaphe 'Archimède' in 1969, north of São Miguel Island, and later identified by Sibuet (1972). See also remarks below, under *Asteroschema inornatum* Koehler, 1906a.

Family Euryalidae Gray, 1840

Genus *Asteroschema* Oerstedt & Lütken, *in* Lütken, 1856

Asteroschema inornatum Koehler, 1906a

?$1888. Euryalide; Simroth: 231.

$1909. *Astrochema inornatum* Kœhler; Koehler: 205, pl. 7, fig. 1.

$1921a. *Astrochema inornatum*, Kœhler; Koehler: 2.

1948. *Asteroschema inornatum* Koehler; Clark: 78.

1985. *Astroschema inornatum* Koehler, 1906; Paterson: 16, fig. 10.

2005. *Asteroschema inornatum* Koehler, 1906; García–Diez *et al*.: 48.

$2005. *Asteroschema inornatum* Koehler, 1906; Stöhr & Segonzac: 4722.4.

2008. *Asteroschema inornatum* Koehler, 1906; Martynov & Litvinova: 78–79, fig. 1B.

2014. *Asteroschema inornatum* Koehler, 1906; Smirnov *et al*.: 194.

Type locality: Bay of Biscay.

See: Koehler (1906a: 30–31, pl. 3, figs. 45, 47; 1921a); Gage *et al.* (1983: 288); Paterson (1985).

Distribution: North Atlantic deep-waters, from off Nova Scotia and the Reykjanes Ridge (S of Iceland) on the Mid-Atlantic Ridge, south of the Charlie-Gibbs Fracture Zone to the Azores and from the Rockall Trough south of the Bay of Biscay to Madeira.

Depth: 1,300–2,300 m (AZO: 1,478–2,300 m).

Habitat: found in association with gorgonians.

Remarks: Simroth (1888) reported a small young euryalid collected in the Azores. Only two species belonging to the order Euryalida are known from the archipelago, *Astroschema inornatum* and *Astrodia tenuispina*, both known from Azorean waters well below 1,000 m. Aside from the small size of the specimen, Simroth (1888) presented no further details and we have no knowledge where this animal could be housed. Nevertheless, Koehler (1909, 1921a) and more recently Stöhr & Segonzac (2005) collected material belonging to *Asteroschema inornatum* in the archipelago, thus confirming this species' presence in the Azores.

Order Ophiacanthida O'Hara *et al*., 2017

Family Ophiacanthidae Ljungman, 1867

Genus *Ophiacantha* Müller & Troschel, 1842

Ophiacantha abyssicola Sars, 1872

$1909. *Ophiacantha abyssicola*, G.-O. Sars; Koehler: 182.

1913. *Ophiacantha abyssicola*, G. O. Sars; Farran: 38–39, fig. 9d.

1927a. *Ophiacantha abyssicola* G.O. Sars; Mortensen: 194, figs. 105.5–6.

1932. *Ophiacantha abyssicola* G.O. Sars; Grieg: 37.

2005. *Ophiacantha abyssicola* Sars, 1871; García-Diez *et al*.: 49.

Type locality: Norway.

See: Sars (1872: 8–10); Mortensen (1927a); Clark (1949: 375); Madsen (1970: 163); Gage *et al.* (1983: 289); Paterson (1985: 47–48, fig. 20); Bartsch (1987: 118–119); Jesus & Abreu (1998: 61); Metaxas & Giffin (2004).

Distribution: North Atlantic; north of Cape Hatteras in the Northeast American coast to Greenland and Iceland, eastwards to Scandinavia, southwards to the Western Sahara, including the Azores, Madeira, Canaries, and the Atlantis Seamount (Meteor).

Depth: 35–3,500 m, an upper bathyal species that may occur in shallow waters at higher latitudes, such as the Norwegian Sea (AZO: 880 m).

Habitat: rock, coral, mud to gravel and detritic substrates; it can form dense beds.

Remarks: the record of *Ophiacantha abyssicola* in the Azores is based on a single small specimen collected by RV ‘Princesse Alice’ (sta 837: N37°55’ W25°24’15”, 880 m) and identified by Koehler (1909).

Ophiacantha aculeata Verrill, 1885a

$^{\$}$2008. *Ophiacantha aculeata* Verrill, 1885; Martynov & Litvinova: 90–91, figs. 7A, 10.

Type locality: off Virginia, USA (N37°50’00” W73°03’50”).

See: Verrill (1885a: 153; 1885b: 443–444); Koehler (1914a: 74–77, pl. 11, figs. 1–2); Martynov & Litvinova (2008).

Distribution: North Atlantic deep-waters, from off Virginia to New England, eastwards to Rockall Trough, the Bay of Biscay to Iberian Basin, including in the Mid-Atlantic Ridge, from Reykjanes Ridge to the north of the Azores.

Depth: 1,650–3,584 m (AZO: 2,954–2,968 m).

Habitat: soft sediments (*Globigerina* ooze).

Remarks: *Ophiacantha aculeata* was recently identified by Martynov & Litvinova (2008) among the material collected by RV ‘G.O. Sars’ (‘MAR–ECO’ expedition) at a station located at the northern border of the Azorean waters (sta 40/367: N42°55’ W30°20’, 2,954–2,968 m). This species has been historically confused with *O. fraterna* Verrill, 1885c (Martynov & Litvinova 2008), a species also considered at one point conspecific or a variety of *O. bidentata* (Bruzelius, 1805). See remarks under the latter species).

Ophiacantha aristata **Koehler, 1895c**

$^{\$}$1896a. *Ophiacantha aristata* Koehler; Koehler: 212.

$^{\$}$1898. *Ophiacantha aristata*, Kœhler; Koehler: 55.

$^{\$}$1906b. *Ophiacantha aristata* Koehler; Koehler: 288–289.

$^{\$}$1909. *Ophiacantha aristata*, Kœhler; Koehler: 183, pl. 26, figs. 5–6**.**

$^{\$}$1921a. *Ophiacantha aristata* Kœhler; Koehler: 2.

1927a. *Ophiacantha aristata* Koehler; Mortensen: 191, 193–194, fig. 107.

1932. *Ophiacantha aristata* Koehler; Grieg: 38.

1938. *Ophiacantha aristata* Kœhler; Nobre: 76–77.

2005. *Ophiacantha aristata* Koehler, 1896; García-Diez *et al.*: 49.

Type locality: Bay of Biscay.

See: Koehler (1896c: 81–86, figs. 43, 44); Mortensen (1927a); Bartsch (1987: 119–120, figs. 11–15); Copley *et al.* (1996: 553); Rodrigues *et al.* (2011: 7, fig. 2).

Distribution: Northeast Atlantic, from the Reykjanes Ridge (S of Iceland) and British Isles to NW Africa, including the Azores and Canaries.

Depth: 658–1,805 m (AZO: 1,095–1,740 m).

Habitat: soft bottoms, mud to sand and on corals.

Remarks: Koehler (1896a, 1898, 1906b, 1909, 1921a) recorded *Ophiacantha aristata* among the material collected by the main oceanographic cruises crossing the Azorean archipelago waters at the time (RVs ‘Hirondelle’, ‘Talisman’, ‘Princesse Alice’). This species is only known in the archipelago from Koehler’s historical reports.

Ophiacantha bidentata**? (Bruzelius, 1805)**

?$^{\$}$1898. *Ophiacantha bidentata*, Retzius; Koehler: 55.

1927a. *Ophiacantha bidentata* (Retzius); Mortensen: 196, figs. 105.1–2.

1938. *Ophiacantha bidentata* (Retzius); Nobre: 72.

1985. *Ophiacantha bidentata* (Retzius, 1805); Paterson: 34–36, fig. 15.

2005. *Ophiacantha bidentata* (Retzius, 1805); García-Diez *et al.*: 49.

2010. *Ophiacantha bidentata* (Retzius, 1805); Micael & Costa: 322.

2011. *Ophiacantha bidentata* (Bruzelius, 1805); Benavides-Serrato *et al.*: 244–245.

2012. *Ophiacantha bidentata* (Bruzelius, 1805); Micael *et al.*: 3.

2014. *Ophiacantha bidentata* (Retzius, 1805); Smirnov *et al.*: 195.

Type locality: Norway.

See: Bruzelius (1805: 33, as *Asterias bidentata*); Koehler (1906b: 289; 1909: 184; 1914a: 80–81); Mortensen (1927a); Jesus & Abreu (1998: 62); Martynov & Litvinova (2008).

Distribution: Arctic (circumpolar) and North Atlantic, from the eastern coast of USA to Greenland and in the eastern Atlantic from South of Iceland to Cape Blanc, including the archipelagos of the ?Azores, Madeira, Canaries and ?Cabo Verde.

Depth: 10–?4,730 m (?AZO: ?1,287 m).

Remarks: when describing *Ophiacantha fraterna*, Verrill (1885c) cautioned that this species had previously been confused with *O. bidentata*, including some of the H.M.S. 'Challenger' material identified by Lyman (1882). Verrill (1885b) also added that O. *bidentata* unlike *O. fraterna* occurs at moderate depths. Later authors consider *O. fraterna* as a junior synonym of *O. bidentata*, or a variety of the latter (*e.g.,* Mortensen 1933a; Paterson 1985). As a result, it is difficult to understand the true geographical and depth range of *O*. *bidentata* (see discussion by Martynov & Litvinova 2008). In view of this and considering that the report of *Ophiacantha bidentata* in the archipelago is based on a single poorly preserved specimen collected at a depth of 1,287 m (Koehler 1898; RV 'Hirondelle', sta 112: N38°48'30", W28°06'16"), the inclusion of this species in the Azorean faunal list should be considered with caution.

Mortensen (1927a) included Cape Verde in the geographical distribution of *O. bidentata*. To the best of our knowledge no animal belonging to this species was ever collected in the archipelago. In an earlier report, Koehler (1906b) recorded this species at *Talisman* deep-water stations located between off NW African coast and Canaries. It is possible that Mortensen (1927a) mistook Koehler's records, which was repeated by subsequent references (*e.g*., Mortensen 1933a, Nobre 1938, Madsen 1947).

Ophiacantha crassidens Verrill, 1885a

$^{\$}$1906a. *Ophiacantha decipiens* nov. sp.; Koehler: 22–23, pl. 2, figs. 26–27.

$^{\$}$1906b. *Ophiacantha decipiens* Koehler; Koehler: 283–284, pl. 20, figs. 31–32.

$^{\$}$1909. *Ophiacantha crassidens*, Verrill; Koehler: 185–186, pl.26, figs. 9–11.

1913. *Ophiacantha crassidens*, Verrill; Farran: 42–43, figs. 9c, 14.

1927a. *Ophiacantha decipiens* Koehler; Mortensen: 188.

1927a. *Ophiacantha crassidens* Verrill; Mortensen: 192–193, fig. 106.

1932. *Ophiacantha crassidens* Verrill; Grieg: 38.

1938. *Ophiacantha decipiens* Kœhler; Nobre: 73.

$1985. *Ophiacantha crassidens* Verrill, 1885; Paterson: 40–41, fig. 17.

2005. *Ophiacantha crassidens* Verrill, 1885; García-Diez *et al.*: 49.

$2005. *Ophiacantha crassidens* Verrill, 1885; Stöhr & Segonzac: 4722.3.

2014. *Ophiacantha crassidens* Verrill, 1855; Smirnov *et al.*: 194.

Type locality: off Cape Hatteras, USA.

See: Mortensen (1927a); Grieg (1932); Paterson (1985).

Distribution: North Atlantic; it is known from west of Cape Hatteras and off Virginia in the West Atlantic and from the British waters to south of the Azores in the East Atlantic.

Depth: 970–3,120 m (AZO: 1,095–2,200 m).

Habitat: soft sediments, sand to mud.

Remarks: Koehler (1906a, b) described *Ophiacantha decipiens* from a specimen collected by RV ‘Talisman’ in the Azores (sta 127, 1883: N38°38’, W28°20’46”, 1,257 m). Koehler (1906a) believed that this species was a close ally to *O. smitti* Ljungman, 1872, a species reported from the archipelago by Stöhr & Segonzac (2005). Koehler (1909) also reported *O. crassidens* from the Azores, based on material collected by RV ‘Princesse Alice’ (sta 703: N39°21’20”, W31°05’45”, 1,360 m; sta 1344: N38°45’30”, W28°07’45”, 1,095 m). Later, Paterson (1985) compared the type material of *O. decipiens* with specimens belonging to *O. crassidens* and found them to be conspecific. More recently, Stöhr & Segonzac (2005) reported an animal belonging to this species from Mount Saldanha, in the southwestern-most waters of the Azores (SEAHMA–1, sta PL181–3: N36°33’38”, W33°24’49”, 2,200 m).

Ophiacantha lineata Koehler, 1896b

$1896b. *Ophiacantha lineata* nov. sp.; Koehler: 247–249.

$1909. *Ophiacantha lineata*, Kœhler; Koehler: 187–188, pl. 25, figs. 6–8.

$1921a. *Ophiacantha lineata* Kœhler; Koehler: 2, 4.

1927a. *Ophiacantha lineata* Koehler; Mortensen: 188.

1972. *Ophiacantha lineata* Koehler; Cherbonnier & Sibuet: 398.

$1985. *Ophiacantha lineata* Koehler, 1896c; Paterson: 42–44, fig. 19.

2005. *Ophiacantha lineata* Koehler, 1909; García-Diez *et al.*: 49.

Type locality: Azores (N38°26’ W26°30’45”).

See: Koehler (1896b, 1909, 1914a: 87); Bartsch (1987: 122–123, figs. 20–21); Paterson (1985).

Distribution: North Atlantic, from Florida eastwards from Rockall to Western Sahara, including the Azores.

Depth: 500–3,175 m (AZO: 1,165–1,378 m).

Habitat: soft sediments, sand with coral and shells.

Remarks: Koehler (1896b, 1909) described a new species, *Ophiacantha lineata* based on specimens collected in the Azores by RV 'Princesse Alice' (sta 578: N38°26'00" W26°30'45", 1,165 m). Koehler (1921a) found further material from the archipelago on a later expedition by RV 'Princesse Alice' (sta 3140: N37°38' W26°01', 1,378 m). In a review, Paterson (1985) re-examined RV 'Princesse Alice's material, updating the original description by Koehler.

Ophiacantha mesembria **Clark, 1915**

$^{\$}$1898. *Ophiacantha pentagona*, Kœhler; var. *armata* n. var.; Koehler: 55–56.

1922. *Ophiacantha mesembria*; Koehler: 60–61.

1927a. *Ophiacantha mesembria* H. L. Clark; Mortensen: 188.

Type locality: off Santa Cruz (Virgin Islands, Caribbean).

See: Clark (1915: 201–202); Jesus & Abreu (1998: 63); Benavides-Serrato *et al.* (2011: 248–249).

Distribution: Northwest Atlantic, known from Florida to the Caribbean islands and Gulf of Mexico eastwards to the Azores and ?Madeira.

Depth: 256–2,870 m (AZO: 2,870 m).

Habitat: soft sediments (clayish sand).

Remarks: Koehler (1898) examined two specimens collected by RV 'Hirondelle' in Azorean waters, which he placed in a variety 'armata' of *O. pentagona*, a species described from the Pacific Ocean. Later, on examination of material from the Pacific collected by RV 'Albatross', Koehler (1922) changed his previous identification of the RV 'Hirondelle' material, and placed them under the Caribbean *O. mesembria*, extending its geographical distribution to the Mid-Atlantic and its vertical distribution from 1,143 m to 2,870 m. This species may also occur at Madeira Archipelago (Jesus & Abreu 1998, as *Ophiacantha* cf. *mesembria*).

Ophiacantha notata Koehler, 1906a

$^{\$}$2005. *Ophiacantha notata* Koehler, 1906; Stöhr & Segonzac: 4722.3.

Type locality: Bay of Biscay (N45°05'00" W7°00'26").

See: Koehler (1906a: 23–24, pl. 2, figs. 28–30; 1906b: 284–286. pl. 20, figs. 36–38); Paterson (1985: 44, fig. 19).

Distribution: only known from the Bay of Biscay and near Menez Gwen in Azores.

Depth: 850–1,226 m (AZO: 850 m).

Remarks: until recently, *Ophiacantha notata* was known only from the type material collected by the RVs 'Travailleur' and 'Talisman' expeditions in the Bay of Biscay. Stöhr & Segonzac reported this rare species from the waters in the vicinity of Menez Gwen, in the southwest of the Azores (SEAHMA–1, DR01: N37°50'32" W31°31'16", 850 m).

Ophiacantha setosa (Bruzelius, 1805)

?1898. *Ophiacantha setosa*, Müller et Troschel; Koehler: 57–58, pl. 8, figs. 37–38.

$^{\$}$1906b. *Ophiacantha setosa* (Retzius); Koehler: 291–292.

$^{\$}$1938. *Ophiacantha setosa* Müller und Troschel; Nobre: 74, fig. 34.2.

1965. *Ophiacantha setosa* (Retz.); Tortonese: 218–220, fig. 102.

See: Bruzelius (1805: 30, as *Asterias setosa*); Rochebrune (1881: 324); Koehler (1921b: 69–70, fig. 45); Tortonese (1965); Paterson (1985: 37–38, fig. 16); Bartsch (1987: 123–124); Koukouras *et al.* (2007: 73).

Distribution: Mediterranean Sea and East Atlantic, from the Bay of Biscay along West African coast as far as Angola, including the archipelagos of the Azores, Canaries and Cabo Verde.

Depth: 5–1,480 m (AZO: ?139–1,257 m).

Habitat: abundant in detritic substrates and a frequent epibiont on gorgonians.

Remarks: the first report of *Ophiacantha setosa* from the Azores can be traced back to Koehler (1898). In the introduction and later in the discussion of the geographical distribution of this species (pages 32 and 58), Koehler remarked that he found this species in the Azores at a depth of 139 m, without giving any further details. However, Koehler (pp. 33, 57, 69) only listed a station sampled by RV 'Hirondelle' located in the Bay of Biscay, at a depth of 135 m. Regardless, the same author (1906b) later identified a specimen belonging to *O. setosa* among the material collected by RV 'Talisman' in the Azores (sta 127, 1883: N38°38' W28°20'46", 1,257 m), which appears to have been re-examined later by Nobre (1938).

Ophiacantha simulans **Koehler, 1895c**

$^{\$}$1909. *Ophiacantha composita*, Kœhler; Koehler: 185. [misidentification]

1983. *Ophiacantha simulans* Koehler, 1896; Gage *et al*.: 291.

1985. *Ophiacantha simulans* Koehler, 1896a; Paterson: 39–40, fig. 17.

2005. *Ophiacantha composita* Koehler, 1907; García-Diez *et al*.: 49 . [based on Koehler 1909]

2008. *Ophiacantha simulans* Koehler, 1896; Martynov & Litvinova: 96, fig. 11B.

2014. *Ophiacantha simulans* Koehler, 1896; Smirnov *et al*.: 196.

Type locality: Bay of Biscay.

See: Koehler (1895c: 465–467, fig. 7; 1896c: 82–84); Mortensen (1933a: 26–29, figs. 11, 12, pl. 3, figs. 5–6); Paterson (1985).

Distribution: North Atlantic, from off North Carolina eastwards to Iceland in the North, southwards to Morocco including the archipelagos of the Azores and Canaries.

Depth: 1,480–3,018 m (AZO: 1,919–3,018 m).

Habitat: soft substrates, mud to muddy sand and corals.

Remarks: Koehler (1906b, 1909) reported small animals collected by the RVs ‘Talisman’, ‘Travailleur’ and ‘Princesse Alice’ in the Bay of Biscay, Canaries and the Azores, which he believed to be *Ophiacantha composita*, a species he described for the Indian Ocean. Furthermore, Koehler (1906b) assumed that the species he had erected earlier based on a single specimen collected by RV ‘Caudan’ in the Bay of Biscay (*Ophiacantha simulans*) was conspecific with the species from Indian Ocean. After the examination of material collected by ‘Ingolf’ and ‘Thor’ cruises in Icelandic waters, Mortensen (1933a) disagreed with Koehler stating that the NE Atlantic animals were *O. simulans*, reinstating the former species. Paterson (1985) re-examined the material from the RVs ‘Talisman’ and ‘Travailleur’ collected in the Bay of Biscay and agreed with Mortensen, assigning Koehler’s *Ophiacantha composita* specimens from the Atlantic to *O. simulans*.

Ophiacantha smitti **Ljungman, 1872**

$^{\$}$2005. *Ophiacantha smitti* Ljungman, 1872; Stöhr & Segonzac: 4722.3.

Type locality: Portugal (N38°10’ W9°25’).

See: Ljungman (1872: 621–622); Lyman (1882: 189, pl. 15, figs. 1–2); Paterson (1985: 46–47, fig. 20); Bartsch (1987: 124–125, figs. 22–24); Jesus & Abreu (1998: 62); Jesus & Fonseca (1999: 345).

Distribution: North Atlantic, from the Bay of Biscay south to off Western Sahara, including the Azores and Madeira; also off Bermuda.

Depth: 75–2,282 m (AZO: 1,550 m).

Habitat: soft bottoms, muddy sand to grey ooze.

Remarks: *Ophiacantha smitti*, a species known from both sides of the Atlantic, is one of the more recent additions to the deep-water echinoderm fauna from the Azores, identify by Stöhr & Segonzac (2005) in a non-vent area near Lucky Strike (RV "L'Atalante", 'Victor 1ère' cruise 'Victor', sta PL33: N37°15'45" W32°13'30", 1,550 m).

Ophiacantha veterna Koehler, 1907a

$^{\$}$1921a. *Ophiacantha veterna* Kœhler; Koehler: 2.

1927a. *Ophiacantha veterna* Koehler; Mortensen: 189.

1985. *Ophiacantha enopla veterna* (Koehler, 1907b); Paterson: 37, fig. 16.

2005. *Ophiacantha enopla veterna* (Koehler 1907); García-Diez *et al.*: 49.

$^{\$}$2005. *Ophiacantha enopla veterna* (Koehler, 1907); Stöhr & Segonzac: 4722.10.

2008. *Ophiacantha veterna* Koehler, 1907; Martynov & Litvinova: 96–97, fig. 11D.

2014. *Ophiacantha enopla* Verrill, 1885; Smirnov *et al.*: 196.

Type locality: North of the Azores.

See: Koehler (1907a: 41–43; 1909: 189–190, pl. 29, figs. 3, 4); Paterson (1985); Stöhr & Segonzac (2005); Martynov & Litvinova (2008).

Distribution: Northeast Atlantic, from Reykjanes Ridge, eastwards from the Bay of Biscay to Western Sahara and Madeira, and southwards in the Mid-Atlantic Ridge to south of the Azores.

Depth: 101–2,460 m (AZO: 1,330–2,300 m).

Habitat: soft substrates, found associated with diverse sessile fauna (*e.g.,* sponges, hydrozoans, gorgonians, colonial tunicates) and co-occurring with *Asteroschema inornatum* Koehler 1906a.

Remarks: the first report of *Ophiacantha veterna* for the Azores was made by Koehler (1921a) based on two individuals collected by RV 'Hirondelle' (sta 3137: N37°00' W25°00', 1,330 m). More recently, Stöhr & Segonzac (2005) identified *Ophiacantha veterna* in the Mid-Atlantic Ridge, at the southwest border of the Azorean waters ('Marvel' cruise, sta PL1199–10: N36°32'16" W33°27'24", 2,300 m), thus substantiating the presence of this species in the archipelago. Paterson (1985) demoted *O. veterna* to a subspecies of the Northwest Atlantic *O. enopla,* a decision that Martynov & Litvinova (2008) later revoked by reinstating the species status.

Genus *Ophiochondrus* Lyman, 1869

Ophiochondrus armatus (Koehler, 1907a)

$^{\$}$1907a. *Ophioplus armatus*, nov. sp.— Koehler: 46.

$^{\$}$1909. *Ophioplus armatus*, Kœhler; Koehler: 203–204, pl. 28, figs. 7–8.

1914a. *Ophiochondrus armatus* (Kœhler); Koehler: 129–131, pl. 14, figs. 2–3, 6.

1927a. *Ophiochondrus armatus* (Koehler); Mortensen: 197–198, figs. 109–110.

2005. *Ophiochondrus armatus* (Koehler, 1909); García-Diez *et al*.: 49.

Type locality: Azores (N38°35’30” W28°05’45”).

See: Koehler (1909; 1914a); Mortensen (1927a).

Distribution: a rare species known only from Florida, Porcupine Seabight (SW of Ireland) and the Azores.

Depth: 287–1,250 m (AZO: 1,250 m).

Habitat: sandy bottoms with corals and shells; epibiont on corals.

Remarks: Koehler (1907a, 1909) described a new species *Ophiochondrus armatus* (= *Ophioplus armatus*) based on specimens collected by RV ‘Princesse Alice’ in the Azores. No other material is known from the archipelago.

Genus *Ophiomitrella* Verrill, 1899

Ophiomitrella cordifera Koehler, 1896b

$^{\$}$1896b. *Ophiomitra cordifera* nov. sp.— Koehler: 250–251.

$^{\$}$1909. *Ophiomitrella cordifera*, (Kœhler); Koehler: 192–193, pl. 29, figs. 1–2.

1927a. *Ophiomitrella clavigera* (Ljungman); Mortensen: 186–187, fig. 103.

$^{\$}$1933a. *Ophiomitrella cordifera*; Mortensen: 40–41.

1980. *Ophiomitrella clavigera* (Ljungman, 1864); Marques: 102.

$^{\$}$1985. *Ophiomitrella cordifera* (Koehler, 1896c); Paterson: 72–73, fig. 28.

1988. *Ophiomitrella clavigera* (Ljungman, 1864); Harvey *et al*.: 170.

2005. *Ophiomitrella clavigera* (Ljungman 1865); García-Diez *et al*.: 49.

Type locality: Azores (N38°52’45” W28°06’00”).

See: Koehler (1896b, 1909); Mortensen (1933a); Paterson (1985).

Distribution: known only from the Azores and Canaries.

Depth: 1,143–1,530 m (AZO: 1,143 m).

Habitat: soft bottoms, mud and sand.

Remarks: Mortensen (1920, 1927a) believed that *Ophiomitrella cordifera* described by Koehler (1896b) from the Azores was conspecific with the *O. clavigera* (Ljungman, 1865). However, on a re-examination of the type material, Mortensen (1933a) reinstated *O. clavigera*. Paterson (1985) agreed and considered the two to be valid species, but kept the Azores under the geographical distribution of both species. In spite of the wide distribution of *O. clavigera* in the Northern Atlantic, We could not find any valid record of this species in the Azores. Thus, it is more than likely that Paterson's (1985) account for the archipelago was a result of a mistake resulting from the historical synonymy of the two species. Subsequent reports of *O. clavigera* from the Azores were based on Paterson's (1985) or Mortensen's (1927a) initial erroneous assumption of synonymy.

Family Ophiodermatidae Ljungman, 1867

Genus *Ophioderma* Müller & Troschel, 1840a

Ophioderma longicauda? (Bruzelius, 1805)

$^{\$}$1865. *Ophiura lævis* Lyman; Lyman: 10, 26.
1914b. *Ophioderma longicauda*; Koehler: 275.
$^{\$}$1915. *Ophioderma longicaudum* (Retzius); Clark: 301.
1921b. *Ophioderma longicauda* Linck; Koehler: 87–89, fig. 58.
1927a. *Ophioderma longicauda* (Retzius); Mortensen: 226.
1965. *Ophioderma longicaudum* (Retz.); Tortonese: 259–261, figs. 118–119.
2002. *Ophioderma longicaudum* (Retzius, 1789); Pérez-Ruzafa *et al.*: 282.
2010. *Ophioderma longicauda* (Bruzelius, 1805); Micael & Costa: 322.
2012. *Ophioderma longicauda* (Bruzelius, 1805); Micael *et al.*: 3.

See: Cadenat (1938: 361, as *Ophioderma longicauda* var. *guineense*); Tortonese (1965); Stöhr *et al.* (2009).

Distribution: Mediterranean Sea and Northeast Atlantic, from Brittany on the west coast of France to Congo, including the archipelagos of the ?Azores, Madeira, Selvagens, Canaries and Cabo Verde.

Depth: 0–70 m, recorded at 120 m in the Gulf of Guinea.

Habitat: hard to coralligenous and muddy substrates, also among algae, under rocks and in *Posidonia* and *Caulerpa* beds.

Type of Development: lecithotrophic larvae, though brooding females were also observed in the Mediterranean Sea.

Remarks: the only known specimen from the Azores was reported by Lyman (1865, as *Ophiura lævis*) based on the collection of the Museum of Comparative Zoology (Harvard University). However, Lyman presented no data on its origin, including the depth, collector or the date. Later, Clark (1915, as *Ophioderma longicaudum*) confirmed Lyman's previous identification, but added no further information. The absence of background information on this specimen makes necessary to include this shallow-water species in the dubious record list, until new material is found that could substantiate the historical records.

Family Ophiomyxidae Ljungman, 1867

Genus *Ophioconis* Lütken, 1869

Ophioconis forbesi **(Heller, 1863)**

$^{\$}$1896a. *Ophioconis forbesi* Lütken; Koehler: 213.
$^{\$}$1898. *Ophioconis forbesi*, Lütken; Koehler: 58.
$^{\$}$1909. *Ophioconis Forbesi*, Heller; Koehler: 141.
1921b. *Ophioconis forbesi* Heller; Koehler: 89–90, fig. 59.
1927a. *Ophioconis Forbesi* (Heller); Mortensen: 227.
1965. *Ophioconis forbesi* (Hell.); Tortonese: 262–263, fig. 120.
1997. *Ophioconis forbesi* Heller, 1868; Pereira: 332.
2005. *Ophioconis forbesi* (Heller, 1863); García-Diez *et al*.: 50.
2010. *Ophioconis forbesi* (Heller, 1862); Micael & Costa: 322.
2012. *Ophioconis forbesi* (Heller, 1862); Micael *et al*.: 3.

Type locality: Adriatic (Mediterranean Sea).

See: Heller (1863: 422–424, pl. 2, figs. 5–8) Koehler (1921b); Tortonese (1965); Cherbonnier & Sibuet (1972: 407–408); Hernández *et al*. (2013: 490).

Distribution: Mediterranean Sea and Northeast Atlantic, from the Bay of Biscay to Moroccan coasts, including the archipelagos of the Azores and Canaries, and the seamounts of Josephine, Seine and Gettysburg.

Depth: 20–230 m (AZO: 98–130 m).

Habitat: sand, gravel and shells to rock; also among coralligenous algae; found in association with *Ophiura albida*.

Remarks: Koehler (1896a, 1898, 1909) identified the only two specimens of *Ophioconis forbesi* known from the Azores, collected by RV 'Hirondelle' (sta 226: N38°31'19" W28°34'31", 130 m) and RV 'Princesse Alice' (sta 882: N38°03'40" W28°34'45", 98 m).

Genus *Ophiomyxa* Müller & Troschel, 1840a

***Ophiomyxa serpentaria* Lyman, 1883**

$^{\$}$1909. *Ophiodera serpentina*, (Lyman); Koehler: 203.
1927a. *Ophiomyxa serpentaria* Lyman; Mortensen: 168, fig. 94a.
1933a. *Ophiomyxa serpentaria* Lyman; Mortensen: 11–14, figs. 1–3.
1985. *Ophiomyxa serpentaria* Lyman, 1883; Paterson: 18–20, fig. 11.
1988. *Ophiomyxa serpentaria* Lyman, 1883; Harvey *et al.*: 168.
2005. *Ophiomyxia serpentaria* Lyman, 1883; García-Diez *et al.*: 48.
2014. *Ophiomyxa serpentaria* Lyman, 1883; Smirnov *et al.*: 194.

Type locality: Faeroe Channel (N59°56' W6°27').

See: Lyman (1883: 274, pl. 8, figs. 114–116); Mortensen (1927a); Cherbonnier (1969: 348); Paterson (1985).

Distribution: Northeast Atlantic, from the Denmark Strait and Iceland southwards to the northwest African coast, including the Azores.

Depth: 450–2,440 m (AZO: 599–1,095 m).

Habitat: sand, rock and coralligenous substrates.

Type of Development: lecithotrophic.

Remarks: *Ophiomyxa serpentaria* is only known in the Azores from three poorly preserved specimens collected by RV 'Princesse Alice' and reported by Koehler (1909) (sta 866: N38°52'50" W27°23'05", 599 m; sta 1344: N38°45'30" W28°07'45", 1,095 m).

Family Ophiotomidae Paterson, 1985

Genus *Ophiocomina* Koehler, *in* Mortensen, 1920

***Ophiocomina nigra* (Abildgaard, *in* Müller, 1789)**
(Fig. 5.8)

$^{\$}$1888. *Ophiocoma nigra* Müller et Troschel; Barrois: 73–74.
$^{\$}$1907b. *Ophiocoma nigra* (Abildgard); Koehler: 326.
$^{\$}$1922. *Ophiocomina nigra*; Koehler: 314–318, pl. 75, figs. 1–5.
1927a. *Ophiocomina nigra* (Abildgaard); Mortensen: 178–179, figs. 83, 100.
1938. *Ophiocomina nigra* (Abildgaard); Nobre: 69–70, fig. 38.
1962. *Ophiocomina nigra* (Abildgaard); Fontaine: 1–8.

1965. *Ophiocomina nigra* (Abildg.); Tortonese: 251–253, fig. 115.

$^{\$}$1983. *Ophiocomina nigra* (Abildgaard); Marques: 3, fig. 4.

1995. *Ophiocomina nigra* (Abildgaard); Moyse & Tyler: 674, fig. 12.6.

1997. *Ophiocomina nigra* (Abildgaard, 1789); Pereira: 332.

2002. *Ophiocomina nigra* (Abildgaard, 1789); Pérez-Ruzafa *et al*.: 283.

$^{\$}$2005. *Ophiocomina nigra*; Cardigos *et al.*: 165.

2010. *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1789); Micael & Costa: 322.

2012. *Ophiocomina nigra* (Abildgaard, *in* O.F. Müller, 1789); Micael *et al*.: 3.

See: Mortensen (1927a); Narasimhamurti (1933); Tortonese (1965); Picton (1993: 40–41); Jesus & Abreu (1998: 62); Stöhr (2005: 569–572, figs. 17A–M).

Distribution: East Atlantic and Mediterranean Sea, from Scandinavia to Portugal and in the Azores, Madeira, Selvagens and Canaries.

Depth: 0–400 m, though rare at depths greater than 100 m (AZO: 6–30 m).

Habitat: gravel to rocky bottoms, usually on moderately sheltered areas; can form dense beds with over 100 animals/m^2.

Type of Development: planktotrophic (35–40 days).

Material examined: DBUA-ECH 070 (Baixa do Cerco, Caloura, SMG, AZO, *c*. N37°42’20” W25°30’30”, 1996.12.5, 15–30 m; 5 spms; D=3–8 mm); DBUA-ECH 128 (FRM, AZO, *c*. N37°16’14” W24°46’52”, 1990.06.08, 6–8 m; 1 spm, D=5 mm).

Description: disc round to pentagonal, covered by minute granules. Radial shields not diamond-shaped rounded middle angles, an obtuse proximal angle and the distal angle forms a small rounded lobe projecting into the interradial space. Adoral shields barely meeting within, extending around the lateral angle of the oral shield, separating it from the ventral arm plates. Two large blunt apical papillae flanked on each side by four oral papillae, inner oral papillae spiniform, pointed and outer papilla enlarged and scale-like. Five relatively long arms, about 4–5 times the disc diameter. Five long slender arm spines; two of ventral ones slightly smaller. Dorsal of arm plates broad and contiguous with a slightly rounded distal margin; first proximal dorsal plates covered by granules. Ventral arm plates continuous, pentagonal with obtuse proximal edge and slightlyconcave distal margin; two tentacle scales over each pore reduced to one in the distal part of the arm; the outer scale slightly larger. Colour (in ethanol) is uniformly white or brown to dark brown on the dorsal side and white or pale brown on the ventral side.

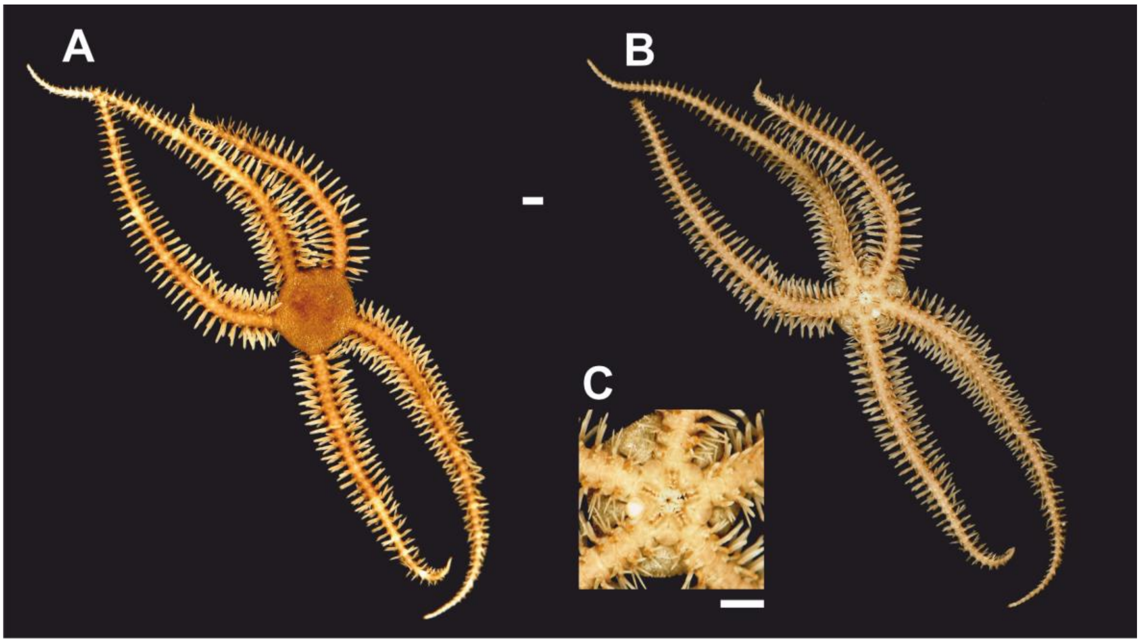


Figure 5.8. *Ophiocomina nigra* (Abildgaard, *in* Müller 1789) (DBUA-ECH 070). Dorsal view (A); ventral view (B); detail of the disc, ventral view (C); scale bars are 1 mm.

Remarks: among the shallow-water echinoderm fauna of the Azores, *Ophiocomina nigra* is quite unique in having a disc covered by small granules giving it an overall smooth appearance. Among the ophiuroids belonging to the family Ophiacanthidae found in the Azores several species also have a disc covered with granules, but only *Ophiacantha bidentata* is known to occur in shallow-waters. However, in this species the disc 'ornamentation' is characterized by rather short stumps (Mortensen 1927a), clearly contrasting with the minute granulation presented by *O. nigra*. Also, *Ophiothrix fragilis* is known to be found in association with *O. nigra* in the Azorean shallow waters (*e.g.,* Koehler 1909) and also has a disc 'ornamentation', but like *O. bidentata*, it is characterized by shorts stumps where the radial plates can be seen clearly (see also remarks under *O. fragilis*).

Ophiocomina nigra is found in all sorts of substrata, though it apparently prefers rocky bottoms (Mortensen 1927a). Nevertheless, Marques (1983) noted that in the Azores, *Ophiocomina nigra* seems particularly common in areas of strong sedimentation and rich in organic matter, such as ports, populated, and industrial areas. Cardigos *et al.* (2005) recorded this species in the area of Dom João de Castro Seamount (between Terceira and São Miguel islands), one of the rare examples in the Azores of a shallow-water hydrothermally-active volcanic seamount (the top of the seamount lies at just 13 m depth; Cardigos *et al*. 2005).

Genus *Ophiotoma* Verrill, 1899

Ophiotoma alberti **(Koehler, 1896b)**

$^{\$}$1896b. *Ophiotrema Alberti* nov. gen. nov. sp.; Koehler: 251–253.

$^{\$}$1909. *Ophiotrema Alberti*, Kœhler; Koehler: 196–198, pl. 28, figs. 1–2.

1927a. *Ophiotrema Alberti* Koehler; Mortensen: 183.

1983. *Ophiotrema alberti* Koehler, 1896; Gage *et al*.: 288.

1985. *Ophiotrema alberti* Koehler 1896c; Paterson: 57–58, fig. 23.

2005. *Ophiotrema alberti* Koehler, 1896; García-Diez *et al*.: 49.

2014. *Ophiotrema alberti* Koehler, 1896; Smirnov *et al*.: 197.

Type locality: Azores (N38°09’00” W23°15’45”).

See: Mortensen (1927a); Paterson (1985); Martynov (2010: 97–103, figs. 66A–E, 67A–C, 68A–I).

Distribution: Northeast Atlantic; recorded from several scattered locations in the Atlantic, including the Reykjanes Ridge area (*c.* N58°30’ W31°29’) and Rockall Trough, south to the Bay of Biscay and the Azores; it was also recorded in the southern hemisphere (S51°07’ W9°31’).

Depth: 1,684–4,354 m (AZO: 4,020 m).

Habitat: soft substrates.

Remarks: *Ophiotoma alberti* was erected by Koehler (1896b, 1909; as *Ophiotrema alberti*) based on two specimens collected by RV ‘Princesse Alice’ in the Azores (sta 527: N38°09’ W23°15’45”, 4,020 m), the only material known so far from the archipelago.

Ophiotoma coriacea**? Lyman, 1883**

?$^{\$}$1909. *Ophiopora Bartletti*, (Lyman); Koehler: 195.

1927a. *Ophiotoma coriacea* Lyman; Mortensen: 187–188, fig. 104.

1985. *Ophiotoma coriacea* Lyman, 1883; Paterson: 57, fig. 23.

1988. *Ophiotoma coriacea* Lyman, 1883; Harvey *et al*.: 169–170.

2005. *Ophiotoma barletti* (Lyman, 1883); García-Diez *et al*.: 49.

2014. *Ophiotoma coriacea* Lyman, 1883; Smirnov *et al*.: 197.

Type locality: off Cape Cod, USA (N41°24’45” W65°35’30”).

See: Lyman (1883: 268–269, pl. 2, figs. 1–3); Farran (1913: 45–46); Mortensen (1933a: 37–39); Paterson (1985); Martynov (2010: 97–103, figs. 66F–H).

Distribution: North Atlantic; from off Cape Cod eastward to Iceland, south to the Bay of Biscay and ?Azores.

Depth: 1,605–4,106 m (AZO: ?3,465 m).

Habitat: soft bottoms, from muddy sand to ooze.

Remarks: Koehler (1909) reported the Caribbean species *Ophiotoma bartletti* (= *Ophiopora bartletti*) from the Azores, based on a single incomplete and deformed specimen, collected by RV 'Princesse Alice' (sta 745: N38°05'00" W23°50'15") at a depth of 3,465 m, much deeper than what is believed to be the normal depth for the Caribbean species. Clark (1915) considered that the Caribbean species *O. bartletti* was conspecific with the East Atlantic *O. coriacea*, an opinion that subsequent authors did not agree with (*e.g.,* Koehler 1922; Mortensen 1933a). Paterson (1985) argued that since all that remains of the type material of the former species were fragments of the arms the synonymy could not be confirmed. We agree with Paterson (1985) that *O. bartletti* is restricted to the Caribbean and tentatively refer Koehler's report of *O. bartletti* to the temperate species *O. coriacea* (see also Farran 1913), despite the fact that *O. coriacea* as such has not been reported from the Azores so far. Inclusion of this species in the Azorean echinoderm fauna should, nevertheless, be considered with caution, considering the poor state of the only known specimen recovered from the Azorean deep waters.

Genus *Ophiotreta* Verrill, 1899

Ophiotreta valenciennesi (Lyman, 1879)

(Fig. 5.9)

$1896b. *Ophiacantha rufescens* sp. nov.; Koehler: 249–250.

1901. *Ophiacantha rufescens* Koehl.; Clark: 250.

$1906b. *Ophiacantha Valenciennesi* Lyman; Koehler: 292.

$1909. *Ophiacantha Valenciennesi* Lyman; Koehler: 188–189, pl. 6, fig. 2.

1927a. *Ophiacantha valenciennesi* Lyman 1879; Mortensen: 189.

$1933a. *Ophiacantha Valenciennesi* Lyman; Mortensen: 35–37, figs. 19b, 21a–e.

1938. *Ophiacantha Valenciennesi* Lyman; Nobre: 77–78.

1980. *Ophiacantha valenciennesi* Lyman, 1878; Marques: 101.

$1985. *Ophiotreta valenciennesi rufescens* Koehler, 1896c; Paterson: 49–50, fig. 21.

2005. *Ophiacantha valenciennesi* Lyman, 1879; García-Diez *et al.*: 49.

$2005. *Ophiotreta valenciennesi rufescens* Koehler, 1896; Stöhr & Segonzac: 4722.10.

2009. *Ophiotreta valenciennesi rufescens* (Koehler, 1896); Mifsud *et al.*: 67, fig. 2.

Type locality: off the Key-Islands**,** Indonesia (S5°43' W132°25').

See: Lyman (1882: 183–184, pl. 26, figs. 7–8, as *Ophiacantha valenciennesi*); Koehler (1914a: 102–103, as *Ophiacantha* (*Ophiotreta*) *valenciennesi*); Mortensen (1933a); O'Hara & Stöhr (2006: 62–63, figs. 5A–D, 17P); Borrero-Pérez *et al.* (2008: 181, figs. 7D, E); Stöhr (2011: 20–21).

Distribution: cosmopolitan, in the Pacific, Atlantic and the Mediterranean Sea, from the Gulf of Mexico and Caribbean, eastwards in the Azores and on the West African waters to Angola.

Depth: 123–1,442 m (AZO: 711–1,442 m).

Habitat: soft to hard substrates; can be found near hydrothermal vents and on cold seeps and in association with *Lophelia* corals.

Material examined: EMEPC G3D4 Ma004 (South of TER, AZO, N38°23'36" W26°54'11", 2007.05.18, 711–790 m; 1 spm, D=9 mm); EMEPC G3D4 Ma018 (South of TER, Azores, N38°23'36" W26°54'11", 2007.05.18, 711–790 m; (SE of TER, AZO, N38°23'36" W26°54'11", 2007.05.18, 711–790 m; 1 spm, D=7 mm).

Description: disc round to sub-pentagonal, covered by thin small imbricating plates bearing low hemispherical rugose granules; only the distalmost tips of the radial shields are visible. Mouth shields arrow-head-shaped (length≈breadth), widest at the mid-distal area, with a lobed distal margin; adoral shields not meeting within, extending around the lateral angle of the oral shield, separating it from the ventral arm plates. Jaws about as wide as long. One or two apical papillae flanked by five oral papillae on each side; proximal oral papillae spiniform, pointed, distal papilla enlarged and scale-like. Dorsal arm plates bell-shaped, with slightly lobed distal margin, contiguous, not bearing small spines on the distal margin. Ventral arm plates wider than long, contiguous with an acute proximal angle and a convex distal margin. Arms mostly broken off at the base, carrying 6 arm spines, the uppermost longest (about 3 segments in length); two small oval tentacle scales over each pore, 1/2 as long as the ventral arm plate, inner scale slightly smaller. Colour brown with slightly darker bands on the arms.

Remarks: Koehler (1896b) described *Ophiacantha rufescens*, based on material collected by RV 'Princesse Alice' in the Azores (sta 584: N38°31' W26°49'15", 845 m). On analysing the specimens collected by RV 'Talisman' off NW Africa and in the Azores (sta 122, 1883: N37°35' W28°20'46", 1,440–1,442 m), Koehler (1906b) placed his

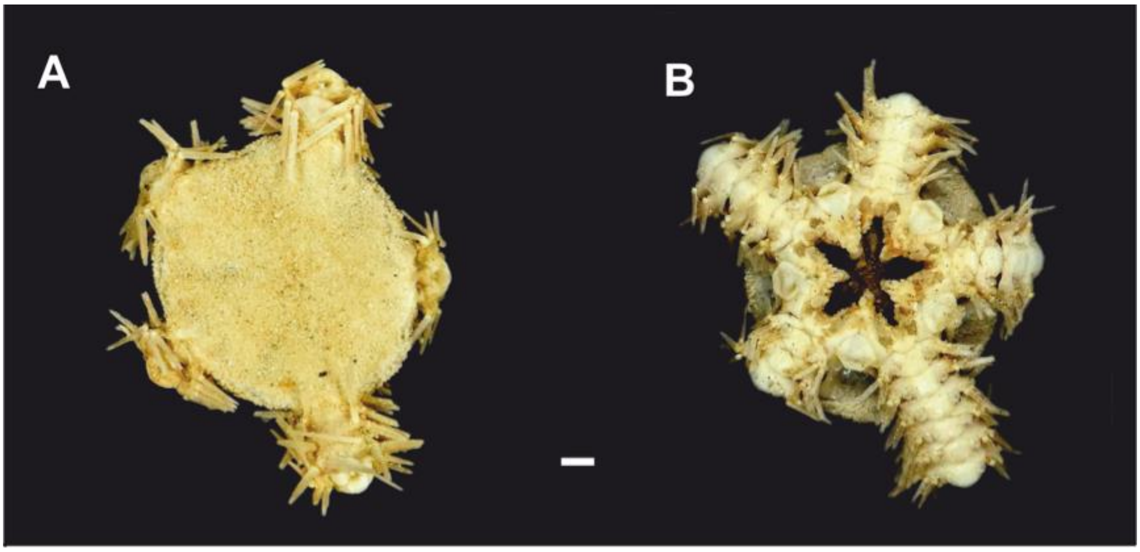


Figure 5.9. *Ophiotreta valenciennesi* (Lyman, 1879) (EMEPC G3D4Ma004). Dorsal view (A); ventral view (B); scale bar is 1 mm.

species in the synonymy of the Pacific species, *O. valenciennesi*. Re-examining material from the RVs ‘Princesse Alice’ and ‘Talisman’, Mortensen (1933a) believed that the Atlantic specimens belonged to a separate variety, retaining Koehler’s form ‘rufescens’ as a subspecies of *O. valenciennesi*. More recently, Stöhr & Segonzac (2005) recorded an animal belonging to this Atlantic subspecies on a block recovered in the area of the hydrothermal vents of Menez Gwen (‘DIVANAUT 1’, sta PL906–14: N37°49’36” W31°31’01”, 848 m). On a study on the New Caledonia brittle stars, Stöhr (2011) revoked the subspecific status of ‘*rufuscens*’, as the diagnostic morphological features were not exclusive of the Atlantic material.

The specimens documented herein agree with the original descriptions presented by Koehler (1896b) under the name of *Ophiacantha rufescens*. For the most part, the Azorean material is also in accordance with the observations by O’Hara & Stöhr (2006) on *O. valenciennesi*. The only conspicuous difference is the presence of small spines at the distal margin of the dorsal arm plates in the Indo-Pacific material. Koehler (1914a) commented that some of the specimens of *O. valenciennesi* collected by RV ‘Albatross’ in Cuban waters also presented this feature. Still, as a rule, the form ‘*rufescens*’ documented in the Atlantic or Mediterranean Sea presents a smooth distal edge of the dorsal plates (*e.g.,* Paterson 1985; Mifsud *et al*. 2009; Borrero-Pérez *et al*. 2008), which agrees with our material. In contrast, Paterson (1985) reported that this subspecies has 7 to 8 arm spines, which clearly contrasts with our observations and with Koehler's (1896b) original description, placing the Azorean material somewhat closer to the typical '*valenciennesi*'. A reduced number of arms spines was also reported in the Columbian specimens by Borrero-Pérez *et al*. (2008).

Ophiotreta valenciennesi was also reported from the archipelago of Cabo Verde (*e.g.,* Koehler 1909; Mortensen 1927a; Nobre 1938). However, such records seem to be based directly or indirectly on the material collected by RV 'Talisman'. At the time, Koehler (1906b) reported the location of the stations using a system of coordinates based on the Paris Meridian. On converting the longitudes to the Greenwich Meridian, it is clear that the reported material came from waters off the coast of NW Africa, outside Cabo Verde waters. It is likely that Paterson's (1985) account of 'off Madeira' as the NE Atlantic geographical limit of *O. valenciennesi* is a result of a misprint. The author most probably have meant to refer to the archipelago of the Azores.

Order Ophioleucida O'Hara *et al*. 2017

Family Ophiernidae O'Hara *et al*. 2017

Genus *Ophiernus* Lyman, 1878

Ophiernus vallincola **Lyman, 1878**

$^{\$}$1878. *Ophiernus vallincola* sp. nov.; Lyman: 122–123, pl. 6, figs. 170–175.

$^{\$}$1882. *Ophiernus vallincola* Lym.; Lyman: 32–33, pl. 24, figs. 16–18, pl. 38, figs. 6–9.

1896b. *Ophiernus abyssalis* nov. sp.; Koehler: 242–243.

$^{\$}$1909. *Ophiernus abyssalis*, Kœhler; Koehler: 143–145, pl. 28, figs. 3, 4.

1927a. *Ophiernus abyssalis* Koehler; Mortensen: 228.

1927a. *Ophiernus vallincola* Lym.; Mortensen: 228.

1977. *Ophiernus vallincola* Lyman; Madsen: 112–114, fig. 2.

$^{\$}$1985. *Ophiernus vallincola* Lyman, 1878; Paterson: 98–99, fig. 40.

2005. *Ophiernus vallincola* Lyman, 1878; García-Diez *et al*.: 49.

2014. *Ophiernus vallincola* Lyman, 1878; Smirnov *et al*.: 207–208.

Type locality: Azores (N37°24' W25°13').

See: Lyman (1878); Madsen (1977); Paterson (1985); Martynov & Litvinova (2008: 83, fig. 3D).

Distribution: cosmopolitan, present in the Pacific, Indian, Atlantic and Southern (Antarctica) oceans; in the Atlantic from the Reykjanes Ridge area (S of Iceland) and the British Isles to Southern African waters, including the archipelagos of the Azores and Madeira.

Depth: 840–4,065 m (AZO: 1,732–1,919 m).

Habitat: soft bottoms, muddy sand to ooze.

Remarks: Lyman (1878, 1882) described a new species *Ophiernus vallincola* based on material collected by RV 'H.M.S. Challenger' selecting a specimen taken in Azores waters as the type. The only other material of this species from the archipelago was reported by Koehler (1909, as *Ophiernus abyssalis*), collected by RV 'Princesse Alice' at several stations.

Order Ophioscolecida O'Hara *et al*., 2017

Family Ophiohelidae Perrier, 1893

Genus *Ophiomyces* Lyman, 1869

Ophiomyces frutectosus Lyman, 1869

$^{\$}$1872. *Ophiomyces frutectosus* Lym.; Ljungman: 621.

1888. *Ophyomyces frutectosus* Lyman; Barrois: 32.

1927a. *Ophiomyces frutectosus* Lyman; Mortensen: 183.

Type locality: off Sand Key (Florida).

See: Lyman (1869: 345–347; 1883: 243); Paterson (1985: 75, fig. 31); Borges *et al*. (2002: 17, fdigs. 8a, b).

Distribution: a Caribbean species, also reported from southern Brazil, the Azores and the Josephine Seamount.

Depth: 50–1,098 m (AZO: 585–1,098 m).

Habitat: soft substrates.

Remarks: on describing *Ophiomyces frutectosus*, Lyman (1869) remarked that he also found two specimens belonging to this species among the material collected by the 'Josephine' cruise in the Josephine Seamount. Later, Ljungman (1872) reported material of this species collected in São Miguel Island (Azores) by RV 'Josephine', at depths (585–1,098 m) well below the species' normal bathymetrical range (141–527 m).

Family Ophioscolecidae Lütken, 1869

Genus *Ophiogeron* Lyman, 1878

Ophiogeron granulatus? (Lyman, 1883)

?$^{\$}$1882. *Ophiogeron edentulus*, Lym.; Lyman: 237, pl. 12, figs. 16–18.

?$^{\$}$1909. *Astrogeron supinus*, (Lyman); Koehler: 199, pl. 29, fig. 7.

1927a. *Astrogeron supinus* (Lyman); Mortensen: 167.

2005. *Astrogeron supinus* (Lyman, 1883); García-Diez *et al*.: 48.

Type locality: Martinique (Caribbean Sea).

See: Lyman (1883: 269–270, as *Ophiosciasma granulatum*); Koehler (1914a: 162, as *Ophiosciasma granulatum*; 162, as *Ophiogeron supinus*); Clark (1941: 70–71).

Distribution: West Atlantic; restricted to the Gulf of Mexico and Caribbean waters, but possibly extending to the Azores.

Depth: 95–511 m in the West Atlantic (?AZO: 1,250–1,647 m).

Habitat: soft bottoms (ooze) with coral and broken shells.

Remarks: Lyman (1878) described *Ophiogeron edentulus* based on the material collected by RV 'H.M.S. Challenger' at a station located in South Pacific waters. Later, Lyman (1882) added material from another RV 'H.M.S. Challenger' station to this species, now located in the Azores (sta 76: N38°11' W27°09', 1,647 m). Mortensen (1927a) believed that the material from this Atlantic station belonged most probably to the Caribbean species *O. granulatus* (= *Astrogeron supinus*). The report of this West Atlantic species in the Azores by Koehler (1909) appears to support this supposition. Furthermore, the present knowledge of *O. edentulus* is still limited to the type material. In view of this, we are inclined to agree with Mortensen and consider *O. edentulus* as restricted to the Pacific waters and thus, tentatively regard Lyman's record of *O. edentulus* as misidentification. On the other hand, the record of *Ophiogeron granulatus* (= *Astrogeron supinus*) in the Azores by Koehler (1909) was based on a small and poorly preserved specimen collected by RV 'Princesse Alice' (sta 1349: N38°35'30" W28°05'45", 1,250 m) at a depth below the normal range for this species. Overall, both 'H.M.S. Challenger' and RV 'Princesse Alice' reports place this species outside its normal geographical and bathymetric range. Thus, the identity of the Azorean material with *Ophiogeron granulatus* should be viewed with caution until new material collected in area can confirm the historical reports.

Genus *Ophiophrura* Clark, 1911b

Ophiophrura tripapillata (Stöhr & Segonzac, 2005)

$^{\$}$2005. *Ophioscolex tripapillatus* sp. nov.; Stöhr & Segonzac: 4722.3–4722.7, fig. 3.

Type locality: Near Menez Gwen, Mid-Atlantic Ridge, Azores (N37°50'56" W31°30'40").

See: Stöhr & Segonzac (2005).

Distribution: Northeast Atlantic, known only from the Azores, the Bay of Biscay, and Iceland.

Depth: 1,015–1,500 m (AZO: 1,015 m).

Habitat: hard substrates (oxidized basalt), with other benthic fauna (*e.g.,* sponges, bryozoans, brachiopods and tunicates).

Remarks: Stöhr & Segonzac (2005) described *Ophioscolex tripapillatus*, based on a specimen collected in the vicinity of Menez Gwen, southwest of the Azores. This species is known only from 5 specimens, collected from widely separated localities.

Order Ophiurida Müller & Troschel, 1840a *sensu* O'Hara et al., 2017

Genus *Anthophiura* Clark, 1911b

Anthophiura ingolfi? Fasmer, 1930

?$^{\$}$1896b. *Ophioglypha minuta* Lyman; Koehler: 242.

? $^{\$}$1909. *Ophioglypha minuta*, Lyman; Koehler: 152–153.

2005. *Aspidophiura minuta* (Lyman, 1878); García-Diez *et al*.: 49.

Type locality: Between Greenland and Iceland (N64°34’ W31°12’).

See: Fasmer (1930: 4–7, figs. 3–5); Vadon & Guille (1984: 593–595, figs. 1A–B, pl. 4, figs. 4–6); Paterson (1985: 140, fig. 53); Améziane (2007: 347).

Distribution: North Atlantic, between Greenland and Iceland south to the Bay of Biscay and the ?Azores; reported also from Reunion Island (Indian Ocean) and New Caledonia (SW Pacific Ocean).

Depth: 1,175–2,862 (?4,020) m (AZO: ?4,020 m).

Habitat: soft bottoms (detreictic mud).

Remarks: Koehler (1909) identified two individuals collected by RV ‘Princesse Alice’ in the Azores as *Anthophiura minuta* (= *Ophioglypha minuta*) (sta 527: N38°09’00” W23°15’45”, 4,020 m). However, he added that the Azorean specimens were different from Lyman’s (1878) type material collected by RV ‘H.M.S. Challenger’ half way between the Antarctic and Australian waters, but identical to the RV ‘Caudan’ animals from the Bay of Biscay (Koehler 1895c, 1896c). Additionally, Koehler (1909) remarked on the very simple structure that characterises the material collected by the RVs ‘H.M.S. Challenger’, ‘Caudan’ and ‘Princesse Alice’, possibly juveniles belonging to two different species. Later, Fasmer (1930) believed that these animals belonged to his newly described species, *Anthophiura ingolfi* based on the description of the disc scaling, an opinion shared by later authors (*e.g.,* Mortensen 1933a; Paterson 1985). However, Fasmer remarked Koehler's material was lost and without its re-examination the presence of *A. ingolfi* in the Azores and the Bay of Biscay could not be confirmed. Paterson (1985) was able to confidently expand the geographical range of Fasmer's species to the Bay of Biscay, based on the material collected by the oceanographic mission 'Biogas'. Thus, and in spite of the absence of confirmed records, we have transferred the Azorean specimens from *A. minuta* (a strictly Pacific species) was transferred to *A*. *ingolfi,* following Fasmer (1930) and Paterson (1985).

Family Astrophiuridae Sladen, 1879
Genus *Ophiophycis* Koehler, 1901

Ophiophycis mirabilis **Koehler, 1901**

(Fig. 5.10)

$^{\$}$1901. *Ophiophycis mirabilis*, nov. sp.; Koehler: 222–225, figs. 1, 2.
$^{\$}$1909. *Ophiophycis mirabilis*, Kœhler; Koehler: 163–164, pl. 26, figs. 3–4.
1927a. *Ophiophycis mirabilis* Koehler; Mortensen: 229.
1969. *Ophiophycis mirabilis*; Cherbonnier: 348.
1972. *Ophiophycis mirabilis* Koehler; Cherbonnier & Sibuet: 419.
1985. *Ophiophycis mirabilis* Koehler, 1901b; Paterson: 141–142, fig. 54.
2005. *Ophiophycis mirabilis* Koehler, 1901; García-Diez *et al*.: 49.
2014. *Ophiophycis mirabilis* Koehler, 1901; Smirnov *et al*.: 203.

Type locality: Azores (N38°26'00" W26°30'45").

See: Koehler (1901); Paterson (1985); Tyler & Zibrowius (1992: 222–223); Martynov & Litvinova (2008: 82, fig. 3A).

Distribution: Northeast Atlantic, from Reykjanes Ridge (South of Iceland) south in the Bay of Biscay and off Portugal, in the Josephine Bank area to the Azores.

Depth: 810–2,150 (?2,871) m (AZO: 1,131–1,201 m).

Habitat: hard substrate and on corals.

Material examined: EMEPC G3D3A Ma004 (Southeast of TER, AZO, N37°56'15" W26°49'00", 2007.05.18, 1,131–1,201 m; 4 spms, D=4–5 mm)

Description: disc pentagonal, fringed spines (modified arm spines), dominated by a large star-shaped centrodorsal and primary radial plates; spines flat with tips of variable shape, from blunt almost square to more acute; a faint knob on the centrodorsal plate; radial shields somewhat tear-drop shaped (length > breadth), longer than half disc radius and contiguous along the mid-portion of the plate; a single row of two plates between each pair of radial shields, the proximal one rectangular and the distal one triangular to heart shaped. One pointed mouth papilla flanked on each side by two to four contiguous block-like papillae. Adoral shields narrow, longer than broad. Mouth shields small (length <1/2 disc radius) and pentagonal. Ventral inter-radial scales rectangular, elongated from the edge of the oral shield to the margin of the disc. None of specimens presented complete arms, either broken at the base or at the first two or three segments. First two dorsal arm plates contiguous and trapezoidal. Ventral arm plates separated; first ventral arm plate is approximately rectangular; subsequent plate somewhat more pentagonal with a straight proximal edge and a slight obtuse distal angle. Tentacle pores including the second oral tentacle pore with one small, round to oval, slightly pointed tentacle scale. Two to three flattened arm spines. Colour (dry) uniformly white.

Remarks: for the most part, the specimens herein described are in accordance with the description by Koehler (1901, 1909) and Paterson (1985). Nevertheless, according to the latter author, the absence of knobs on the dorsal disc and arm plates in *O. mirabilis* is one of the main differences between this species and the closely resembling *Ophiomisidium pulchellum* (Thomson, 1877). Our specimens presented faint knobs on the centrodorsal plates identical to what was figured by Martynov & Litvinova (2008: 82, fig. 3A). Conversely, on a redescription of *O. pulchellum* by Borges & Campos (2011), no such knobs are described. Apparently, the presence of knobs on the centrodorsal plate is variable and thus not diagnostic. Notwithstanding, according to Paterson (1985) the plate shape and arrangement in the ventral interradial area can also be used to distinguish *Ophiophycis mirabilis* from *Ophiomisidium pulchellum* or *Ophiomisidium speciosum* Koehler, 1914a. Our material as in *O. mirabilis*, there is a single large rectangular plate between the edge of the disc and the mouth plate, which contrasts with the sub-trapezoidal elongate plate described for the *Ophiomisidium* species.

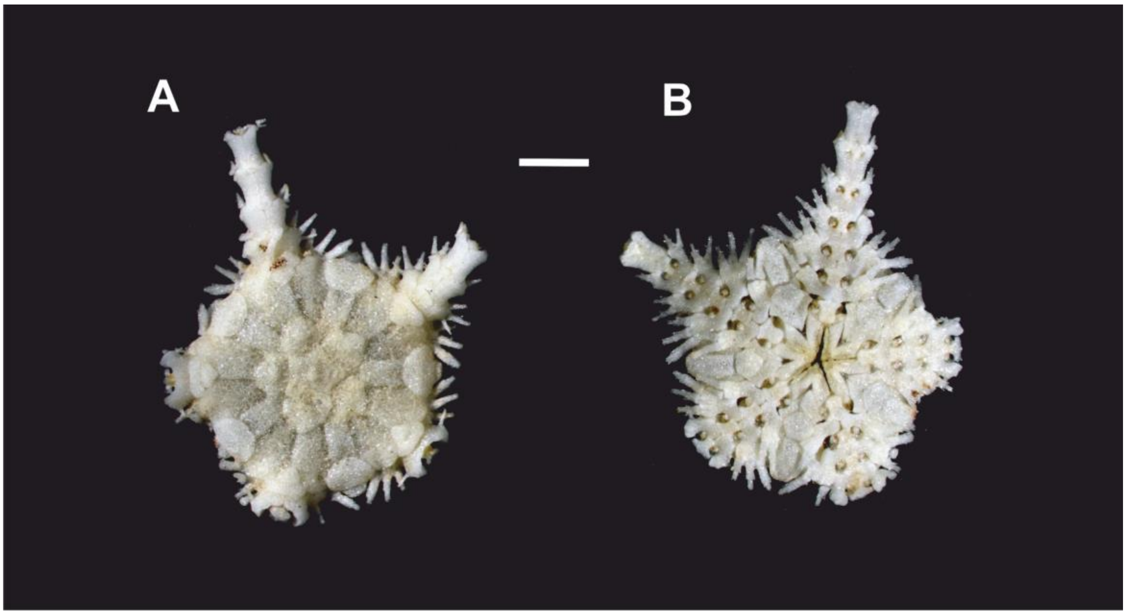


Figure 5.10. *Ophiophycis mirabilis* Koehler, 1901 (EMEPC G3D3A Ma004). Dorsal view (A); ventral view (B); scale bar is 1 mm**.**

Koehler (1901, 1909) described *Ophiophycis mirabilis* based on two specimens collected by RV ‘Princesse Alice’ in the Azores (sta 578: N38°26’00” W26°30’45”, 1,165 m). Later, this deep-water ophiuroid was reported from the Bay of Biscay (Cherbonnier 1969; Cherbonnier & Sibuet 1972; Paterson 1985) expanding the species’ geographical range to the continental European waters. More recently, Martynov & Litvinova (2008) found *O. mirabilis* on the Reykjanes Ridge, south of Iceland. Tyler & Zibrowius (1992) observed this species on hard substrates (using fissures in the rock) in steep slopes of the Porcupine deep-waters (SW Ireland) and they believed that this could be the reason why this species is rarely documented since this behaviour makes it very difficult to sample. Fortunately, the specimens examined here were recovered among the rock samples collected during a geological survey in the Azores deep-waters by EMEPC that helped to further confirm the presence of this species in the area.

Family Ophiopyrgidae Perrier, 1893

Genus *Amphiophiura* Matsumoto, 1915

Amphiophiura convexa **(Lyman, 1878)**

$^{\$}$1909. *Ophioglypha convexa*, Lyman; Koehler: 149–150, pl. 25, figs. 1–2.

1927a. *Amphiophiura convexa* (Lyman); Mortensen: 231.

1932. *Ophiura convexa* Lyman; Grieg: 32.

$^{\$}$1972. *Amphiophiura convexa* (Lyman); Cherbonnier & Sibuet: 408.

1985. *Amphiophiura bullata convexa* (Lyman, 1878); Paterson: 132–133, fig. 51.

2005. *Amphiophiura bullata convexa* (Lyman, 1878); García-Diez *et al*.: 49.

2008. *Amphiophiura convexa* (Lyman, 1878); Martynov & Litvinova: 81, fig. 2D.

2014. *Amphiophiura bullata convexa* (Lyman, 1878); Smirnov *et al*.: 201.

Type locality: E of Japan, Pacific.

See: Lyman (1878: 84, pl. 3, figs. 83–84, as *Ophioglypha convexa*); Paterson (1985).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian Oceans; in the west Atlantic from Labrador basin to off New England and in the East Atlantic, from Reykjanes Ridge south to the Bay of Biscay, Azores, Canaries and ?Madeira; also reported from Vema Fracture zone, off Central African coast (24°02'S 14°41'W) and Demerara Abyssal Plain, off northern South America.

Depth: 1,950–6,810 m (AZO: 3,665–4,261 m).

Habitat: soft bottoms (ooze).

Remarks: Koehler (1909, 1914a) remarked on the variability present in *Amphiophiura convexa* (= *Ophioglypha convexa*), which in certain aspects of its morphology resembles *A*. *bullata* (Thomson, 1877). Paterson (1985) based on the variability of the dorsal plating of the disc, assumed *A*. *convexa* to be a subspecies of *A*. *bullata*. Martynov & Litvinova (2008) disagreed and maintained the specific status, a view followed herein.

Jesus & Abreu (1998) reported an '*Amphiophiura* cf. *bullata convexa*' from Madeira shallow-waters, between 20 and 100 m. In the North Atlantic, the genus *Amphiophiura* includes strictly deep-water species that tend to live well below 1,000 m (Paterson 1985; Smirnov 2014). In light of this, we doubt that the material reported by Jesus & Abreu (1998) belongs to *A. convexa* or even the genus *Amphiophiura*.

Genus *Ophiopleura* Duncan, 1878

Ophiopleura inermis (Lyman, 1878)

$^{\$}$1921a. *Ophiura aurantiaca* Verrill; Koehler: 5.

1927a. *Ophiopleura aurantiaca* (Verrill); Mortensen: 251–252, fig. 137.

1933a. *Ophiopleura aurantiaca* (Verrill); Mortensen: 92–94, fig. 50.

1983. *Ophiopleura inermis* (Lyman, 1878); Gage *et al*.: 295.

1985. *Ophiopleura inermis* (Lyman, 1878); Paterson: 128, fig. 48.

2008. *Ophiopleura inermis* (Lyman, 1878); Martynov & Litvinova: 82–83, fig. 3B.

Type locality: Off Tristan da Cunha Island.

See: Lyman (1878: 95–96, pl. 5, figs. 123–125, as *Ophioglypha inermis*); Paterson (1985); Jesus & Abreu (1998: 63); Martynov & Litvinova (2008).

Distribution: Atlantic species, known from Greenland and Iceland south to off Martha's Vineyard (Massachusetts) in the west and to the Bay of Biscay, the Azores, Madeira and Canaries in the east; also found in the south of the Charlie-Gibbs Fracture Zone and off Tristan da Cunha.

Depth: 150–1,875 m (AZO: 1,740 m).

Habitat: hard to soft sediments.

Remarks: Koehler (1921a) reported the only specimen of *Ophiopleura aurantiaca* (as *Ophiura aurantiaca*) known from the Azores waters (RV 'Hirondelle II', sta 3150: N38°01' W25°21', 1,740 m), a species later found to be conspecific with *Ophiopleura inermis* (Mortensen 1933a; Gage *et al*. 1983).

Genus *Ophioplinthus* Lyman, 1878

Ophioplinthus inornata (Lyman, 1878)

$^{\$}$1906b. *Ophioglypha inornata* Lyman; Koehler: 262–263
1927a. *Homalophiura inornata* (Lym.); Mortensen: 231.
$^{\$}$1948. *Ophiura inornata* (Lyman); Clark: 78.
1985. *Ophiurolepis inornata* (Lyman, 1878); Paterson: 138–139, fig. 53.
2014. *Ophiurolepis inornata* (Lyman, 1878); Smirnov *et al*.: 206.

Type locality: off S. Paulo Rocks (N1°47' W24°26').

See: Lyman (1878: 97, pl. 2, figs. 26–27); Mortensen (1936: 329); Paterson (1985); Martynov & Litvinova (2008: 85–7, figs. 6G).

Distribution: cosmopolitan, recorded in the Pacific, Indian, Atlantic and Southern oceans; in the Atlantic from South America, Falkland Islands, Caribbean, Saint Paul Rocks, eastwards to off Cape Blanc (NW Africa), including the Azores.

Depth: 242–3,385 m (AZO: 2,995–3,200 m).

Habitat: soft sediments (*Globigerina* ooze).

Development: non-brooding, direct or lecithotrophic development.

Remarks: the presence of *O. inornata* in the Azores was first reported by Koehler (1906b; 'Talisman', sta 131, 1883: N38°28', W25°05'46", 2995 m). Later, Clark (1948) also identified material belonging to this species from the Azores, but referred to it as from west of Gibraltar (‘Atlantis’ sta 15: N35°37', W30°51'; 3,200 m).

Ophioplinthus pseudotessellata Martynov & Litvinova, 2008

$^{\$}$2008. *Ophioplinthus pseudotessellata* sp. nov.; Martynov & Litvinova: 89–90, figs. 4B, D, 5D–G.

Type locality: North of the Azores (N42°55’ W30°20’).

See: Martynov & Litvinova (2008).

Distribution: known only from the type locality, in the Mid-Atlantic Ridge north of the Azores.

Depth: AZO: 2,954–2,968 m.

Remarks: *Ophioplinthus pseudotessellata* is only known by type collected at the north border of the Azorean waters.

Ophioplinthus tessellata (Verrill, 1894)

$^{\$}$1896a. *Ophioglypha tessellata* Verrill; Koehler: 203–204.

$^{\$}$1898. *Ophioglypha tessellata*, Verrill; Koehler: 37–40, pl. 7, figs. 34, 36.

$^{\$}$1909. *Ophioglypha tessellata*, Verrill; Koehler: 156–157, pl. 25, figs. 12–13, pl. 27, figs. 5–6.

1927a. *Homalophiura tesselata* (Verrill); Mortensen: 231.

1932. *Ophiura tessellata* Verrill; Grieg: 33.

1933a. *Homalophiura tesselata* (Verrill); Mortensen: 91–92, pl. 3, fig. 17.

$^{\$}$1972. *Homalophiura tesselata* (Verrill); Cherbonnier & Sibuet: 408–409.

1985. *Homophiura tessellata* (Verrill, 1894) n. comb; Paterson: 137–138, fig. 52.

2005. *Homophiura tessellata* (Verrill, 1894); García-Diez *et al*.: 49.

2008. *Ophioplinthus tessellata* (Verrill, 1894) comb. nov.; Martynov & Litvinova: 83–88, figs. 4A,C, 5A–C.

2014. *Homophiura tessellata* (Verrill, 1894); Smirnov *et al*.: 202.

Type locality: east coast of North America, between N39°35’ and N41°47’.

See: Verrill (1894: 290–293, as *Ophioglypha tessellata*); Paterson (1985); Martynov & Litvinova (2008).

Distribution: North Atlantic, from Greenland to south of Block Island (off the coast of Rhode Island), eastwards from south of Iceland, in European waters south to Cabo Verde, and along the Mid-Atlantic Ridge south to the Azores.

Depth: 433–4,706 m (AZO: 1,919–2,870 m).

Habitat: soft substrates.

Type of Development: lecithotrophic.

Remarks: Koehler (1906b, 1909) reported *O. tessellata* in the Azores ('Talisman', sta 248: N41°40'41", W26°44'09", 2870 m; 'Princesse Alice', sta 738: N37°40', W26°26'15", 1919 m). Later, Cherbonnier & Sibuet (1977) also recorded this relatively large species in the area (*Noratlante*, sta P65B10: N36°58'02", W26°20', 2870 m). No other material was reported in the Azores.

Family Ophiosphalmidae O'Hara *et al*. 2018

Genus *Ophiomusium* Lyman, 1869

Ophiomusium lymani **Thomson, 1873**

$1878. *Ophiomusium Lymani* Wyv. Thom.; Lyman: 113.
$1882. *Ophiomusium lymani*, Wyv. Thom.; Lyman: 90.
$1896a. *Ophiomusium lymani* Wyville-Thomson; Koehler: 204.
$1898. *Ophiomusium Lymani*, Wyville Thomson; Koehler: 42.
$1906b. *Ophiomusium Lymani* Wyville Thomson; Koehler: 264–265.
$1909. *Ophiomusium Lymani*, Wyville Thomson; Koehler: 161, pl. 3, fig. 4, pl. 4, fig. 1.
$1921a. *Ophiomusium Lymani* Wyville Thomson; Koehler: 3.
$1972. *Ophiomusium lymani* W. Thomson, 1873; Sibuet: 122.
$1985. *Ophiomusium lymani* Wyville Thomson, 1873; Paterson: 147–148, fig. 58.
1992. *Ophiomusium lymani*; Pérès: 254, 255, 257, 258.
2005. *Ophiomusium lymani* Wyville Thomson, 1873; García-Diez *et al*.: 49.

Type locality: Rockall Trough, off SW of Ireland.

See: Gage & Tyler (1982); Gage *et al.* (1983: 299–300); Paterson (1985).

Distribution: cosmopolitan, recorded in the Atlantic, Pacific and Indian Oceans; in the Atlantic from the Davis Strait to Caribbean waters, eastwards from Iceland to southern Namibia, including the Azores, Canaries and Tristan da Cunha.

Depth: 651–4,829 m (AZO: 1,384–3,300 m).

Habitat: soft sediments, clay, mud to ooze; an opportunistic scavenger or carnivore that moves over or nestles into the sediment surface without burrowing; an opportunistic scavenger or carnivore.

Type of Development: lecithotrophic.

Remarks: *Ophiomusium lymani* was reported by almost every historical oceanographic expedition made in the Azores waters (*e.g.,* RVs 'H.M.S. Challenger', 'Hirondelle', RV 'Princesse Alice'). This recurrence agrees with Pérès (1992), who commented that this species appears to be quite abundant in the Azores at depths of between 2,000 and 3,300 m.

Genus *Ophiosphalma* Clark, 1941

***Ophiosphalma armigerum* (Lyman, 1878)**

$1896b. *Ophiomusium planum* Lyman; Koehler: 242.

$1906b. *Ophiomusium planum* Lyman; Koehler: 265–266.

$1909. *Ophiomusium planum*, Lyman; Koehler: 162, pl. 29, figs. 11.

1927a. *Ophiomusium planum* Lyman; Mortensen: 252.

1932. *Ophiomusium planum* Lyman; Grieg: 36.

1938. *Ophiomusium planum* Lyman; Nobre: 145.

$1948. *Opiomusium armigerum* Lyman; Clark: 78.

$1972. *Ophiosphalma armigerum* (Lyman); Cherbonnier & Sibuet: 416.

2005. *Ophiosphalma planum* (Lyman, 1878); García-Diez *et al*.: 49.

Type locality: between Tristan da Cunha and South American continent (S37°29’, W27°31’).

See: Lyman (1878: 108, 109–110, pl. 1, figs. 21–22, as *Ophiomusium armigerum*); Paterson (1985: 149, fig. 58).

Distribution: Atlantic, East coast of United States from off Virginia to the Caribbean Sea and Gulf of Mexico, south to off South America, in the East Atlantic known from the Bay of Biscay to NW Africa, including the Azores, Madeira and Canaries.

Depth: 260–5,110 m, mainly found from 3,000–5,000 m (AZO: 2,870–5,005 m).

Habitat: soft sediments, clay, mud to ooze.

Remarks: the species *Ophiomusium planum* was reported from the Azores by Koehler (1896b, 1906b, 1909) and Cherbonnier & Sibuet (1972), based on material collected by RVs ‘Princesse Alice’, ‘Talisman’ and ‘Noratlante’. Clark (1948) reported *Opiomusium armigerum* collected by RV ‘Atlantis’ in the archipelago. Paterson (1985) found these species to be conspecific and established the synonymy, with *O. armigerum* having the priority.

Family Ophiuridae Müller & Troschel, 1840a

Genus *Ophiocten* Lütken, 1855

***Ophiocten affinis*? (Lütken, 1858)**

?$1888. *Ophioglypha affinis* Lym.; Simroth: 231.

1997. *Ophiura affinis* (Lütken 1858); Pereira: 333.

2010. *Ophiocten affinis* (Lütken, 1858); Micael & Costa: 322.

2012. *Ophiocten affinis* (Lütken, 1858); Micael *et al*.: 3.

Type locality: Norway.

See: Lütken (1858: 45–46, pl. 2, figs. 10a–b, as *Ophiura affinis*); Mortensen (1927a: 244–245, figs. 132, as *Ophiura affinis*; 1936: 337, fig. 48b, as *Ophiocten amitinum* var. *simulans*); Grieg (1932: 33); Cherbonnier (1969: 348, as *Ophiura affinis*); Paterson (1982); Jesus & Abreu (1998: 63, as *Ophiura affinis*); Picton (1993: 52–53, as *Ophiura affinis*); Sumida *et al*. (1998: 282–285, 295–297, fig. 9); Theroux & Wigley (1998: 28, as *Ophiocten scutatum*).

Distribution: North Atlantic, from Nova Scotia and Newfoundland, eastwards from Iceland, Faroe, Scandinavian and British waters, along the European Shelf south to Cape Bojador, the ?Azores and Madeira; the subspecies *O. affinis simulans* can be found in South Africa.

Depth: 8–550 m (AZO:?).

Habitat: soft substrates, silt, sand, shingle to silt covered rocks.

Type of Development: lecithotrophic.

Remarks: the presence of *Ophiocten affinis* in the Azores is based on a single record by Simroth (1888). However, no additional information was given by the author and there is no trace where the specimen could be housed (or later reviewed). The presence of this species in the archipelago should be considered with caution, until new material collected in the area can corroborate this historical record.

***Ophiocten centobi* Paterson *et al*., 1982**

$2005. *Ophiocten centobi* Paterson, Tyler & Gage, 1982; Stöhr & Segonzac: 4722.12–13.

Type locality: Bay of Biscay (N47°44’ W08°21’).

See: Paterson *et al.* (1982: 119–121, figs. 6–7); Stöhr & Segonzac (2005).

Distribution: known only from the Bay of Biscay and in the vicinity of the deep-water hydrothermal systems on the Mid-Atlantic Ridge south of the Azores, such as Lucky Strike and Rainbow.

Depth: 1,680–2,837 m (AZO).

Habitat: coral and gravel detritic substrates (non-vent environments); also among mytilid bivalves, pteropod shells and *Cynachira* sponges.

Remarks: *Ophiocten centobi* was only known from the type material from the Bay of Biscay until Stöhr & Segonzac (2005) reported it from the vicinity of deep-sea hydrothermal vent fields in the Mid-Atlantic Ridge, south of the Azores.

Ophiocten hastatum Lyman, 1878

$^{\$}$1878. *Ophiocten hastatum* sp. nov.; Lyman: 103, pl. 5, figs. 133–134.

$^{\$}$1882. *Ophiocten hastatum*, Lym.; Lyman: 82–83, pl. 9, figs. 10–11.

$^{\$}$1896a. *Ophiocten longispinum* nov. sp.; Koehler: 204–205.

$^{\$}$1898. *Ophiocten hastatum* Lyman; Koehler: 42–44, 73, pl. 7, figs. 32, 33.

$^{\$}$1909. *Ophiocten hastatum*, Lyman; Koehler: 165.

1927a. *Ophiocten hastatum* Lyman; Mortensen: 246.

1982. *Ophiura hastata* (Lyman); Guille: 80, figs. 5, 6, 7a–b.

$^{\$}$1982. *Ophiocten hastatum* Lyman, 1878; Paterson *et al.*: 117–119, fig. 5.

1985. *Ophiocten hastatum* Lyman, 1878; Paterson: 129, fig. 49.

2004. *Ophiocten hastatum* Lyman 1878; Gage *et al.*: 849–864, figs. 1–84.

2005. *Ophiocten hastatum* Lyman, 1878; García-Diez *et al.*: 49.

$^{\$}$2008. *Ophiocten hastatum* Lyman, 1878; Martynov & Litvinova: 83, fig. 3C.

2014. *Ophiocten hastatum* Lyman, 1878; Smirnov *et al.*: 202–203.

Type locality: off Marion Island, Southern Ocean (S46°46' E45°31').

See: Lyman (1878); Paterson *et al.* (1982); Guille (1982); Gage *et al.* (2004); Martynov & Litvinova (2008).

Distribution: cosmopolitan, found in the Atlantic, Southern, and Pacific Oceans; in the Atlantic from Labrador basin east in the Rockall Trough south to the Bay of Biscay, including the Mid-Atlantic Ridge from Reykjanes Ridge south to the Azores; with exception of the reports for the Labrador Basin, all other records for the West Atlantic are misidentifications of *O. gracilis*.

Depth: 843–4,700 m (AZO: 1,830–2,107 m).

Habitat: soft bottoms, muddy sand to ooze; opportunistic.

Type of Development: planktotrophic.

Remarks: Lyman (1878, 1882) described *Ophiocten hastatum* on the basis of material taken by RV 'H.M.S. Challenger' in Southern Ocean deep-waters. Lyman (1878, 1882) also found two specimens of this species among the material collected by the same cruise in Azorean waters (sta 78: N37°24' W25°13', 1,830 m). On a preliminary report, Koehler (1896a) described a new species *Ophiocten longispinum* from the material collected by RV 'Hirondelle' in the Azores (sta 184: N40°05' W27°27'46", 1,850 m).

Later, Koehler (1898) recanted his previous identification, changing it to *O. hastatum* and completed Lyman's original description of this species using RV 'Hirondelle' material from the archipelago. Koehler (1909) also identified this species at several RV 'Princesse Alice' stations located inside Azorean waters. More recently, Martynov & Litvinova (2008) identified this species in Azorean northern waters (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 42/368: N42°48' W29°38', 2,063–2,107 m).

Genus *Ophioctenella* Tyler *et al.*, 1995

Ophioctenella acies **Tyler *et al.*, 1995**

$^{\$}$2005. *Ophioctenella acies* Tyler *et al.* 1995; Stöhr & Segonzac: 4722.13–14, figs. 2, 7.

Type locality: Mid-Atlantic Ridge.

See: Tyler *et al.* (1995); Stöhr & Segonzac (2005); Desbruyères *et al.* (2006: 483, figs. 1–3).

Distribution: Atlantic, along the Mid-Atlantic Ridge from Lucky Strike (SW Azores) south to Snake Pit (N23°22' W44°56'), westwards from Blake Plateau and Florida Escarpment to south of Barbados.

Depth: 1,626–3,500 m, though it seems to reach higher densities at depths greater than 3,000 m (AZO: 1,626–1,727 m).

Habitat: restricted to chemosynthetic areas, found at hydrothermal vents and methane cold seeps, usually in association with deep sea mytilid beds.

Development: probable planktotrophic development.

Remarks: *Ophioctenella acies* appears to be the only echinoderm species restricted to active vent sites known to occur in the Azores. In one of the few echinoderm studies from deep-sea reducing environments in the North Atlantic, Stöhr & Segonzac (2005) identify several animals of *O. acies* from Lucky Strike, but found this species conspicuously absent from hydrothermal vents of Menez Gwen.

Genus *Ophiura* Lamarck, 1801

Ophiura albida **Forbes, 1839**

$^{\$}$1869. *Ophioglypha albida*; Lyman: 319.

$^{\$}$1872. *Ophioglypha albida* (Forbes); Ljungman: 620.

1888. *Ophioglypha albida* Forbes; Barrois: 32.

$^{\$}$1888. *Ophioglypha albida* Lyman; Barrois: 32, 72, 133.

$^{\$}$1915. *Ophiura albida* Forbes 1839; Clark: 318.

1927a. *Ophiura albida* Forbes; Mortensen: 239–240, figs. 128.5–6.

1938. *Ophiura albida* Forbes; Nobre: 91.

1965. *Ophiura albida* Forbes; Tortonese: 272–274, figs. 99B, 125.

1995. *Ophiura albida* Forbes; Moyse & Tyler: 673, fig. 12.6.

1997. *Ophiura albida* Forbes, 1839; Pereira: 332–333.

2010. *Ophiura albida* Forbes, 1839; Micael & Costa: 322.

2012. *Ophiura albida* Forbes, 1839; Micael *et al.*: 3.

Type locality: Irish waters.

See: Forbes (1839: 125–126, pl. 4, figs. 5–6); Mortensen (1927a); Tortonese (1965); Picton (1993: 52–53); Tyler *et al.* (2005: 189); Koukouras *et al.* (2007: 80).

Distribution: Mediterranean Sea and Northeast Atlantic; from Iceland to Portugal, including the Azores.

Depth: 2–1,030 m (AZO: 20–458 m).

Habitat: gravel, muddy sand or on silty areas between rocks.

Type of Development: planktotrophic.

Remarks: historically, *O*. *albida* is known in the Azores by relatively few records. It was first collected by *Josephine* expedition in Ponta Delgada (São Miguel Island) at 274–458 m depth. This material was examined by Lyman (1869), Ljungman (1872) and later by H.L. Clark (1915). Barrois (1888) also reported this species in the same area, but at much shallower depths, about 20 to 25 m. The scarcity of records could be explained by the species preferred habitat in the archipelago. This ophiuroid appears to live mainly on soft bottoms at depths between 20 and 458 m. Soft-bottom environments were extensively sampled by oceanographic cruises in the archipelago, but rarely at depths shallower than 500 m.

Ophiura imprudens (Koehler, 1906a)

$^{\$}$1906a. *Ophioglypha imprudens* nov. sp.; Koehler: 8–10, pl. 1, figs. 7–8.

$^{\$}$1906b. *Ophioglypha imprudens* Koehler; Koehler: 256–257, pl. 18, figs. 9–10.

1927a. *Ophiura imprudens* (Koehler); Mortensen: 234.

1983. *Ophiura imprudens* (Koehler, 1906); Gage *et al.*: 298.

$^{\$}$1985. *Ophiura (Ophiura) imprudens* (Koehler, 1906); Paterson: 117–118, fig. 42.

1998. *Ophiura (Ophiura) imprudens* (Koehler, 1906); Jesus & Abreu: 63.

Type locality: Azores (N38°23’00” W28°49’46”).

See: Paterson (1985); Jesus & Fonseca (1999: 347).

Distribution: Northeast Atlantic, known for the Azores, Madeira, Rockall Bank and Portuguese mainland.

Depth: 75–560 m (AZO: 560 m).

Habitat: soft bottoms, sandy gravel to muddy sediments.

Remarks: *Ophiura imprudens* is only known from the archipelago by the type specimen. See also remarks under *O. carnea* Lütken, 1858.

Ophiura ljungmani (Lyman, 1878)

$1878. *Ophioglypha lepida* sp. nov.; Lyman: 70–71, pl. 3, figs. 71–73.
$1882. *Ophioglypha lepida*, Lym.; Lyman: 43–44, pl. 4, figs. 1–3.
$1909. *Ophioglypha Ljungmanni*, Lyman; Koehler: 152.
$1909. *Ophioglypha Thouleti*, Kœhler; Koehler: 158–159, pl. 6, fig. 6; pl. 26, figs. 1–2.
$1921a. *Ophiura Ljungmanni* (Lyman); Koehler: 3.
1927a. *Ophiura lepida* (Lyman); Mortensen: 234.
1927a. *Ophiura Ljungmani* (Lyman); Mortensen: 240–242, fig. 130.
$1985. *Ophiura* (*Ophiura*) *ljungmani* (Lyman, 1878); Paterson: 118–120, fig. 44.
2002. *Ophiura ljungmani* (Lyman 1878); Borges *et al*.: 27–31, figs. 15a–c, 16a–f, 17a–d, 18a–c.
2005. *Ophiura ljungmani* (Lyman, 1878); García-Diez *et al*.: 49.
$2005. *Ophiura ljungmani* (Lyman, 1878); Stöhr & Segonzac: 4722.3
2008. *Ophiura ljungmani* Lyman, 1878; Hernández-Herrejon *et al.*: 101–102, figs. 3E–F.
$2008. *Ophiura ljungmani* (Lyman, 1878); Martynov & Litvinova: 80, fig. 1D.
2014. *Ophiura (Ophiura) ljungmani* (Lyman, 1878); Smirnov *et al*.: 205.

Type locality: Brazil (S09°07' W34°50').

See: Lyman (1882); Mortensen (1933a: 83–84); Paterson (1985); Borges *et al.* (2002).

Distribution: Atlantic, from Labrador Basin to Brazil, eastwards from Iceland to southern Africa, including the Azores, Madeira, Canaries and Ascension Island.

Depth: 101–6,398 m (AZO: 789–2,968 m).

Habitat: mainly soft bottoms, coralligenous sand, mud to ooze; can form large aggregations.

Type of Development: planktotrophic.

Remarks: *Ophiura ljungmani* was reported from the Azorean waters under three different names: *Ophioglypha lepida* by Lyman (1878, 1882; RV 'H.M.S. Challenger'), *Ophioglypha ljungmanni* by Koehler (1909, 1921a; RV 'Princesse Alice') and *Ophioglypha thouleti* by Koehler (1909, 1921a; RV 'Princesse Alice'). Later, Koehler

(1914a) found his species O. *thouleti* to be identical with Lyman's *O. ljungmanni*, but kept Lyman's *O. lepida* as a separate species. In turn, Mortensen (1933a) found the diagnosing characters that separate *O. lepida* from *O. ljungmani* negligible (mostly size/age dependent) and concluded that they are conspecific. Paterson (1985) re-examined the original material of *O. lepida* by Lyman, including a specimen collected in the Azorean waters (RV 'H.M.S. Challenger', sta 76: N38°11' W27°09', 1,646 m), further substantiating the synonymy.

***Ophiura saurura* (Verrill, 1894)**

$^{\$}$2008. *Ophiura saurura* (Verrill, 1894) comb. nov.; Martynov & Litvinova: 80–81, figs. 2A–C.

Type locality: off Georges Bank, NE America.

See: Verrill (1894: 288–290, as *Ophioglypha saurura*); Koehler (1898: 40–42, pl. 6, figs. 19–21, as *Ophioglypha aspera*); Paterson (1985: 134–135, fig. 50, as *Amphiophiura saurura*); Martynov & Litvinova (2008).

Distribution: North Atlantic, off Nantucket and Newfoundland, eastwards from south of Iceland to the Bay of Biscay, reported from the Reykjanes Ridge and from the Mid-Atlantic Ridge from the Charlie-Gibbs Fracture Zone to North of the Azores.

Depth: 844–2,979 m (AZO: 2,063–2,968 m).

Habitat: soft bottoms.

Remarks: *Ophiura saurura* was recently reported by Martynov & Litvinova (2008) from the material collected by RV 'G.O. Sars' ('MAR–ECO' expedition) at two stations located in the extreme north of the Azorean waters (N42°55'–N42°48' W30°20'–W29°38', 2,063–2,968 m), the species' southernmost known record.

Subgenus *Dictenophiura* Clark, 1923a

***Ophiura* (*Dictenophiura*) *carnea carnea* Lütken, 1858**

(Fig. 5.11)

$^{\$}$1909. *Ophioglypha carnea*, (Lütken); Koehler: 147–148.

1913. *Ophiura carnea* Ltk.; Farran: 29–30, figs. 2–3.

1927a. *Ophiura carnea* M. Sars; Mortensen: 243, figs. 131.3–4.

1965. *Dictenophiura carnea* (Lütk.); Tortonese: 267.

2005. *Ophiura carnea* (Lutken, 1858); García-Diez *et al.*: 49.

Type locality: Bergen, Norway.

See: Lütken (1858: 41, pl. 1, figs. 6a–b); Farran (1913); Pérès (1964: 19); Cherbonnier (1969: 345, 346, 1970: 1269); Madsen (1970: 233–234, fig. 46); Paterson (1985: 117, fig. 42); Copley *et al.* (1996: 553).

Distribution: Northeast Atlantic and Mediterranean Sea, from Reykjanes Ridge (south of Iceland), Scandinavia and Faeroe Islands to Senegal, including the Azores and ?Cabo Verde archipelagos and Gorringe Seamount; the subspecies O. *carnea skoogi* (Koehler, 1923) is known from tropical West Africa, from Dakar to Angola.

Depth: 14–2,857 m (AZO: 14–599 m).

Habitat: soft (mud, sand, gravel, detritic) to hard substrates.

Type of Development: planktotrophic.

Material examined: DBUA-ECH 065 (Vila Franca do Campo, SMG, AZO, *c.* N37°42'50" W25°25'58", 1991.08.03, 70–80 m; 4 spms, D=5–6 mm); DBUA-ECH 066 (Água d'Alto, SMG, AZO, *c.* N37°42'55" W25°28'27", 1991.07.30; 4 spms, D=5 mm); DBUA-ECH 068 (off Ribeira das Tainhas, Vila Franca do Campo, SMG, AZO, N37°42'16" W25°24'45", 2006.07.21, 72 m; 2 spms, D=3–4 mm); DBUA-ECH 134 (Vila Franca do Campo, SMG, AZO, N37°42'43" W25°21'33", 2006.07.26, 38 m; 4 spms, D=3–5 mm); DBUA-ECH 135 (Vila Franca do Campo, SMG, AZO, N37°41'39" W25°27'11", 2006.07.21, 95–121 m; 1 spm, D=4 mm); DBUA-ECH 136 (off Praia de Água d'Alto, SMG, AZO, N37°42'24" W25°28'59", 2006.07.26, 66 m; 2 spms, D=4–5 mm); DBUA-ECH 137 (off Ribeira das Tainhas, SMG, AZO, N37°41'57" W25°25'08", 2006.07.24, 144–198 m; 1 spm, D=6 mm); DBUA-ECH 332 (off Praia da Vinha da Areia, SMG, AZO, N37°42'15" W25°24'28", 2006.07.21, 14 m; 1 spm, D=4 mm); DBUA-ECH 333 (off Ponta Garça, SMG, AZO, N37°42'01" W25°23'07", 2006.09.05, 318 m; 1 spm, D=4 mm); DBUA-ECH 335 (off Vila Franca do Campo, SMG, AZO, N37°41'52" W25°23'13", 2006.07.21, 46–47 m; 1 spm, D=3 mm).

Description: disc round to subpentagonal, high with almost vertical sides; five short arms mostly broken off at the tip, about twice the D; disc scales rather coarse and naked, with distinct centrodorsal and primary plates. Radial shields rounded to almost teardrop-shaped in larger specimens (length > breadth), contiguous distally, about one third of the disc radius in length. Arm combs prominent, almost vertical, extending up towards the dorsal surface of the disc; outer comb with about 10 to 12 conical and slightly rounded spinelets; inner comb with smaller and pointed spinelets. Innermost dorsal plate with a distinct groove. One pointed apical papilla flanked on each side by one triangular and two block-like oral papillae. Adoral shields narrow, slightly curved in appearance. Oral shields rounded pentagonal somewhat elongated (length > breadth) about one third to one half of the disc radius, with an obtuse proximal angle and a convex distal edge. Genital papillae small, pointed. Second oral tentacle slit, with three to four rounded tentacle scales on each side increasing to five to six in the larger specimens (D = 6 mm). Dorsal arm plates fan-shaped, distal edge with a weak point, contiguous only on the first 2–3 proximal arm segments and swollen in profile. First ventral arm plate triangular to trapezoidal; subsequent plates become more rounded with an obtuse proximal angle and a rounded distal edge; they are separated from one another. First proximal tentacle pores large with one larger rounded tentacle scaleopposing one to two smaller ones; in largest specimens (D = 6 mm), one to two extra scales are also present, summing the total tentacle scales per pore to 4–5; the number of tentacle scales is reduced to one by the fourth proximal arm segment. Lateral arm plates swollen, with three relatively small arm spines of about the same size and evenly spaced, distally decreasing progressively in size. Colour (in ethanol): most specimens presented a more or less uniform white colour pattern, with dorsal side of the disc slightly darker with clear white radial shields; the original colour seems better preserved in one specimen (DBUA-ECH 332, Fig. 5.11), having the dorsal surface of the disc light brown and the arms banded light pink, white and light brown; ventral surface uniformly white or cream.

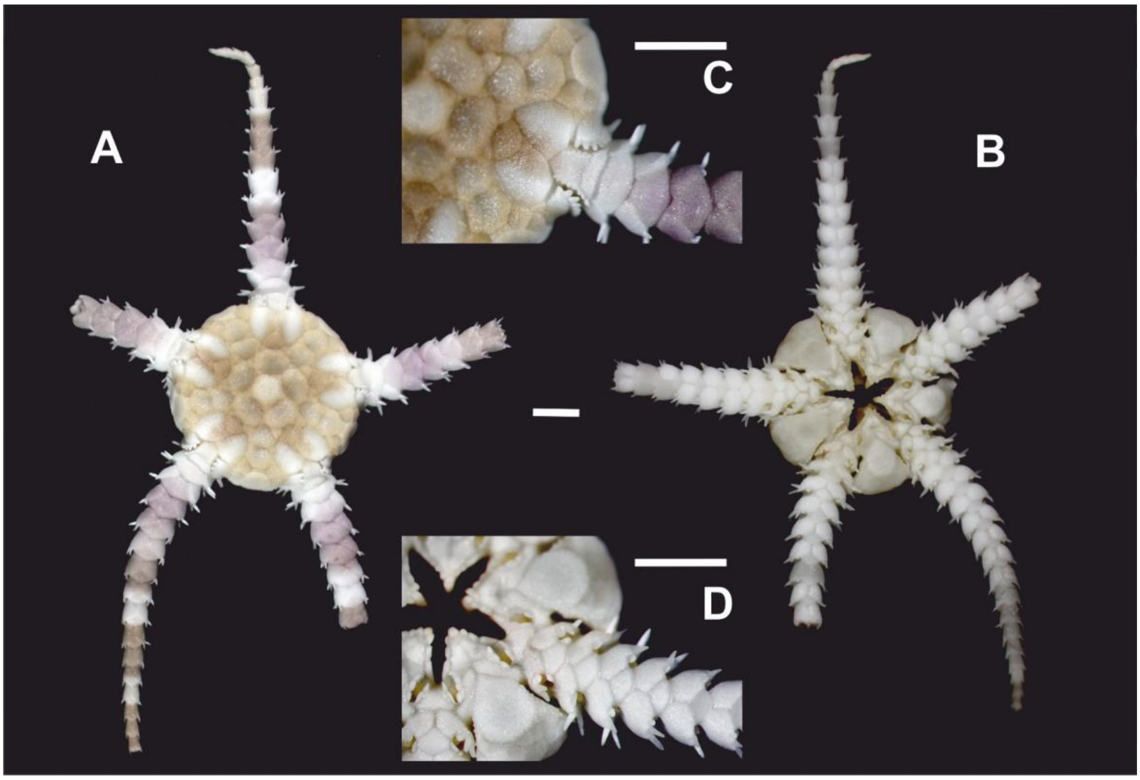


Figure 5.11. *Ophiura (Dictenophiura) carnea carnea* (DBUA-ECH 332). Dorsal view (A); ventral view (B); detail of the disc and arm, dorsal view (C) and ventral view (D); scale bars are 1 mm.

Remarks: the examined specimens share many diagnosing characters of *O. carnea*, distinct from the close resembling *O. albida* and *O. imprudens*: a thick almost vertical disc; comparatively small arms; well developed almost vertical arm combs; a distinct longitudinal furrow in the inner-most dorsal arm-plate; arm plates with overall swollen appearance; small rounded radial shields and somewhat longer oral shields. The examined specimens did not present the arm spines arranged as described by Paterson (1985) in *O. carnea* (*i.e.*, two adjacent to the tentacle pore and another towards the dorsal surface). However, this appears to be a variable character in this species, and animals of this species may present arm spines arranged in an evenly manner (*e.g.*, Koehler 1898, Mortensen 1927a, Glück *et al*. 2012). Previously, *O. carnea* was known in the Azores based on a single specimen collected by *Princesse Alice* (sta 866: N38°52’50”, W27°23’05”, 599 m; Koehler 1909).

Clark (1923a: 361) selected *O. carnea* as the genotype of *Dictenophiura*, a genus characterised by a longitudinal furrow dividing the inner-most dorsal plate. Madsen (1970: 234) downgraded *Dictenophiura* to a subgenus of *Ophiura*, on the basis that this is not a constant character in *O. carnea*, occasionally absent in larger specimens (see also Mortensen 1933a: 82). In view of this, we agree with Paterson (1985: 118, table 3), that this species closely resembles *O. imprudens*. In the absence of a medium furrow in the inner-most dorsal plate, *O. carnea* differs only slightly from *O. imprudens*: by the shape/size of the radial and mouth plates. Also, the arm combs in *O. imprudens* appear not to be prominent as in *O. carnea*. The former species is known by very little material, a total of seven reported specimens (Koehler 1906a, Gage *et al*. 1985). As more material becomes available, it will be necessary to re-address *O. imprudens* specific status in relation to *O. carnea*. Additionally, the subspecies African *O. carnea skoogi* is distinguished from *O. carnea carnea* by relatively more swollen dorsal and lateral arm plates (Mortensen 1936). We believe that our material belongs to the NE Atlantic variety despite the remarks by Madsen (1970: 234), who observed that *O. carnea skoogi* can only be diagnosed with certainty in fully grown animals (6–7 mm disc diameter).

Koehler (1923) included Cape Verde in the geographical distribution of *O. carnea*, which was repeated by subsequent references (*e.g.*, Koehler 1924, Mortensen 1927a, 1936, Tortonese 1965, Madsen 1970). We could not trace the original material on which Koehler (1923) based his record, though the occurrence of this species in Cape Verde is not unlikely considering the wide distribution of *O. carnea* in East Atlantic waters.

Subgenus *Ophiura* Lamarck, 1816

***Ophiura* (*Ophiura*) *mundata* (Koehler, 1906a)**

$^{\$}$1896b. *Ophioglypha irrorata* Lyman; Koehler: 241.

$^{\$}$1909. *Ophioglypha mundata*, Kœhler; Koehler: 153, pl. 27, figs. 7–8.

1933a. *Ophiura* (*Ophiuroglypha*) *mundata* Koehler; Mortensen: 88–89, figs. 48d–e, pl. 3, figs. 11–12.

1985. *Ophiura* (*Ophiura*) *mundata* (Koehler, 1906); Paterson: 127–128, fig. 48.

2005. *Ophiura mundata* Koehler, 1906; García-Diez *et al.*: 49.

2014. *Ophiura* (*Ophiura*) *mundata* (Koehler, 1906); Smirnov *et al.*: 205.

Type locality: waters between Canaries and NW Africa.

See: Koehler (1906a: 10–11, pl. 1, figs. 4–6, as *Ophioglypha mundata*); Paterson (1985).

Distribution: North Atlantic, from Labrador Basin eastwards to Iceland and south from the Bay of Biscay to Morocco, including the Azores and Canaries.

Depth: 1,674–4,315 m (AZO: 1,919–4,020 m).

Habitat: soft substrates.

Remarks: Koehler (1909) stated that his early identifications of *Ophiura irrorata* (Lyman, 1878) including the ones based on the material collected by RV ‘Princesse Alice’ in Azorean waters (Koehler 1896b) were in reality *O. mundata*. Later Koehler (1914a) considered the later species as conspecific with *O. irrorata*, a warm-temperate cosmopolitan species. At one time, Mortensen (1927a) also considered a junior synonymy of *O. irrorata*, an opinion that Mortensen (1933a) later revoked. In turn, Paterson (1985) commented on how *O. mundata* closely resembles *O. saurura* (Verrill, 1884) (= *Amphiophiura saurura*), suggesting that further studies should be carried out in order to determinate whether those forms were conspecific.

Subgenus *Ophiuroglypha* Hertz, 1927

***Ophiura* (*Ophiuroglypha*) *concreta* (Koehler, 1901)**

$^{\$}$1906b. *Ophioglypha concreta* Koehler; Koehler: 261.

1927a. *Ophiura concreta* (Koehler); Mortensen: 233.

1932. *Ophiura concreta* Koehler; Grieg: 32.

$^{\$}$1972. *Ophiura concreta* (Koehler); Cherbonnier & Sibuet: 414, 415.

?$^{\$}$2008. *Ophiura irrorata* (Lyman, 1878); Martynov & Litvinova: 79–80, fig. 1C.

Type locality: Cabo Verde (N14°47′ W24°31′45″).

See: Koehler (1901: 228–230, figs. 6–8; 1909: 148–149, pl. 25, figs. 3–5, as *Ophioglypha concreta*); Paterson (1985: 125, fig. 47, as *Ophiura irrorata concreta*).

Distribution: East Atlantic, from the Bay of Biscay south to Cabo Verde, and east to the Azores, reported as well off South African deep-waters.

Depth: 1,885–3,120 m (AZO: 2,845–2,995 m).

Habitat: soft substrates (muddy sand).

Remarks: Koehler (1901) described a new species *Ophioglypha concreta* based on a specimen collected by RV ‘Princesse Alice’ in Cabo Verde, and later identified a small specimen as belonging to the same species from the material collected by RV ‘Talisman’ in Azorean waters (sta 131, 1883: N38°38′ W25°5′46″, 2,995 m). On the re-examination of the type specimen of *O. concreta*, found *O. concreta* to be identical with *O. irrorata* in almost every aspect, ascribing no specific value to differences in the arrangement or number of arm spines. In view of this, Paterson proposed to demote this species to a subspecies of *O. irrorata* restricted to the East Atlantic. Nevertheless, he also noted that the distinct characters of *O. concreta* were constant over a wide range of sizes and geographical areas. In contrast, Martynov & Litvinova (2008) disputed the subspecific division of *O. irrorata*. According to them several subspecies should not live syntopically as in the case of *O. i. irrorata* and *O. i. concreta*, both known from the Bay of Biscay. Another example of co-existence can be found in Grieg (1932), who identified both forms in the material collected by RV ‘Michael Sars’ north of the Azores (sta 88: N45°26′ W25°45′, 3,120 m). However, Martynov & Litvinova (2008) were unsure if they represented two separate species or rather a single polymorphic species. In view of this, we have opted for a more conservative approach and maintain the historical species *O. concreta* separate from *O. irrorata*. Presently, *O. concreta* is known with certainty in the Azores only by historical records of Koehler (1906b; RV ‘Talisman’) and Cherbonnier & Sibuet (1972; ‘Noratlante’ cruise). See below remarks under *Ophiura irrorata*.

***Ophiura* (*Ophiuroglypha*) *irrorata*? (Lyman, 1878)**

1896b. *Ophioglypha irrorata* Lyman; Koehler: 241

1932. *Ophiura irrorata* Lyman; Grieg: 32.

?$2008. *Ophiura irrorata* (Lyman, 1878); Martynov & Litvinova: 79–80, fig. 1C.

Type locality: off South Africa.

See: Lyman (1878: 73–74, pl. 4, figs. 106–108, as *Ophioglypha irrorata*); Paterson (1985: 122–125, figs. 46–47, as *Ophiura irrorata irrorata*).

Distribution: cosmopolitan, in all oceans except Arctic; in the Atlantic from Cape Cod, eastwards from SW Iceland to NW Africa, including the Azores; reported elsewhere off South African deep-waters.

Depth: 403–7,340 m, most common at depths over 2,000 m (?AZO: 3,005–3,050 m).

Habitat: soft substrates (*e.g.,* ooze).

Remarks: the first report of *O. irrorata* from the archipelago was made by Koehler (1896b, as *Ophioglypha irrorata*), later changed to *O. mundata* (Koehler 1909). The report of *O. irrorata* by Grieg (1932) from the Azores was either based on the first report by Koehler (1896b) or by Mortensen (1927a) who at the time believed both species were conspecific (see remarks under *O. mundata*). More recently, Martynov & Litvinova (2008) identified a single specimen belonging to the species *O. irrorata* in the north of the Azores (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 46/372: N42°46' W29°16', 3,005–3,050 m). As Martynov & Litvinova disputed the subspecific status of *O. concreta* as a subspecies of *O. irrorata*, it is not clear whether the individual belonged to the *O. irrorata sensu stricto* or to *O. concreta*. *Ophiura irrorata* is cosmopolitan species and thus, likely to occur in the Azores deepwaters. However, taking into account the taxonomical background of this species, we considered its presence in the Azores as uncertain (see above remarks under *O. concreta* and *O. mundata*).

Class Asteroidea de Blainville, 1830

Order Velatida Perrier, 1884

Family Myxasteridae Perrier, 1885b

Genus *Pythonaster* Sladen, *in* Thomson & Murray, 1885

Pythonaster atlantidis Clark, 1948

$1948. *Pythonaster atlantidis* n. sp.; Clark: 76–77.

$1992. *Pythonaster atlantidis* A.H. Clark; Clark & Downey: 339.

$2012. *Pythonaster atlantidis* A.H. Clark 1948; Mah *et al.*: 60–61, figs. 3A–D.

2014. *Pythonaster atlantidis* A.H. Clark, 1948; Dilman: 37.

Type locality: Azores (N35°37' W30°51').

See: Clark (1948); Clark & Downey (1992); Mah *et al.* (2012).

Distribution: North Atlantic, from Hudson Canyon (N38°25' W70°52') east to the Porcupine Abyssal Plain (SW Ireland) and southern Azorean waters.

Depth: 2,976–4,877 m (AZO: 3,200 m).

Development: possibly direct development.

Remarks: Clark (1948) described a new species of *Pythonaster* based on a single specimen collected by RV 'Atlantis', at the border between the Azorean and Meteor Seamount waters (sta 15: N35°37', W30°51', 3,200 m). New records have shown that this species is more widespread in the North Atlantic, from Hudson Canyon, off the coast of New Jersey in the west (Mah *et al.* 2012) to the Porcupine Abyssal Plane, SW Ireland in the east (Howell *et al.* 2002).

Family Pterasteridae Perrier, 1875

Genus *Calyptraster* Sladen, 1882

Calyptraster personatus (Perrier, 1885c)

$^{\$}$1894. *Cryptaster personatus* sp. nov.; Perrier: 191, pl. 14, fig. 3.

1927a. *Cryptaster personatus* Perrier; Mortensen: 101.

1947. *Calyptraster personatus* (Perrier); Madsen: 3–7, figs. 1–2.

$^{\$}$1972. *Calyptraster personatus* (Perrier); Cherbonnier & Sibuet: 383.

1973. *Calyptraster personatus* (Perrier); Downey: 80, pl. 35, figs. C, D.

1975. *Calyptraster personatus* (Perrier); Sibuet: 108.

1979. *Calyptraster coa* Sladen, 1882; Walenkamp: 64–72, figs. 19, 23–25, pl. 14.

$^{\$}$1992. *Calyptraster personatus* (Perrier); Clark & Downey: 309–310, pl. 75, figs. C–D.

2014. *Calyptraster personatus* (Perrier, 1885); Dilman: 34.

Type locality: Azores (N38°38'00" W25°05'46").

See: Downey (1973); Clark & Downey (1992).

Distribution: Atlantic, in the west recorded to the Gulf of Mexico and Caribbean waters and in the east from the Gulf of Cadiz to the Gulf of Guinea, including the Azores.

Depth: 2,151–6,560 m (AZO: 2,871–2,995 m).

Habitat: soft sediments.

Remarks: Perrier (1894) described a monotypic genus *Cryptaster* to accommodate *C. personatus* from the Azores. Madsen (1947) believed that this species was conspecific with *Calyptraster coa* Sladen, 1882 from the south-east of Pernambuco (Brazil), distinguished only by a strongly musculated dorsal membrane. Madsen argued that the diagnosing characters selected by Sladen in the genus *Calyptraster* (which it was also monotypic at the time) had no generic value (and possible also no specific value) and established the synonymy with Perrier's genus *Cryptaster*. Nonetheless, Madsen kept *C. coa* and *C. personatus* separated, as he believed that further studies should be conducted before considering these as geographic varieties of the same species. Walenkamp (1979) compared Sladen' syntypes and his own specimens from Guyana with *C. personatus* specimens from Bay of Cadiz (Madsen 1947) and from Gulf of Guinea (Sibuet 1975) and found all to be identical. Walenkamp also assumed that the material reported from the Azores by Cherbonnier & Sibuet (1972; *Jean Charcot*, *Noratlante* cruise, sta P. 65, B10: N36°58'2", W26°20', 2,871 m) belonged to *C. coa*. On the re-examination of the type material of *C. personatus*, Clark & Downey (1992: 308) found Perrier's original description of this species misleading and reinstated the species status. Clark & Downey (1992) also commented on the apparent bathymetric partition between these species, as *C. coa* occurs at depths shallower than 1,000 m whereas *C. personatus* occurs at depths below 2,000 m. Thus, the report of the western *C. coa* to the Azores is erroneous.

Genus *Hymenaster* Thomson, 1873

Hymenaster anomalus Sladen, 1882

$^{\$}$2008. *Hymenaster anomalus* Sladen, 1882; Dilman: 141.

Type locality: Mid-Atlantic Ridge, North of Tristan da Cunha (S32°24' W13°05').

See: Sladen (1889: 512–514, pl. 89, figs. 3–4, pl. 91, figs. 4–6); Downey (1973: 75, pl. 32: figs. A–B); Clark & Downey (1992: 315–316, figs. 49a–c, pl. 76, figs. C–D).

Distribution: Western Atlantic, known from Straits of Florida, Gulf of Mexico and Tristan da Cunha, also from the Mid-Atlantic Ridge north of the Azores.

Depth: 1,984–3,050 m (AZO: 2,954–3,050 m).

Habitat: soft sediments (pteropod ooze).

Remarks: the West Atlantic *Hymenaster anomalus* was recently recorded from northern Azorean waters by Dilman (2008), expanding its geographical range to the Mid-Atlantic Ridge northwest waters.

Hymenaster giboryi Perrier, 1894

$^{\$}$1909. *Hymenaster Giboryi*, Perrier; Koehler: 93, pl. 1, figs. 2–3.

1927a. *Hymenaster Giboryi* Perrier; Mortensen: 106.

1972. *Hymenaster giboryi* Perrier, 1894; Cherbonnier & Sibuet: 381–382.

1976. *Hymenaster giboryi* Perrier, 1894; Sibuet: 298.

1992. *Hymenaster giboryi* Perrier; Clark & Downey: 316–317 figs. 51f–h.

2005. *Hymenaster giboryi* Perrier, 1894; García-Diez *et al.*: 47.

2014. *Hymenaster giboryi* Perrier, 1885; Dilman: 35.

Type locality: between the Azores and Portugal (N42°19’00” W21°15’46”).

See: Perrier (1894: 189–190, pl. 14, fig. 1); Clark & Downey (1992).

Distribution: North Atlantic, from off Newfoundland, southwards to off Jamaica and eastwards to Rockall Trough and to waters between Azores and Iberian Peninsula.

Depth: 1,919–4,275 m (AZO: 1,919–4,261 m).

Habitat: soft substrates, mud or *Globigerina* ooze.

Remarks: *Hymenaster giboryi* is known only from a few specimens collected at discrete locations throughout the North Atlantic.

Hymenaster pellucidus Thomson, 1873

$^{\$}$1896a. *Hymenaster pellucidus*, Wyville-Thomson; Perrier: 40.

2005. *Hymenaster pellucidus* Thompson, 1873; García-Diez *et al*.: 47.

$^{\$}$2008. *Hymenaster pellucidus* Wyville Thomson, 1873; Dilman: 142.

2014. *Hymenaster pellucidus* Thomson, 1873; Dilman: 35.

Type locality: Faeroe Channel (N60°21’ W05°41’).

See: Sladen (1889: 521–522, pl. 92, figs. 6–7, pl. 93, figs. 10–12); Clark & Downey (1992: 319–320, figs. 50a–b, pl. 77, figs. C–D); Janies (1995).

Distribution: circumboreal, in the Atlantic and Pacific Oceans; from the Arctic waters south to northern South America (*c.* N7°) in the West Atlantic and south to Portugal in the East Atlantic, and in the Mid-Atlantic Ridge from the Reykjanes Ridge and the Charlie-Gibbs Fracture Zone to the Azores.

Depth: 13–3,240 m (AZO: 2,870–3,050 m).

Habitat: soft sediments (ooze, mud sand, shell-sand, gravel) to hard substrates.

Development: lecithotrophic (brachiolaria larvae), brooded internally until late juvenile stage is reached (approximately one month.

Remarks: the first report of *Hymenaster pellucidus* from the Azores by Perrier (1896a; RV 'Hirondelle', sta 248: N41°40'41" W26°44'9", 2,870 m; specimens lost) was considered doubtful by later authors (*e.g.,* Koehler 1909; Mortensen 1927a; Grieg 1932) as it was generally considered an exclusively Arctic cold-water species. However, Dilman (2008) recently identified this species among the material collected from the Mid-Atlantic Ridge in northern Azorean waters (RV 'G.O. Sars' 'MAR–ECO' cruise, sta 46/372: N42°46' W29°16', 3,005–3,050 m) thus substantiating the presence of this species in the archipelago.

Hymenaster roseus Koehler, 1907a

$^{\$}$1907a. *Hymenaster roseus*, nov. sp.; Koehler: 21–23.

$^{\$}$1909. *Hymenaster roseus*, Kœhler; Koehler: 94–95, pl. 20, figs. 1, 11.

1927a. *Hymenaster roseus* Koehler; Mortensen: 106.

?$^{\$}$1976. *Hymenaster roseus* Koehler; Sibuet: 293–295, fig. 5A.

$^{\$}$1992. *Hymenaster roseus* Koehler; Clark & Downey: 322–323, pl. 78, figs. E–F.

2005. *Hymenaster roseus* Koehler, 1907; García-Diez *et al.*: 47.

2014. *Hymenaster roseus* Koehler, 1907; Dilman: 36.

Type locality: Azores.

See: Koehler (1909); Clark & Downey (1992).

Distribution: known only from the Azores.

Depth: 1,846–2,102(?2,370) m (AZO).

Habitat: soft substrates, muddy sand to *Globigerina* ooze.

Remarks: Koehler (1907a, 1909) described *Hymenaster roseus*, though clearly stating that the material collected by RV 'Princesse Alice' in the Azores was in a very poor state. Sibuet (1976) found a specimen quite close to this species original description among the material collected south of São Miguel Island (RV 'Jean Charcot', 'Biacores' cruise, sta 163BL: N37°26'30" W26°02'30", 2,370 m). However, Sibuet observed that the type material of *H. roseus* was in such deteriorate condition that any valid comparison was impossible. Clark & Downey (1992) re-examined Koehler's original material and reinforced this concern remarking that the state of preservation of the type material was such that rendered it useless. These authors considered the reasons for Koehler erecting a new species rather weak, as the diagnosing characters are shared with many *Hymenaster* species. Furthermore, they observed that Koehler's specimens are quite small. Clark & Downey (1992) stated that in the future *H. roseus* could prove to be an invalid species.

***Hymenaster tenuispinus* Sibuet, 1976**

$^{\$}$1976. *Hymenaster tenuispinus* nov. sp.; Sibuet: 289–291, fig. 3.

Type locality: off Brittany, France (N47°34' W8°38').

See: Sibuet (1976); Clark & Downey (1992: 323).

Distribution: Northeast Atlantic, from west of Brittany (France) south to North of Galicia (Spain) in the Bay of Biscay and west to the Azores.

Depth: 2,120–2,245 m (AZO: 2,120 m).

Remarks: the relatively unknown *Hymenaster tenuispinus* was described by Sibuet (1976) to encompass specimens collected in the Bay of Biscay. Sibu*et* also identified this species among the material taken in the southwest of Flores Island by the RV 'Jean Charcot' during the expedition 'Biacores' (sta 131BL: N39°04'30" W32°43'30", 2,120 m). Recently, Dilman (2013) noted that some of the specimens collected in the Charlie-Gibbs Fracture Zone north of the Azores shared characters with *H. tenuispinus* and the sub-Antarctic *H. coccinatus*. According to Dilman, these two species differ only by the number of adambulacral and oral spines, a character that appears to be size-related. *Hymenaster tenuispinus* may prove to be a junior synonym based on juveniles or subadults of *H. coccinatus,* a species previously thought to be restricted to the waters between Marion and the Crozet Islands.

Genus *Pteraster* Müller & Troschel, 1842

***Pteraster personatus* Sladen, 1891**

$^{\$}$1909. *Pteraster reductus*, Kœhler; Koehler: 96–97, pl. 3, figs. 8–9, pl. 20, fig. 10.

1927a. *Pteraster reductus* Koehler; Mortensen: 102.

1932. *Pteraster reductus* Koehler; Grieg: 28–29, pl. 5, figs. 6–7.

1972. *Pteraster reductus* Koehler; Cherbonnier & Sibuet: 380.

1973. *Pteraster personatus* Sladen; Downey: 76–77, pl. 32, figs. C–D.

1983. *Pteraster reductus* Koehler, 1907; Gage *et al.*: 282.

1992. *Pteraster personatus* Sladen; Clark & Downey: 334, pl. 82, figs. A–B.

2005. *Pteraster personatus* Sladen, 1891; García-Diez *et al*.: 48.

2011. *Pteraster personatus* Sladen 1891; Benavides-Serrato *et al*.: 187.

2014. *Pteraster personatus* Sladen, 1891; Dilman: 36.

Type locality: Porcupine Seabight, SW of Ireland (N51°01' W11°50').

See: Downey (1973); Clark & Downey (1992); Benavides-Serrato *et al.* (2011).

Distribution: North Atlantic, in the west reported from Labrador and the Gulf of Mexico; in the east recorded from the Rockall Trough and SW of Ireland to ?Mauritania, including the Azores.

Depth: 480–2,870 m (AZO: 1,846–2,870 m).

Habitat: soft substrates, mud to muddy sand.

Remarks: Koehler (1909) described a new species *Pteraster reductus* based on small poorly preserved specimens collected by RV 'Princesse Alice' at several stations located within the Azores waters. Koehler remarked that his new species was closely related with *Pteraster personatus* but differing particularly on the smaller size. Later, Downey (1973) argued that *P. reductus* represents juveniles of *P. personatus* dismissing the diagnosing differences selected by Koehler as size-dependent .No other material is known from the archipelago.

Superorder Forcipulatacea Blake, 1987

Order Brisingida Fisher, 1928

Family Brisingidae Sars, 1875

Genus *Hymenodiscus* Perrier, 1884

Hymenodiscus coronata (Sars, 1872)

$1896a. *Brisinga coronata*, O. Sars; Perrier: 20.

$1909. *Brisinga coronata*, Sars; Koehler: 122–123.

$1921a. *Brisinga coronata* G. O. Sars; Koehler: 2.

1927a. *Brisingella coronata* (G. O. Sars); Mortensen: 127.

1938. *Brisingella coronata* (G. O. Sars); Nobre: 28–31, fig. 3.

1983. *Brisingella coronata* (G. O. Sars, 1871); Gage *et al*.: 285.

1986. *Brisingella coronata* (G.O. Sars, 1871); Downey: 13–15, fig. 6.

1992. *Brisingella coronata* (G.O. Sars); Clark & Downey: 468–469, figs. 67b, 70b, pl. 108, fig. F.

2005. *Brisingella coronata* (Sars, 1871); García-Diez *et al*.: 48.

2006. *Hymenodiscus coronata* (G.O. Sars, 1872); Dilman: 183.

2014. *Hymenodiscus coronata* (G.O. Sars, 1872); Dilman: 38.

Type locality: off Lofoten Island, Norway.

See: Downey (1986); Clark & Downey (1992); Howell *et al.* (2003); Mecho *et al.* (2014: 285–286, fig. 4).

Distribution: Mediterranean Sea and Northeast Atlantic, from Norway and Reykjanes Ridge to off Banc d'Arguin (Mauritania) and ?Cabo Verde, including the Azores and Canaries.

Depth: 100–2,904 m (AZO: 919–2,870 m).

Habitat: soft bottoms, sand, mud to *Globigerina* ooze; a suspension feeder (copepods) and a predator.

Type of Development: lecithotrophic.

Remarks: from the Azores, *Hymenodiscus coronata* is only known from the historical reports by Perrier (1896a) and Koehler (1909, 1921a) based on material collected by the RVs ‘Talisman’ and ‘Princesse Alice’ at several stations. The southern-most record of this of species appears to be located off Banc d'Arguin, and not in Cape Verde as reported by the related literature (*e.g*., Mortensen 1927a, Grieg 1932, Downey 1986, A.M. Clark & Downey 1992, Dilman 2014). The RV ‘Talisman’ reports published the station locations using a French coordinate system (Paris Meridian). Later authors may not have been aware of this and might have placed Perrier (1894)’s record near the archipelago waters, instead of the continental NW African waters (sta 96, 1883: N19°19'00", W18°01'46").

Family Freyellidae Downey, 1986

Genus *Freyastera* Downey, 1986

Freyastera sexradiata (Perrier, 1885c)

$^{\$}$1909. *Freyella sexradiata*, Perrier; Koehler: 129–130, pl. 23, fig. 6.

1927a. *Freyella sexradiata* Perrier; Mortensen: 122.

1972. *Freyella sexradiata* Perrier; Cherbonnier & Sibuet: 388.

1983. *Freyella sexradiata* (Perrier, 1885); Gage *et al.*: 285.

1986. *Freyastera sexradiata* (Perrier, 1885), new combination; Downey: 40–41, fig. 20.

1992. *Freyastera sexradiata* (Perrier); Clark & Downey: 481–482, figs. 74c–d.

2005. *Freyastera sexradiata* (Perrier, 1885); García-Diez *et al.*: 48.

2014. *Freyastera sexradiata* (Perrier, 1885); Dilman: 38–39.

Type locality: Between the Azores and the Iberian Peninsula (N42°19’00” W21°15’46”).

See: Perrier (1894: 82, 89–90, pl. 3, fig. 2, as *Freyella sexradiata*); Downey (1986); Clark & Downey (1992).

Distribution: North Atlantic deep-waters, from the Porcupine Abyssal Plain (SW of Ireland) southwards to Gibraltar and westwards to North America including the Azores.

Depth: 4,020–5,110 m (AZO: 4,020 m).

Habitat: soft substrates, mud to *Globigerina* ooze.

Remarks: the only known record of *Freyastera sexradiata* in the Azores was made by Koehler (1909) based on two discs and several arm fragments collected by RV 'Princesse Alice' (sta 527: N38°09' W23°15'45", 4,020 m). The scarcity of records in the Azores might be explained by the great depths at which this species lives and the frail structure that characterises this sea star, as *F. sexradiata* was never recovered intact (Clark & Downey 1992).

Genus *Freyella* Perrier, 1885d

Freyella elegans (Verrill, 1884)

1932. *Freyella spinosa*; Grieg: 31.
$^{\$}$1972. *Freyella spinosa* Perrier; Cherbonnier & Sibuet: 385.
1983. *Freyella spinosa* Perrier, 1894; Gage *et al*.: 285.
$^{\$}$2008. *Freyella elegans* (Verrill, 1884); Dilman: 148.
2013. *Freyella elegans* (Verrill, 1884); Dilman: 584.
2014. *Freyella elegans* (Verrill, 1884); Dilman: 39.

Type locality: off New England.

See: Sibuet (1975: 108); Tyler *et al.* (1984); Downey (1986: 43–46, fig. 22); Clark & Downey (1992: 484–485, fig. 69f, pl. 113, figs. A, B); Tyler & Zibrowius (1992: 222, fig. 5g, as *F. spinosa*); Howell *et al.* (2003).

Distribution: Atlantic, from North Carolina northwards to Greenland and eastwards to Europe, including the Porcupine Abyssal Plain, southwards along West Africa to Namibia, including the Mid-Atlantic Azorean waters.

Depth: 1,600–4,849 m (AZO: 2,063–3,050 m).

Habitat: suspension feeder (copepods, crustacean remains, foraminiferans) on soft bottoms or attached to the rock surface and dead gorgonians.

Type of Development: lecithotrophic.

Remarks: *Freyella elegans* is a highly variable species, widely distributed throughout the Atlantic deep waters. Grieg (1932) placed the Azores as the western geographical limit known at the time for *F. spinosa*, a form now known to be conspecific with *F. elegans* (see Downey 1986). At the time, no material of either species was reported from Azorean waters but between the archipelago and the European continental shores by Perrier (1894, as *Freyella spinosa* var. *abyssicola*). Later, Cherbonnier & Sibuet (1972, as *Freyella spinosa*) identified two specimens collected within the Azorean waters (RV 'Jean Charcot', 'Noratlante' cruise, sta P65B10: N36°58'2" W26°20', 2,871 m). Recently, Dilman (2008) identified material belonging to this species in the northern waters of the Azores, substantiating the presence of *F. elegans* in the archipelago.

Order Forcipulatida Perrier, 1884

Family Asteriidae Gray, 1840

Genus *Asterias Linnaeus, 1758*

Asterias rubens? Linnaeus, 1758

?$^{\$}$1896a. *Asterias polaris*, Gray; Perrier: 38.

$^{\$}$1924. *Asterias rubens* Linnaeus, 1758 — $^{\$}$Koehler : 10.

1997. *Leptasterias (Hexasterias) polaris* (Müller & Troschel, 1842); Pereira: 336.

2005. *Ctenodiscus crispatus* (Retzius, 1805); García-Diez *et al*.: 47.

2010. *Ctenodiscus crispatus* (Retzius, 1805); Micael & Costa: 322.

2010. *Leptasterias polaris* (Müller & Troschel, 1842); Micael & Costa: 321.

2012. *Ctenodiscus crispatus* (Retzius, 1805); Micael *et al*.: 5.

Type locality: Greenland.

See: Mortensen (1927a: 139–141, Fig. 79); Clark & Downey (1992: 422–423, fig. 67c, pl. 100, figs. C–D); Wirtz & Debelius (2003: 180).

Distribution: North Atlantic, in the west from Labrador south to Carolinas (occasionally also Florida); and in the east White Sea and Iceland south to southern Portugal and ?Azores .

Depth: 0–900 m (?AZO: intertidal).

Habitat: all sorts of substrates.

Type of Development: brooding.

Remarks: Perrier (1896a) reported a species '*Asterias polaris* Gray' (family Asteriidae, order Forcipulata) from the Azorean rocky intertidal (RV 'Hirondelle', sta 104, Bay of Porto Pim, Horta, Faial Island). The name as this author listed it is not present in Gray (1840, 1866). Fisher's review (1923, 1930) listed *Asterias polaris* under the synonymy of two (very different) Arctic species: the paxillosid *Ctenodiscus crispatus* (Bruzelius, 1805) (= *Asterias polaris* Sabine, 1824) and the forcipulatid *Leptasterias polaris* (Müller & Troschel, 1842) (= *Asteracanthion polaris* Müller & Troschel, 1842) (see also Clark & Downey 1992). In Azorean faunal lists one or both of these species are mentioned, however, none of the authors explained their choice, nor commented on the unusual presence of an Arctic species in the Azores. García-Diez *et al*. (2005) and Micael *et al*. (2012) selected the first species, *Ctenodiscus crispatus*. Pereira (1997) chose the latter species, *Leptasterias polaris* and Micael & Costa (2010) listed both. Notwithstanding, Perrier (1875) acknowledged Sabine's *Asterias polaris* as a junior synonym of *Ctenodiscus corniculatus* (= '*Astropecten polaris* Gray') now accepted as *C. crispatus*. In contrast, Perrier (1896a) grouped the Azorean *A. polaris* together with *A. rubens* (the genus' type species), as both members of the order Forcipulatida. Previously, Norman (1965) had disagreed with the replacement of the Linnaean genus *Asterias* by Müller & Troschel (1840b) not realising that with the suppression of *Asteracanthion,* two species would arise with the same name.

The problematic taxonomical position of Müller & Troschel (1840b) species' was only resolved much later by Fisher (1923, 1930). Thus, it is apparent that Perrier was referring to *L. polaris* as described by Müller & Troschel (1842). Regardless, Koehler (1924: 102–103) stated in a small footnote that the two small specimens identified by Perrier (1896a) as *L. polaris* were in reality six-armed individuals of *A. rubens*. In contrast with arctic *L. polaris*, the geographical range of *A. rubens* extends to the southern latitudes of South Carolina (or Florida) and Portugal (A.M. Clark & Downey 1992), making it a more likely inhabitant of the Azores warmer waters. The unusual number of arms observed in the material from the Azores could be the reason for Perrier's misidentification. Unlike the six-armed *L. polaris*, *A. rubens* is characterized by having typically five arms. Occasionally, abnormal animals may have as many as eight arms (Koehler 1924, Mortensen 1927a).

The material of *A. rubens* was collected in the rocky intertidal waters of Porto Pim Bay (*c*. N38°31'29", W28°37'38"). The only other sea star species collected at this RV 'Hirondelle' station was *Marthasterias glacialis*, making other common inhabitants of Azores conspicuously absent. Among these, *Coscinasterias tenuispina* (Lamarck, 1816) and *Luidia ciliaris* (Philippi, 1837) are the only non-pentamerous species. In view of this, it is possible that both Perrier and Koehler may have misidentified *Hirondelle* specimens with juveniles of the closely related *C. tenuispina* (see text below). However, this seems unlikely as Koehler was familiarized with these species. Nonetheless, Porto Pim Bay is located in Horta city, near the old installations of Department of Oceanography and Fisheries. This area of easy access is one of the most survey waters in the Azores. However, no new material belonging to *A. rubens* has ever been collected since RV 'Hirondelle' cruise*.* These two small specimens of *A. rubens* may represent the arrival of this species in the Azores, but for some reason failed to settle in the archipelago. For the above reasons, we have considered the presence of this species in the archipelago shallow waters as doubtful.

Genus *Coscinasterias* Verrill, 1867

Coscinasterias tenuispina **(Lamarck, 1816)**
(Fig. 5.12)

$1888. *Asterias tenuispina* Lamarck; Barrois: 70.

$1909. *Asterias tenuispina*, Lamarck; Koehler: 122.

1914b. *Asterias tenuispina*; Koehler: 275.

1921b. *Coscinasterias tenuispina* (Lamarck); Koehler: 26, fig. 19.

1921. *Asterias tenuispina* Lamk.; Mortensen: 224.

$1924. *Coscinasterias tenuispina* (Lamk.); Nobre: 88.

1927a. *Coscinasterias tenuispinus* (Lamarck); Mortensen: 138.

$1930. *Coscinasterias tenuispina* (Lamk.); Nobre: 68.

$1938. *Coscinasterias tenuispina* (Lamk.); Nobre: 36–37, fig. 10, 11.

$1983. *Coscinasterias tenuispina* (Lamarck, 1816); Marques: 2.

1992. *Coscinasterias tenuispina* (Lamarck); Clark & Downey: 427–428, figs. 63h, i, pl. 101, figs. A, B.

1997. *Coscinasterias tenuispina* (Lamarck, 1816); Pereira: 335.

$1998. *Coscinasterias tenuispina*; Morton *et al*.: 120, 169, figs. 6.2O, 8.8S.

2002. *Coscinasterias tenuispina* (Lamarck, 1816); Pérez-Ruzafa *et al*.: 280–281.

2010. *Coscinasterias tenuispina* (Lamarck, 1816); Micael & Costa: 321.

2012. *Coscinasterias tenuispina* (Lamarck, 1816); Micael *et al.*: 2, 3–4.

See: Verrill (1915: 19–20, pl. 26, figs. 2, pl. 17, fig. 4); Clark (1933: 30–31, as *Stolasterias tenuispina*); Nataf & Cherbonnier (1975: 825); Clark & Downey (1992); Jesus & Abreu (1998: 61); Waters & Roy (2003); Koukouras *et al.* (2007: 70).

Distribution: on tropical-subtropical waters of the Mediterranean Sea and Atlantic Ocean; in the west, from North Carolina south to Brazil including Bermuda, and in the east from the Bay of Biscay to Sierra Leone , including the Azores, Madeira, Selvagens, Canaries, Cabo Verde and Saint Helena.

Depth: 0–165 m (AZO: 0–12 m).

Habitat: typical inhabitant of rocky shores; also found on biogenic detritus, sandy to silty sand substrates, under stones and in the meadows of *Zostera* and *Posidonia*.

Type of Development: probably planktotrophic (inferred from the genus); also asexual reproduction through fission.

Material examined: DBUA-ECH 077 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06; 6 spms, R=32–68 mm, r=4–7 mm); DBUA-ECH 108 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06; 3 spms, R=30–110 mm, r=3–10 mm); DBUA-ECH 114 (Lajes, PIX, AZO, *c.* N38°23’22” W28°15’04”, 2 m; 4 spms, R=7–25 mm, r=1–3 mm)**;** DBUA-ECH 122 (São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2012.11.16, intertidal; 1 spm, R=3 mm, r=1 mm); DBUA-ECH 184 (Poços, Capelas, SMG, AZO, *c.* N37°50'06" W25°40'10", 1996.07.18, 12 m; 1 spm, R=3 mm, r=1 mm); DBUA-ECH 407 (Marina, Vila do Porto, SMA, AZO, N36°56'42" W25°08'50", 2016.07.5, 1 m; 1 spm, R=76 mm, r=8 mm).

Description: disc small, with six to nine arms, rather long and slender, slightly angular and of unequal size, being larger of one side relative to the other. Most specimens with two to three madreporites; exceptionally three specimens exhibited a single madreporite, but also signs of recent self-division (shape of the disc half circumference; smallest arms less than a quarter the size of the remaining arms) (DBUA-ECH 077c, 114c, 184). Abactinal skeleton strong, with three regular longitudinal series of primary plates, each carrying a single aciculate spine encircled by a large wreath of crossed pedicellaria; only one dorsal (carinate) series in the smaller specimens (R <7 mm). Spines in the disc irregularly distributed not forming a pentagon. Superomarginal plates with an irregular patch of fine crystal bodies; alternating plates bear single aciculate spines encircled by large wreath of crossed pedicellaria. Inferomarginals bear two oblique spines somewhat flattened, with similar sizes as superomarginals; marginal spine with crossed pedicellaria surrounding only the outer

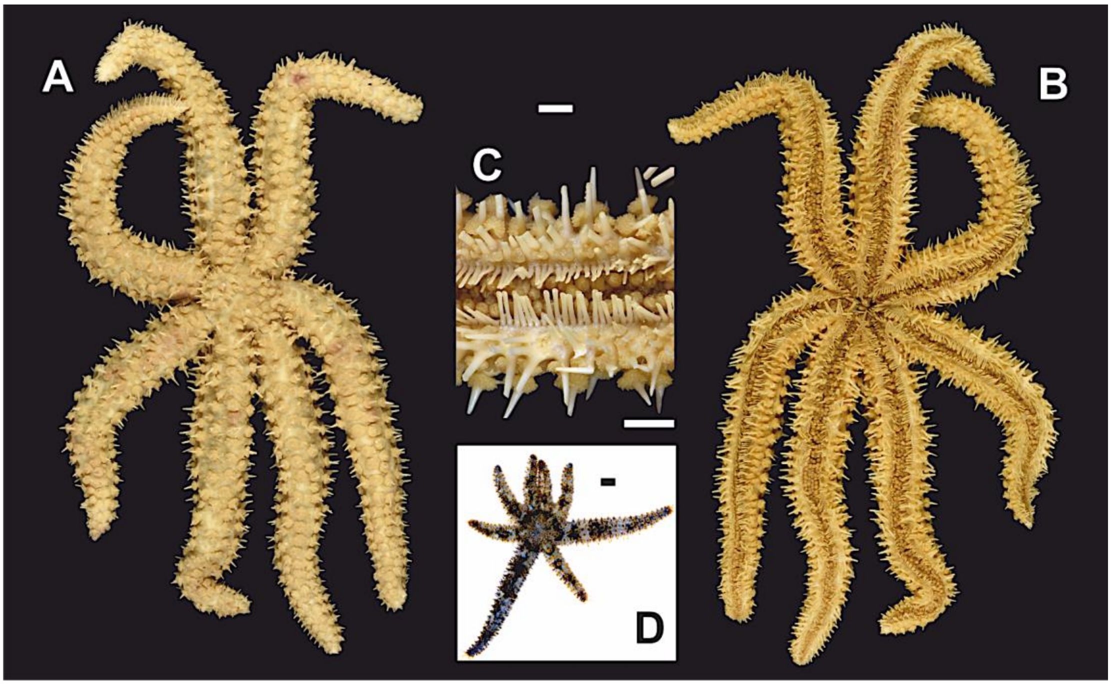


Figure 5.12. *Coscinasterias tenuispina* (Lamarck, 1816) (DBUA-ECH 357: A–C; DBUA-ECH 407: D). Dorsal view (A); ventral view (B); detail of the arm, ventral view (C); blue colour morph; scale bars are 10 mm (A, B, D) and 5 mm (C).

side; larger specimens(R >40 mm) occasionally presented a third (interactinal) spine in the proximal area between the inferomarginal and the adambulacral plates, about the same size and shape as the nearest inferomarginal; the presence or position along the arms of this additional spine was not constant between specimens or between arms of the same specimen. Adambulacral plates generally bearing one long flattened spine with no attached pedicellaria (monocanthid); in larger specimens (R >7 mm), a second spine was occasionally present, though its presence was irregular, normally restricted to the proximal area of the arms; in the largest specimen (DBUA-ECH 108; R=110 mm) this additional spine was observed to about two thirds from the arm base. Crossed pedicellaria with enlarged terminal teeth larger than the median terminal teeth; lanceolate straight pedicellaria long and scattered throughout surface, particularly numerous between the arms. Colour (alive): dorsal side brown or purplish-blue with darker and lighter specks; crossed pedicellaria and tube feet bright orange; ventrally cream; colour (in ethanol) from uniform whitish to cream. Shells of the marine gastropod *Anachis avaroides* Nordsieck, 1975 were found in the stomach of the specimen DBUA-ECH 407.

Remarks: among species belonging to the genus *Coscinasterias*, *C. tenuispina* closely resembles *C. calamaria* (Gray, 1840) a species known from South African and Australian waters. These two species differ only by the shape of the pedicellaria, as in *C. tenuispina* the crossed pedicellaria present an enlarged tooth and the straight pedicellaria present short stubs at the tips. Clark & Downey (1992) remarked that the separation between the two species should eventually be downgraded to a subspecific level, as *C. tenuispina* from Brazil seemed to present somewhat intermediary characteristics. More recently, Waters & Roy (2003) conducted a phylogenetic analysis on the genus, and their findings contradicted the previous authors' hypothesis and pointed to a closer relationship between *C. calamaria* and *C. acutispina* (Stimpson, 1862), a north Pacific species. On the other hand, Waters & Roy support a subspecific separation of *C. tenuispina* populations from the Brazil. Nevertheless, these authors cautioned that further studies should be conducted on Brazilian animals since the differences observed by Clark & Downey were based on juvenile specimens, thus inconclusive from a morphological point of view. In a study on the asteroids from northeastern Brazil, Gondim *et al*. (2014) appear to support the Waters & Roy's contention as their own observations fail to support any clear morphological separation. The colour pattern was also present by Clark & Downey (1992) as a possible source of variation among populations through the geographic range of *C. tenuispina*. However, the colour in this species is rapidly shed through the preservation process. Specimens housed in the DBUA-ECH collection presented features typical of *C. tenuispina*, on the appearance of both straight and crossed pedicellaria. Even the appearance of a second adambulacral in a species or genus otherwise known to be monocanthid was already documented by Verrill (1914) as merely individual variations. The observed brown colour pattern was also found in other areas in the Atlantic (*e.g.,* Pérez-Ruzafa *et al*. 2002; Wirtz & Debelius 2003; Hernández *et al*. 2013). The blue colour morph observed in one of the specimens (Fig. 5.12D) appears to be also found in Bermuda, NW Atlantic (Clark 1933).

C. tenuispina can be easily distinguished from the only other fissiparous sea star known to the Azores *Sclerasterias richardi* (see above) by the distribution of crossed pedicellaria, as in the latter species these pedicellaria are found dispersed on the aboral surface and not organized in wreaths around the spines as in the former.

Also, the non-fissiparous sea star *Marthasterias glacialis* another common inhabitant of the Azorean shallow waters can be easily distinguished from *C. tenuispina* by having five arms and never more than one madreporite.

Genus *Marthasterias* Jullien, 1878

Marthasterias glacialis **(Linnaeus, 1758)**

(Fig. 5.13)

$^{\$}$1842. *Asteracanthion glacialis* Nob.; Müller & Troschel: 14–15.

$^{\$}$1861. *Asterias glacialis* Lam.; Drouët: 211.

1888. *Asterias glacialis* Lamarck; Barrois: 31.

$^{\$}$1888. *Asterias glacialis* O.-F. Müller; Barrois: 32, 69, 113, 114.

$^{\$}$1888. *Asterias glacialis* L.; Simroth: 231, 232.

$^{\$}$1894. *Stolasterias glacialis*, Linck; Perrier: 109.

$^{\$}$1896a. *Stolasterias madeirensis*, Stimpson; Perrier: 37.

$^{\$}$1909. *Asterias glacialis*, Linné; Koehler: 116.

1914b. *Asterias glacialis*; Koehler: 269.

$^{\$}$1923a. *Marthasterias glacialis*; Clark: 305.

$^{\$}$1924. *Asterias glacialis* (L.); Nobre: 88.

1927a. *Marthasterias glacialis* (Linnæus); Mortensen: 143–144, fig. 82.

$^{\$}$1928. *Marthasterias glacialis* (Müller); Fisher: 130, pl. 42, fig. 4, pl. 43, fig. 6

$^{\$}$1930. *Asterias glacialis* (L.); Nobre: 68.

$^{\$}$1938. *Marthasterias glacialis* Linné, 1758; Cadenat: 349.

1938. *Marthasterias glacialis* (L.); Nobre: 34–36, fig. 8, 9.

$^{\$}$1951. *Marthasterias glacialis* var. *rarispina* (Perrier); Clark: 211–212.

$^{\$}$1955. *Marthasterias glacialis* L.; Chapman: 400.

$^{\$}$1965. *Marthasterias glacialis* (L.); Tortonese: 188–192, figs. 89, 91.

$^{\$}$1983. *Marthasterias glacialis* (Linné, 1758); Marques: 2.

1992. *Marthasterias glacialis* (Linnaeus); Clark & Downey: 443–445, fig. 67d, pl. 101, fig. C.

1995. *Marthasterias glacialis* (Linnaeus); Moyse & Tyler: 671, fig. 12.4.

1997. *Marthasterias glacialis* (Linnaeus, 1758); Pereira: 335.

$^{\$}$1998. *Marthasterias glacialis*; Morton *et al.*: 62, figs.3.4Y, 3.7P, 8.1K.

1999. *Marthasterias glacialis* (Linnaeus, 1758); Pérez-Ruzafa *et al.*: 49.

2002. *Marthasterias glacialis* (Linnaeus, 1758); Pérez-Ruzafa *et al.*: 281–282.

2005. *Marthasterias glacialis* (Linnaeus, 1758); García-Diez *et al*.: 48.

$^{\$}$2006. *Marthasterias glacialis* (Linnaeus 1758); Micael *et al*.: 5.

2010. *Marthasterias glacialis* (Linnaeus, 1758); Micael & Costa: 321.

$^{\$}$2010. *Marthasterias glacialis* (Linnaeus, 1758); Micael *et al*.: 329.

2012. *Marthasterias glacialis* (Linnaeus, 1758); Micael *et al*.: 4–5.

See: Mortensen (1927a); Delavault & Cognetti (1961); Clark & Downey (1992); Picton (1993: 36); Koukouras *et al.* (2007: 71).

Distribution: Mediterranean Sea and East Atlantic; from Iceland and Finmark along the European and West African coasts to ?South Africa, including the archipelagos of the Azores, Madeira, Selvagens, Canaries and Cabo Verde.

Depth: 0–180 m (rarely below 50 m) (AZO: 0–35 m).

Habitat: found on rocky shores, on biogenic detritus, sandy to silty sand substrates, and in *Zostera* and *Posidonia* meadows; feeds mainly on molluscs but also on fishes, crustaceans and other echinoderms.

Type of Development: planktotrophic; typically gonochoristic, though some cases of hermaphroditism have been reported in the Tyrrhenian Sea.

Material examined: DBUA-ECH 103 (Piscina da Lagoa, SMG, AZO, *c.* N37°44’29” W25°34’27”, 25.07.1996, 15 m; 1 spm, R=83 mm, r=9 mm); DBUA-ECH 104 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06.08, 6–8 m; 1 spm, R=13 mm, r=3 mm); DBUA-ECH 105 (Rosto do Cão, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1997.02.26, 10 m; 2 spms, R=84–101 mm, r=9); DBUA-ECH 106 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06; 2 spms, R=100–147 mm, r=12–17 mm); DBUA-ECH 110 (Poços, São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.04.14; 1 spm, R=60 mm, r=8 mm); DBUA-ECH 111 (Vila do Porto, SMA, AZO, *c.* N36°56’42” W25°08’50”, 1990.06; 2 spms, R=79–142 mm, r=11–80 mm); DBUA-ECH 205 (Baixa de João Lopes, SMA, AZO, *c.* N37°01’13” W25°10’05”, 2014.06.26, 30–35 m; 1 spms, R=1 mm, r=0.5 mm).

Description: disc subpentagular with scattered spines forming a more or less distinct pentagon; R/r from two to thirteen in smaller specimens (D=1–5 mm, respectively) up to 8–11 fold in larger specimens; a larger individual (R=142 mm; DBUA-ECH 111) was flattened by an inadequate preservation container resulting in a proportion R to r of two fold. Five arms with pentagonal cross-section, long tapering distally. Abactinal skeleton strong, with three longitudinal series of primary plates; the plates in mid-dorsal line of the arm forming a conspicuous regular series, zigzagging distally with one up to two (occasionally three, in larger specimens of R ≥78 mm) stout conical spines, encircled by a large wreath of crossed pedicellaria; the dorsolateral series on each side reduced particularly distally, partially spinose with spines (when present) usually smaller than the carinal ones in all specimens except in the smallest ones (R ≤13 mm), where they are absent. Superomarginal plates as in the mid-dorsal arm area, arranged

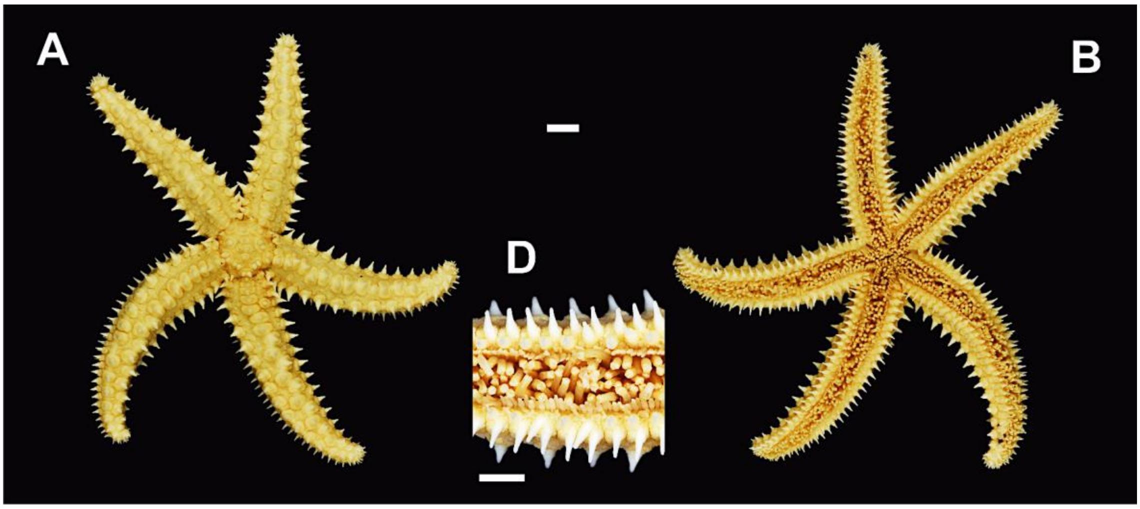


Figure 5.13. *Marthasterias glacialis* (Linnaeus, 1758) (DBUA-ECH 103). Dorsal view (A); ventral view (B); detail of the arm, ventral view (C); scale bars are 10 mm.

in a regular series with one to two spines, slightly exceeding in length the carinal ones; also surrounded by wreath of crossed pedicellaria. Inferomarginal with two oblique spines slightly flattened and of similar length to the abactinal ones; the outer one with crossed pedicellaria surrounding only the outer side. A single spineless actinal series. Adambulacral plates monocanthid. Long lanceolate straight pedicellaria scattered on the ventral surface, particularly within the furrow. Valves of crossed pedicellaria with a slightly enlarged tooth on each side of the terminal lip. Colour (in ethanol): all white, with the exception of a small specimen (DBUA-ECH 104), which is light brown with darker brownish spots giving an overall stripped appearance.

Remarks: *Marthasterias glacialis* is highly polymorphic and has a wide geographical distribution, qualities that have resulted in the description of several synonyms, subspecies and varieties. The validity of these subspecies did not reunite consensus as many believed to be ecophenotypic variations associated with specific environmental conditions (depth, *e.g.,* Mortensen 1933b; Tortonese, 1965; latitude, *e.g.,* Clark 1951). Historically, *M. glacialis* in the Azores was attributed to the form '*rarispina*' by Clark (1951), a variety originally described as a South African species by Perrier (1875). Its diagnosing characters are essentially focused on the absence of spines on the dorsolateral plate series (*e.g.,* Perrier 1875; Clark 1923a). On the other side of the spectrum is the form '*africana*', another South African variety distinct by its many irregularly arranged abactinal spines (Mortensen 1933b; Clark 1974). However, Mortensen (1933b) realized the existence of intermediate forms and classified these as 'not very distinct varieties'. Unlike the previous observations by Clark (1951), the specimens from the Azores housed in the DBUA-ECH collection appear to be identical to the ones from South Africa, figured by Mortensen (1933b: pl. 16, fig. 3) as an example of an intermediate form of the variety '*rarispina*' characterized by having a reduced number of spines in the dorsolateral series. In contrast, the carinal plate series in the DBUA-ECH specimens also presented a somewhat zigzagged arrangement in the distal part of the arms. This feature was associated with the typical form '*rarispina*' by Clark (1951). However, the smallest specimens (R ≤3 mm) in DBUA-ECH collection displayed a naked dorsolateral series and the spines on carinal series are not arranged in a zigzagged manner. Regardless, the observed variations found in Azorean animals are not exclusive in the North Atlantic and were also reported in specimens from Madeira, Canaries, Portugal and the Mediterranean Sea (Ludwig 1897; Nobre 1930; Clark 1951; Clark & Downey 1992). The colouration pattern has been appointed as another source of variation in *M. glacialis*, which can vary between yellow, green, blue, brown and even pink. In the Azores, large specimens are typically described as blackish with the spinose plates conspicuously white, see for example Wirtz & Debellius (2003). However, small specimens (*e.g.,* DBUA-ECH 103, R=83 mm) may present a colouration pattern similar to typical *Coscinasterias tenuispina*, light brown to yellowish-white blotched with darker brownish or orange, giving an overall stripped appearance (see remarks under *C. tenuispina*). A more recent study by Wright and co-workers (2016) concluded that *rarispina* and *africana* varieties from South Africa could not be distinguished at a morphological and genetic level. On the other hand comparisons with sequences previously published by Pérez-Portela *et al* (2010) from the European shores and Azores showed that South African populations could represent a distinct species.

Genus *Sclerasterias* Perrier, 1891

***Sclerasterias richardi*? (Perrier, *in* Milne-Edwards, 1882)**
(Fig. 5.14)

$^{\$}$2017b. *Sclerasterias richardi* (Perrier, *in* Milne-Edwards 1882); Madeira *at al.*: 11–18

Type locality: Mediterranean Sea

See: Perrier (*in* Milne-Edwards 1882: 20–21, as *Asterias richardi*; 1894: 109–112, pl. 9, fig. 4, as *Hydrasterias richardi*); Ludwig (1897: 403–418, pl. 12, figs. 18–22); Falconetti *et al.* (1976, 1977).

Distribution: known only from the Mediterranean Sea, ?Azores and Cabo Verde.

Depth: 80–710 m (AZO: 135 m).

Habitat: soft, detritic to hard substrata.

Type of Development: planktotrophic; also asexual reproduction through fission.

Material examined: DBUA-ECH 357 (Vila Franca do Campo, SMG, AZO, N37°41’42” W25°25’22”, 2006.07.17, 135 m; 3 spms, R=5–6 mm, r=1 mm).

Description: two specimens presenting six arms of unequal sizes (three larger and three smaller) and one animal with three arms of similar dimensions to the larger arms of the six-rayed specimens. Arms broad, pentagonal in cross-section, narrowing gradually into a round arm tip covered by the terminal plate; arms weakly attached to the disc.

Reticular plating on the arms arranged in fairly regular longitudinal plate series (carinal, dorsolateral, superomarginal, inferomarginal, adambulacral); arm plates with a round four-lobed shape with exception of the small bridge-like dorsolateral plates. Papulae occupying the interstices between plates, forming two longitudinal rows on each side of the arm. Arm spines forming fairly regular longitudinal series. Carinal plates carrying up to three short and round spines bearing small spinelets at their tips. Dorsolateral plates bearing one small spine. Superomarginal plates armed with two spines similar in size and shape to the carinal and dorsolateral ones. Spine number and size gradually reduced to one small spine near the arm tip in both carinal and superomarginal plates and none in the dorsolateral plates. Inferomarginal plates with one or two flattened, spatulate to clavate enlarged spines, arranged obliquely and slightly enlarged towards the tip. Adambulacral plates diplacanthid bearing two flattened spines arranged obliquely with the internal spines slightly smaller than the external one. Dorsal surface of all specimens partially damaged, preserving at least two madreporites (S-shaped) near the interradial edges; disc also densely covered with small spines, identical in size and shape to those found on the dorsal surface of the arms. Numerous crossed pedicellaria almost as large as the dorsal spines dispersed over the body surface, not forming a wreath around the spines; presence of a slightly enlarged unpaired tooth on the outer face of each valve of the crossed pedicellaria.

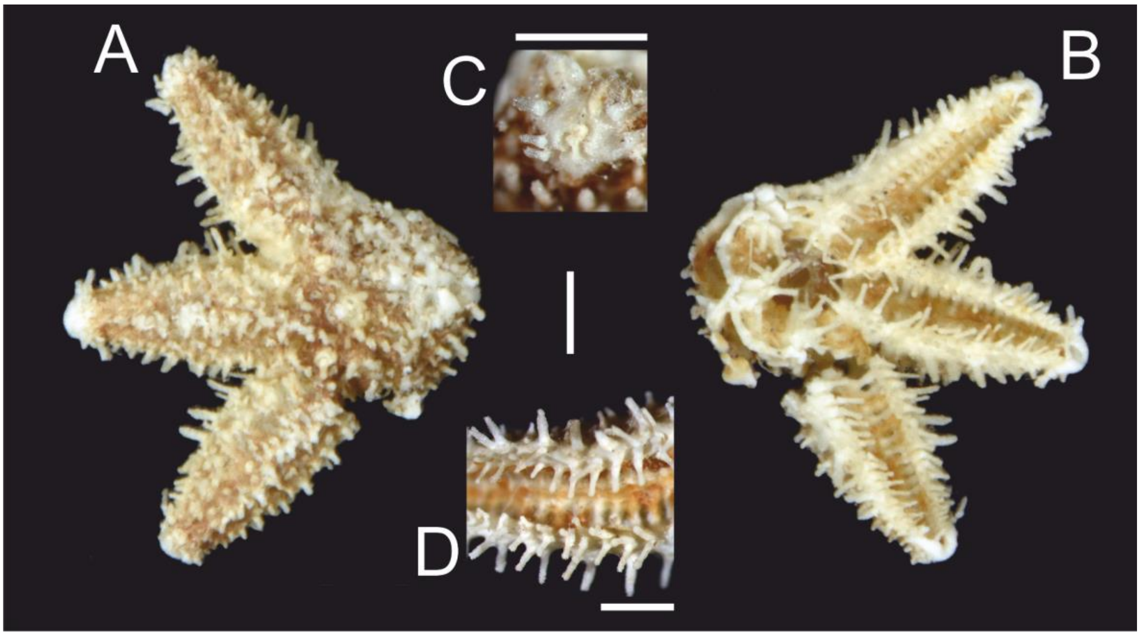


Figure 5.14. *Sclerasterias richardi* (Perrier, in Milne-Edwards, 1882) (DBUA-ECH 357). Dorsal view (a); ventral view (b); detail of the arm, ventral view (c); scale bars are 1 mm.

Straight pedicellaria felipedal, slightly larger than the crossed pedicellaria and restricted to the interradial areas.

Remarks: currently, only two other *Sclerasterias* species are known to the NE Atlantic and Mediterranean Sea: *S. neglecta* (Perrier, 1891) (Bay of Biscay and Mediterranean Sea, 166–887 m) and *S. guernei* Perrier, 1891 (Bay of Biscay, 160–490 m) (A.M. Clark & Downey 1992). Unlike *S. richardi*, the crossed pedicellaria in these species is distributed in a fashion typical of the genus (*i.e.* in wreaths around the spines; Perrier 1891: 264) and none is known to asexually reproduce by fission. Nonetheless, neither the fissiparous nature nor the distribution of the crossed pedicellaria observed in S. *richardi* appears to be unique in *Sclerasterias*. While adults of Hawaiian *S. euplecta* present all the typical characters of the genus, the juvenile stages were described by Fisher [1906, as *Coscinasterias* (*Distolasterias*) *euplecta*] as fissiparous and presenting a scattered distribution of crossed pedicellaria. These observations have led Fisher (1928) to believe that *S. richardi* was also a juvenile of another *Sclerasterias*, possibly *S. neglecta*. Later, Clark & Downey (1992) further suggested that *S. richardi* was an invalid species since the description by Perrier (*in* Milne-Edwards 1882, 1894) was based on immature specimens. However, the smallest known specimens of both *S. neglecta* and *S. guernei* (R = 15 mm, r = 3 mm and R = 17 mm, r = ? mm, respectively) were described as having five arms with crossed pedicellaria arranged in circles around the spines (Perrier 1891, 1896a). More recently, Mastrototaro & Mifsud (2008) argued that the unequal number and size of the arms, the presence of multiple madreporites and the documented sexual reproduction by Falconetti and co-workers (1976, 1977) suffice to prove that it was a valid species. Though we agree with Mastrototaro & Mifsud (2008), the position of *S. richardi* (or even of *S. euplecta*) should be re-addressed in future revisions of this genus.

The only other fissiparous sea star known from the coastal waters of the Azores *Coscinasterias tenuispina* (see below) can be easily distinguished from *S. richardi* by the arrangement of the crossed pedicellaria in wreaths around the spines and by the monocanthid arrangement of the adambulacral spines. Furthermore, *C. tenuispina* appears to be restricted to the first few meters in the Azores (≤12 m) as opposed to much deeper local record of *S. richardi* (135 m). *Sclerasterias richardi* is one of the latest additions to the Azores echinoderm fauna. Madeira *et al*. (2017b) have identified the specimens herein enumerated among the material collected off the coast of Vila Franca do Campo (São Miguel Island) by the *International Workshop of Malacology and Marine Biology* (2006), one of the rare efforts in the Azores targeting deeper coastal waters (*i.e*. between 50 m and 200 m depth). Nevertheless, the specimens were small and probably immature shedding some doubt on whether they belong to an established population or represent a recent arrival, a question that can only be answered in future studies as further material becomes available.

Family Pedicellasteridae Perrier, 1884

Genus *Hydrasterias* Sladen, 1889

Hydrasterias sexradiata **(Perrier, *in* Milne-Edwards, 1882)**

$^{\$}$1909. *Pedicellaster sexradiatus*, Perrier; Koehler: 110–111, pl. 2, fig. 4.

?$^{\$}$1909. *Stellosphæra mirabilis*, Kœhler et Vaney; Koehler: 131–136, pl. 24, fig. 1–10.

1921. *Pedicellaster sexradiatus* Perrier; Mortensen: 224.

1927a. *Pedicellaster sexradiatus* E. Perrier; Mortensen: 130.

$^{\$}$1949. *Hydrasterias ophidion* Sladen; Clark: 375.

$^{\$}$1972. *Pedicellaster .sexradiatus* E. Perrier 1882; Sibuet: 121.

1983. *Hydrasterias sexradiata* (Perrier, 1882); Gage *et al*.: 285–286.

1992. *Hydrasterias sexradiata* (Perrier); Clark & Downey: 410, figs. 62c–d.

1992. *Pedicellaster sexradiatus;* Pérès: 254, 255.

2005. *Hydrasterias sexradiata* (Perrier, *in* Milne-Edwards, 1882); García-Diez *et al*.: 48.

2006. *Hydrasterias sexradiata* (Perrier, 1882); Dilman: 185.

2008. *Hydrasterias sexradiata* (Perrier, 1882); Dilman: 147.

2013. *Hydrasterias sexradiata* (Perrier, 1882); Dilman: 583.

2014. *Hydrasterias sexradiata* (Perrier, 1882); Dilman: 37–38.

Type locality: off Portugal (between *c.* N40°–N38°W12°).

See: Perrier (*in* Milne-Edwards 1882: 46–47; 1894: 100–102, pl. 9, fig. 2, as *Pedicellaster sexradiatus*); Clark & Downey (1992).

Distribution: Northeast Atlantic, from the Rockall Trough and the Bay of Biscay, southwards to ?Cabo Verde and on the Mid-Atlantic Ridge from the Reykjanes Ridge to the Azores.

Depth: 599–4,260 m (AZO: 599–3,465 m).

Habitat: soft substrates, from *Globigerina* ooze to sand.

Type of Development: planktotrophic.

Remarks: Koehler (1909) identified specimens of '*Stellosphaera mirabilis*' collected by RV 'Princesse Alice', at stations located within Azorean waters. Mortensen (1921, 1927a) believed that this was actually the larval form of *H. sexradiata*, in an advanced stage of metamorphosis. According to Clark & Downey (1992), this is yet to be confirmed. The western Atlantic *Hydrasterias ophidion* was reported from the Azores by Clark (1949), based on his identification of material collected by RV 'Atlantis' (sta 20: N37°50'30" W26°00'00", 2,562 m). Later, Dilman (2014) placed Clark's material under *H. sexradiata*, a known native to the Azorean deep waters. Additionally, the inclusion of Cabo Verde Archipelago in the geographical distribution of *Hydrasterias sexradiata* in the bibliography (*e.g.,* Mortensen 1927a; Clark & Downey 1992) is possibly based on a misprint by Koehler (1909), who remarked that the material of this species was collected by RV 'Princesse Alice' between the Azores and Cabo Verde, though all listed stations are positioned in the Azores region.

Family Stichasteridae Perrier, 1885b

Genus *Neomorphaster* Sladen, 1889

***Neomorphaster margaritaceus* (Perrier, *in* Milne-Edwards, 1882)**

$^{\$}$1885c. *Stichaster talismani*, sp. nov.; Perrier: 22–24.

$^{\$}$1889. *Neomorphaster eustichus*, n. sp.; Sladen: 438–439, pl. 66, figs. 3–4, pl. 67, figs. 9–10.

1889. *Stichaster talismani*; Sladen: 431.

$^{\$}$1891. *Calycaster monecus*, species nova; Perrier: 262–264.

$^{\$}$1892. *Neomorphaster eustichus*; Bell: 87.

$^{\$}$1894. *Gastraster margaritaceus*, E. Perrier; Perrier: 103–105, pl. 9, Fig. 4.

$^{\$}$1894. *Neomorphaster Talismani*, E. Perrier; Perrier: 134–137, pl. 10, fig. 2.

1895c*. Neomorphaster Parfaiti* E. Perrier; Koehler: 443–444.

1895c*. Neomorphaster eustichus;* Koehler: 444.

$^{\$}$1896a. *Neomorphaster* Talismani, E. Perrier; Perrier: 30.

$^{\$}$1896a. *Calycaster monœcus*, E. Perrier; Perrier: 28–29, pl. 2, figs. 2, 2a, pl. 3, figs. 3, 3a.

$^{\$}$1909. *Neomorphaster Talismani*, (Perrier); Koehler: 107–108, pl. 6, fig. 5.

$^{\$}$1921a. *Neomorphaster Talismani* (Perrier); Koehler: 2.

1927a. *Neomorphaster talismani* E. Perrier; Mortensen: 134–135, fig. 76.

1927a. *Gastraster margaritaceus* Perrier; Mortensen: 137–138, fig. 78.

1930. *Gastraster margaritaceus* (Perrier); Fisher: 207.

1930. *Neomorphaster talismani* Perrier; Fisher: 212.

1932. *Calycaster monaecus* Ed Perrier; Grieg: 44.

1992. *Neomorphaster margaritaceus* new comb. (Perrier); Clark & Downey: 406, figs. 61g–h, pl. 99, figs. A–D.

1999. *Neomorphaster margaritaceus* (Perrier, 1882); Ringvold: 471.

1999. *Neomorphaster margaritaceus* (Perrier, 1882); Sneli: 251.

2005. *Neomorphaster margaritaceus* (Perrier, 1882); García-Diez *et al*.: 48.

Type locality: Bay of Biscay (N44°05'00" W7°05'46").

See: Perrier (*in* Milne-Edwards 1882: 46, as *Pedicellaster margaritaceus*); Clark & Downey (1992); Sneli (1999); Dilman (2008: 147).

Distribution: Northeast Atlantic, from Faroe waters southwards in the Rockall Trough to the archipelagos of the Azores and Canaries; reported as well to the Faraday Seamount in the Mid-Atlantic Ridge.

Depth: 400–2,102(?5,413) m (AZO: 938–2,102 m).

Habitat: soft substrates, from pteropod ooze, mud to sand; also on gravel and hard substrates.

Remarks: Koehler (1909) identified material belonging to *Neomorphaster margaritaceus* (= *Neomorphaster talismani*) collected between the Azores and Canaries by RV 'Princesse Alice' at a depth of 5,413 m (sta 1787: N31°07' W24°03'07'). Koehler commented on the possibility of mislabelling, since the station was far too deep for the occurrence of this species. Later works considered this depth as an exception but nevertheless valid (*e.g.,* Mortensen 1927a; Harvey *et al*. 1988; Clark & Downey 1992). We are inclined to agree with Koehler (1909) as the second deepest record reported in the bibliography is of 2,102 m (RV 'Princesse Alice', sta 624: N38°59'00" W28°18'05") and most of all other records tend to be well above this 2,000 m limit.

Family Zoroasteridae Sladen, 1889
Genus *Zoroaster* Thomson, 1873

Zoroaster fulgens Thomson, 1873

$^\$$1885c. *Zoroaster longicauda*, sp. nov.; Perrier: 19–21.
$^\$$1891. *Prognaster Grimaldii*, species nova; Perrier: 259–262.
$^\$$1894. *Prognaster* longicauda, sp. nov.; Perrier: 120–125, pl. 10, fig. 1.
$^\$$1896a. *Prognaster Grimaldii*, Perrier; Perrier: 23–25, pl. 2, figs. 1, 1a, 1b.
1927a. *Zoroaster longicauda* Perrier; Mortensen: 131.
1975. *Zoroaster fulgens* W. Thomson; Sibuet: 108.
$^\$$2008. *Zoroaster fulgens* Wyville Thomson, 1873; Dilman: 147.

Type locality: Faroe Channel (lectotype).

See: Farran (1913: 19–22, pl. 1, fig. 3); Mortensen (1927a: 132–133, fig. 75); Downey (1970: 15–17); Clark & Downey (1992: 403–404, figs. 61c–d, 67a, pl. 96, figs. G–H); Tyler *et al.* (1984); Sneli (1999: 250–251, fig. 6); Benavides-Serrato *et al.* (2011: 204–205).

Distribution: Atlantic Ocean, from Newfoundland south to Brazil, eastwards from south of Iceland and the Faroe Channel south to Angola, including the Azores, Canaries and Cabo Verde.

Depth: (?120) 220–4,810 m (AZO: 2,870–3,050 m).

Habitat: soft substrates (ooze, muddy sand, sand to gravel).

Type of Development: lecithotrophic.

Remarks: *Zoroaster fulgens* presents a high degree of variation throughout its geographic and depth range and was described under several synonyms and varieties (see Downey 1970). Historically, the presence of this species in the Azorean waters was recorded under the names *Zoroaster longicauda* (= *Prognaster longicauda*) (Perrier 1885c, 1894; RV 'Talisman') and *Prognaster grimaldii* (Perrier 1891, 1896a; RV 'Hirondelle'). Both species were known only from the material described by Perrier and in the latter case was known only from the Azores. Downey (1970) considered these species as junior synonyms of *Z. fulgens* though he had some concerns in the case of *Z. longicauda*. Later, Clark & Downey (1992) reunited all specimens attributed to the genus previously under the name Z. *fulgens*, including the two Azorean species. More recently, Dilman (2008) reported material belonging to *Z. fulgens* collected by RV 'G.O. Sars' ('MAR–ECO' cruise) in northern Azorean waters, removing any remaining doubts of its occurrence in the archipelago.

In her review on this species, Downey (1970) noted that *Z. fulgens* from the northern part of its range tends to be more spinose and more robust and is generally found below 1,830 m. In contrast, on southern part of its range, this species can be found at depths as shallow as 365 m and tend to have a more compact skeleton, less spinose and slender arms. In turn, Howell *et al*. (2004) identified three depth related morphotypes in Porcupine Seabight (SW of Ireland): a robust form (925–1,750 m), a slender form (1,300–2,200 m) and a long-armed form (3,300–4,020 m). Genetic analysis revealed that these forms are reproductively isolated, and the shallower robust morphotype might represent a distinct species. The known depth range of *Z. fulgens* in the Azores is between the depth intervals recorded by Howell *et al*. (2004) for the two deeper forms. The arm length/disc radius ratio presented by Perrier (1894, 1896a) for *Z. longicauda* (from 2995 m depth) and for *P. grimaldii* (from 2870 m depth) were respectively 16 and 15, both well above the 9.7 given by Howell *et al*. (2004) for the long-armed form. More recently, Dilman (2008) reported material belonging to *Z. fulgens* collected by *G.O. Sars* (*MAR–ECO* cruise) from in northern Azorean waters depths between 2954 and 3050, but gave no descriptions.

Superorder Valvatacea Blake, 1987
Order Notomyotida Ludwig, 1910
Family Benthopectinidae Verrill, 1899
Genus *Cheiraster* Studer, 1883
Subgenus *Cheiraster* Studer, 1883

***Cheiraster* (*Cheiraster*) *sepitus* (Verrill, 1885a)**

$1889. *Pontaster venustus* n. sp.; Sladen: 52–55, pl. 8, figs. 5, 6, pl. 12, figs. 5, 6.

$1894. *Pontaster venustus*, Sladen; Perrier: 287–288.

$1896a. *Pontaster venustus*, Sladen; Perrier: 47.

$1909. *Pontaster venustus*, Sladen; Koehler: 14–15, pl. 1, fig. 13.

$1921a. *Pectinaster* (*Pontaster*) *venustus* Sladen; Koehler: 2.

$1981. *Cheiraster* (*Cheiraster*) *sepitus* (Verrill); Clark: 117–118, figs. 4i–r, 5c.

1988. *Cheiraster sepitus* (Verrill, 1885); Harvey *et al*.: 160–161.

1992. *Cheiraster* (*Cheiraster*) *sepitus* (Verrill); Clark & Downey: 129–130, figs. 22d–e, 23b, pl. 31, figs. D–H.

2005. *Cheiraster sepitus* (Verrill, 1885); García-Diez *et al*.: 47.

2011. *Cheiraster* (*Cheiraster*) *sepitus* (Verrill, 1885); Benavides-Serrato *et al*.: 142.

Type locality: S of Cape Sable, Nova Scotia, USA.

See: Clark (1981); Clark & Downey (1992); Benavides–Serrato *et al.* (2011).

Distribution: North Atlantic, from Nova Scotia south to the Caribbean, east from west of Iceland and the Rockall Trough southwards to the Cabo Verde area including the Azores.

Depth: 304–3,706 m, mostly 1,000–2,000 m (AZO: 1,165–3,706 m).

Habitat: soft bottoms, muddy sand to ooze.

Remarks: the inaccurate original description of the type material by Verrill (1885a) and subsequent multiplicity of synonymies resulted in an unclear geographical and bathymetric range for *Cheiraster sepitus* (Clark 1981; Clark & Downey 1992).

Genus *Pectinaster* Perrier, 1885c

Pectinaster filholi Perrier, 1885c

$1894. *Pectinaster Filholi*; Perrier: 280–285, pl. 18, figs. 2a–b, pl. 20, figs. 3a–d.

1927a. *Pectinaster Filholi* Perrier; Mortensen: 71.

1972. *Pectinaster filholi* Perrier; Cherbonnier & Sibuet: 378.

1981. *Pectinaster filholi* Perrier, 1885; Clark: 118–121.

1983. *Pectinaster filholi* Perrier, 1885; Gage *et al*.: 277.

$1992. *Pectinaster filholi* Perrier; Clark & Downey: 139–140, figs. 21b, 22l–m, pl. 34, figs. A–C.

2006. *Pectinaster filholi* Perrier, 1885; Dilman: 184.

2008. *Pectinaster filholi* Perrier, 1885; Dilman: 139.

2013. *Pectinaster filholi* Perrier, 1885; Dilman: 569.

2014. *Pectinaster filholi*, Perrier 1885; Dilman: 31.

Type locality: off Cap Blanc.

See: Clark (1981); Clark & Downey (1992).

Distribution: Atlantic; in the west from south of Nova Scotia to Delaware; in the east from the Rockall Trough southwards to South Africa and on the Mid-Atlantic Ridge, from the Reykjanes Ridge (South of Iceland) south to the Charlie-Gibbs Fracture Zone and the Azores; also reported off the River Plate, South America.

Depth: 1,258–4,850 m (AZO: 1,258 m).

Habitat: soft sediment, mud or *Globigerina* ooze.

Type of Development: lecithotrophic.

Remarks: Perrier (1885c, 1894) described the deep sea asteroid *Pectinaster filholi* based on the material collected by RV 'Talisman', which included the only known specimen from Azorean waters (sta 126, 1883: N38°37' W28°20'46", 1,258 m), the same specimen re-examined later by Clark & Downey (1992).

Order Paxillosida Perrier, 1884

Family Astropectinidae Gray, 1840

Genus *Astropecten* Gray, 1840

***Astropecten aranciacus*? (Linnaeus, 1758)**

?$^{\$}$1950. *Astropecten aranciacus* (Linné 1758); Madsen: 180–181.

Type locality: Mediterranean Sea.

See: Hörstadius (1938); Tortonese (1965: 137–140, figs. 60–61); Zulliger *et al.* (2009).

Distribution: Eastern Atlantic and Mediterranean Sea; from Portugal south to Angola, including the archipelagos of the ?Azores, Madeira, Canaries and Cabo Verde.

Depth: 1–183 m.

Habitat: soft sediments (biogenic detritus to sandy silt bottoms); also in *Zostera* and *Posidonia* prairies.

Type of Development: planktotrophic (*c*. 60–80 days).

Remarks: the presence of *Astropecten aranciacus* in Azores is based on a single specimen reported by Madsen (1950) with no further collection data (?Copenhagen Museum). The presence of this species in the Azores would be expected considering the widespread distribution of this species in the north-eastern Atlantic, including most of the archipelagos (Zulliger *et al*. 2009). However, the lack of any other animals from the islands of this well-known shallow-water species casts some doubt on Madsen's report suggesting the possibility of a mislabelled specimen. The presence of *A. aranciacus* in the Azores should, therefore, be considered with caution until new material of this species is retrieved from the archipelago's waters.

***Astropecten hermatophilus* Sladen, 1883**

(Fig. 5.15)

$^{\$}$1883. *Astropecten hermatophilus*, n. sp.; Sladen: 257–259.

$^{\$}$1888. *Astropecten pentacanthus* Phil.; Simroth: 231.

$^{\$}$1889. *Astropecten hermatophilus*, Sladen; Sladen: 207–208, pl. 33, figs. 5–6, pl. 37, figs. 7–9).

1897. *Astropecten pentacanthus* (Delle Chiaje); Ludwig: 39–47, pl. 2, fig. 5, pl. 6, fig. 8.

1914b. *Astropecten irregularis* var. *pentacanthus*; Koehler: 273.

$^{\$}$1917. *Astropecten hermatophilus* Sladen; Döderlein: 91–92, 172, pl. 3, figs. 8, 9, 9a.

1927a. *Astropecten hermatophilus* Sladen; Mortensen: 57.

1950. *Astropecten irregularis* f. *pentacanthus* (Delle Chiaje 1825); Madsen: 169–170.

$^{\$}$1992. *Astropecten hermatophilus* Sladen; Clark & Downey: 36, figs. 11h–j, pl. 8D, E.

1997. *Astropecten hermatophilus* Sladen, 1883; Pereira: 335.

2010. *Astropecten hermatophilus* Sladen, 1883; Micael & Costa: 322.

2012. *Astropecten hermatophilus* Sladen, 1883; Micael *et al.*: 5.

Type locality: Azores (N38°38’00” W28°28’30”).

See: Sladen (1883, 1889); Clark & Downey (1992); Moreno-Batet & Bacallado (1980: 124, fig. 2).

Distribution: Northeast Atlantic; known from the Azores, Canaries and Gulf of Guinea.

Depth: 10–165(?823) m [AZO: 10–165 (?823) m].

Habitat: buried in soft substrates, mud or sand, feeding on small infaunal organisms, *e.g.,* bivalve *Ervilia castanea* (Montagu, 1803).

Material examined: DBUA-ECH 056 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2009.12.03, 10 m; 2 dry spms, R=16–24 mm, r=5–7 mm); DBUA-ECH 057 [Cerco, Caloura (buried in sand), SMG, AZO, *c.* N37°42’26” W25°30’37”, 2010.08.13, 20 m; 1 dry spm; R=7, r=3 mm]; DBUA-ECH 059 (SMG, AZO; 2 spms, R=20–27 mm, r=6–8 mm); DBUA-ECH 060 (SMG, AZO; 2 spms, R=19–20 mm, r=7); DBUA-ECH 061 (Vila Franca do Campo, SMG, AZO, *c.* N37°42’50” W25°25’58”; 3 spms, R=6–8 mm, r=3 mm); DBUA-ECH 062 (Água d’Alto, SMG, AZO, *c.* N37°42’55” W25°28’27”, 1993.07.29; 7 spms, R=7–10 mm, r=3–4 mm); DBUA-ECH 098 (Horta, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2010.6.25, 15 m; 1 spm, R=20 mm, r=7 mm); DBUA-ECH 099 (SMG, AZO; 1 spm, R=15 mm, r=6 mm); DBUA-ECH 101 (SMG, AZO; 2 spm, R=20–27 mm, r=7–9 mm); DBUA-ECH 102 (SMG, AZO; 1 spm, R=19 mm, r=6 mm); DBUA-ECH 116 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2011.07, 20 m; 1 spm, R=4 mm, r=2 mm); DBUA-ECH 167 (SMG, AZO; 3 spms, R=5–6 mm, r=2–3 mm).

Description: body pentagonal, flattened dorsoventrally, with five broadly triangular arms. R/r ratio between 2.2–2.3 in the smaller specimens (R <7 mm) to 3.2–3.4 in the larger (R >16 mm); paxillar area much broader than the marginal one, densely covered by paxillae, particularly in the area of the epiproctal cone, which is especially prominent in smaller individuals (R <10 mm). Paxillar spinelets with swollen rounded blunt tips giving an overall granulose aspect to the paxillar area; maximum number of paxillar spinelets present variable, from less than six marginal spinelets with no central

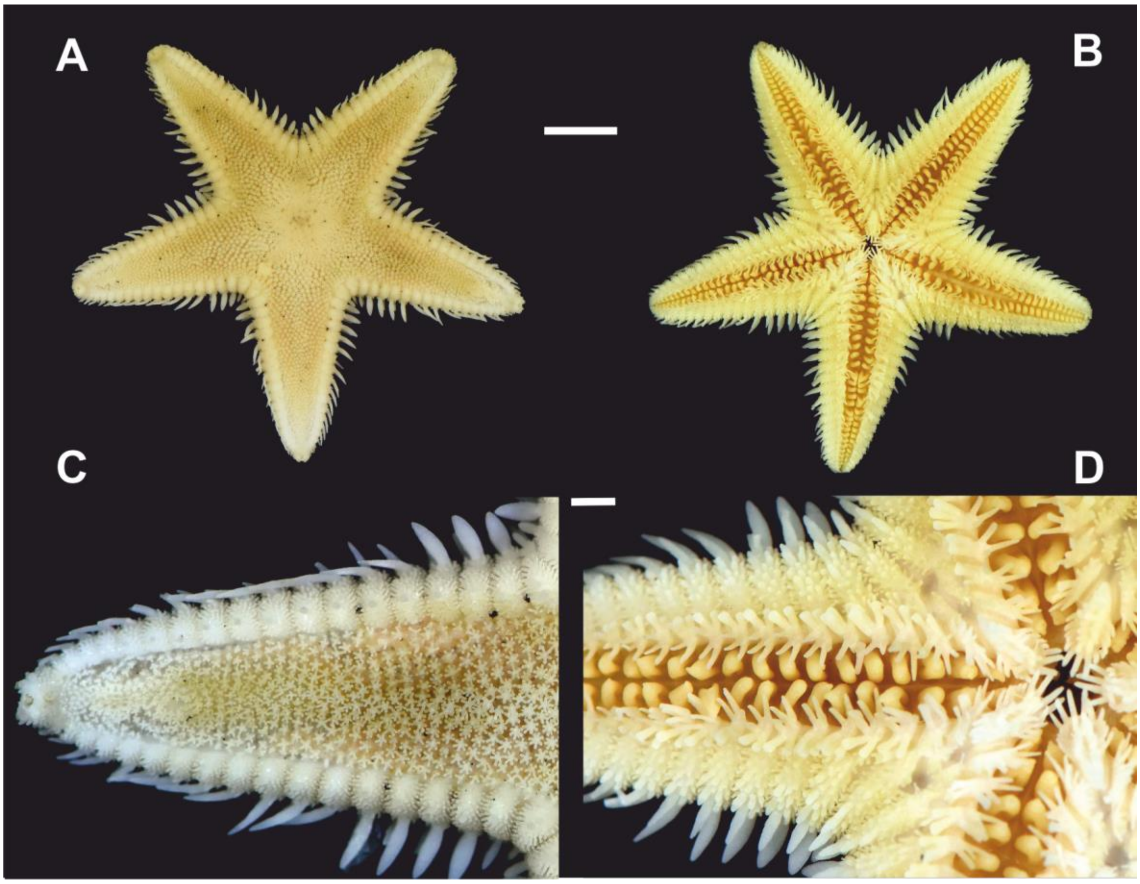


Figure 5.15. *Astropecten hermatophilus* Sladen, 1883 (DBUA-ECH 059). Dorsal view (A); ventral view (B); detail of the arm dorsal view (C); detail of the oral area and arm (D); scale bars are 5 mm (A, B) 1 mm (C, D).

spinelet in the smaller specimens (R <7 mm) to ten to eleven spinelets surrounding up to six central spinelets in the larger specimens (R=27 mm); central spinelets shorter and more rounded (blunt) than the marginal ones. Madreporite oval. Superomarginal plates small, narrow, tumid, vertical and granulose with a stubby spine or larger tubercle on some or all plates; occasionally a second spine is also present in one or two of the innermost plates on each side of the median interradial line. Number of superomarginal plates (SM) varies proportionally with size, from about 0,5–0,7 SM/R in smaller specimens (R <6 mm) up to 1,0–1,2 SM/R in larger specimens (R >19 mm). In smaller specimens (R <10 mm), each inferomarginal plate has a compressed, lanceolate spine followed by a similar spine, which is about two-thirds shorter. Both spines are aligned slightly oblique to the median line of the plate and become progressively slender towards the tip of the arm. In larger specimens, a third spine is generally present, though its maximum size is less than half the size of the adjacent spine and it tends to disappear distally. On the inferomarginal plates towards the tip of the arm, in larger specimens (R >15 mm), a third spine is sometimes present next to the largest spine, though very short (a third or less the size of the largest spine) and very slender, having thus the appearance of a supplementary spinelet. Three adambulacral furrow spines truncate or rounded. Subambulacral spines in two rows, broadly truncate, larger than furrow spines; on few of the innermost plates of the larger specimens (<20 mm) one or two supplementary spinelets may be present; no pedicellaria; dorsal paxillar area whitish-yellow to brown with superomarginals and ventral surface white. Shells of the marine bivalve *Ervilia castanae* were found in the stomachs of the many of the specimens.

Remarks: *Astropecten* with over 150 described species worldwide (Zulliger & Lessios 2010) is one of the most difficult shallow-water asteroid genera, encompassing highly polymorphic species with several described subspecies, local varieties and intermediate forms among sympatric species. Thorough the years several authors attempted to revise this genus (*e.g.,* Döderlein 1917; Clark & Downey 1992; Zulliger & Lessios 2010) though the matter still remains far from resolved. The history of the echinoderm faunal studies in the Azores is a good example of how difficult this genus is. Of a total of five species of *Astropecten* reported at one time to the archipelago, two were dismissed as erroneous since they proved to have been based on misidentifications [*A. irregularis pentacanthus* (Delle Chiaje, 1827)] or on invalid synonymy [*A. bispinosus* (Otto, 1823)]; another two were considered as dubious due to substantiated concerns on the validity of the identifications or on the provenance of the reported specimens [*A. aranciacus* (Linnaeus, 1758) and *A. platyacanthus* (Philippi, 1837)]. Ultimately, the only astropectinid known with certainty from the Azores is *A. hermatophilus*. This species was described by Sladen (1883, 1889) based on a specimen collected by RV 'H.M.S. Challenger' in the Azores (sta 75: N38°38' W28°28'30", 823 m). In 1888, Simroth included the Mediterranean *A. pentacanthus* among the species collected by him in the Azores. Later, Döderlein (1917) re-identified Simroth material as *A. hermatophilus*. Almost one hundred years later, *A. hermatophilus* was also reported from the Canaries (Moreno-Batet & Bacallado 1980) and the Gulf of Guinea (Clark & Downey 1992). The latter species is only known from small animals; the type specimen as described by Sladen (1889) is one of the largest specimens known (R=25 mm) (see also Döderlein 1917; Moreno-Batet & Bacallado 1980; Clark & Downey 1992). This feature led some authors to question the validity of the species (*e.g.,* Clark & Downey 1992; Zulliger & Lessios 2010). Regardless, on comparing our largest specimen (R = 27 mm) we could clearly recognize the original description and illustrations by Sladen (1889). As our material included specimens covering a relatively large size spectrum, it was possible to conclude that deviations from the type were size-dependent (*e.g.,* number of paxillar spinelets, number of inferomarginal fringe spines). Additionally, some of the specimens observed herein had shells of the bivalve *Ervilia castanae* in their stomachs and in many instances the shells of this little bivalve were almost as big as the sea star disc.

The depth range of *Astropecten hermatophilus* seems quite remarkable. Sladen (1883, 1889) erected this species on the basis of an animal collected by RV 'H.M.S. Challenger', between Faial and São Jorge islands at a reported depth of 823 m (450 ftms). Interestingly, at the same station he identified as well *Ophidiaster ophidianus* (Lamarck, 1816) and *Hacelia attenuata* Gray, 1840 (= *Ophidiaster attenuatus*), both strictly littoral species. Sladen also reported *Chaetaster longipes* (Bruzelius, 1805) for the same station; though not littoral this species tends to occur at much shallower waters than 820 m. At first instance, it seems that the depth data presented for station 75 should be much shallower than the one presented by Sladen. In contrast, Agassiz (1881) working with the RV 'H.M.S. Challenger' echinoids indicated two sets of depth values of 92–165 m (50–90 ftms) and 823 m (450 ftms) for station 75, though the species identified by the author among the material from station 75 have a wider known bathymetrical range than the species mentioned above (*e.g., Genocidaris maculata* Agassiz, 1869). Thus, the echinoderms altogether found at this station indicate problems relating to the depth data, and Agassiz's (1881) shallower depth values appear more realistic. One has to keep in mind that HMS Challenger dredged three times at station 75, which is in an area of high bottom relief and thus delivered material from different depths (namely 50, 90, and 450 fathoms according to the ship log (Thomson & Murray 1885). Apparently, all the material resulting from these three dredges was attributed to station 75, thus causing the confusion mentioned above.

Astropecten platyacanthus? (Philippi, 1837)

?$^{\$}$1888. *Astropecten platyacanthus* Müller et Troschel; Barrois: 71.

1897. *Astropecten bispinosus* (Otto); Ludwig: 16–31, pl. 2, fig. 6, pl. 6, fig. 6.

1914b. *Astropecten platyacanthus*; Koehler: 274.

1921b. *Astropecten bispinosus* Otto; Koehler: 46–47, fig. 33, 34.

1927a. *Astropecten bispinosus* Otto; Mortensen: 56.

1934. *Astropecten bispinosus* (Otto); Parenzan: 211–216, fig. 7.

1938. *Astropecten bispinosus* (Otto); Nobre: 51–52, figs. 23, 24.

1950. *Astropecten bispinosus* (Otto 1823); Madsen: 181–182.

1965. *Astropecten bispinosus* (Otto); Tortonese: 140–141, fig. 62.

1997. *Astropecten platyacanthus* (Philippi 1837); Pereira: 336.

2010. *Astropecten bispinosus* (Otto, 1823); Micael & Costa: 322.

2012. *Astropecten bispinosus* (Otto, 1823); Micael *et al.*: 5.

Type locality: Mediterranean Sea.

See: Tortonese (1965: 142–143, figs. 63, 64).

Distribution: Mediterranean Sea; reported also from the ?Azores.

Depth: 2–64 m (?AZO: 15–20 m).

Habitat: soft substrates, on sand and mud.

Remarks: the first and only record of *Astropecten platyacanthus* in the archipelago was reported by Barrois (1888), based on the identification by Ludwig. Historically, *Astropecten platyacanthus* was considered by many authors as a variety of *A. bispinosus* (Otto, 1823). In his review of the Mediterranean sea stars Ludwig (1897) re-assigned Barrois (1888) record under the later species, a decision repeated in later literature. Clark & Downey (1992) considered both *A*. *bispinosus* and *A*. *platyacanthus* endemic to the Mediterranean, and stated that the reports from the Atlantic were based on misidentifications or doubtful locality data. Pereira (1997) concludes that the occurrence of this species in the Azores is possible but unlikely. See above remarks under *A*. *hermatophilus*.

Genus *Dytaster* Sladen, 1889

Species *Dytaster grandis* (Verrill, 1884)

Dytaster grandis grandis (Verrill, 1884)

$^{\$}$1889. *Dytaster biserialis*, n. sp.; Sladen: 77–79, pl. 13, figs. 3, 4.

1894. *Dytaster biserialis*; Perrier: 299.

$1909. *Dytaster agassizi*, Perrier; Koehler: 22, pl 4, fig. 7, pl. 6, fig. 1.

$1909. *Dytaster rigidus*, Perrier; Koehler: 25, pl. 3, fig. 6.

1927a. *Dytaster biserialis* Sladen; Mortensen: 54.

1927a. *Dytaster Agassizi* Perrier; Mortensen: 55.

1927a. *Dytaster rigidus* Perrier; Mortensen: 55.

1972. *Dytaster agassizi* Perrier; Cherbonnier & Sibuet: 377.

1975. *Dytaster agassizi* Perrier; Sibuet: 101.

1992. *Dytaster grandis grandis* (Verrill); Clark & Downey: 53, figs. 13a–c, pl. 15, figs. A, B.

2005. *Dytaster grandis grandis* (Verrill, 1884); García-Diez *et al*.: 46.

$2008. *Dytaster grandis grandis* (Verrill, 1884); Dilman: 132–134.

2013. *Dytaster grandis* (Verrill, 1884); Dilman: 566.

2014. *Dytaster grandis* (Verrill, 1884); Dilman: 26.

Type locality: east coast of USA (from Cape Hatteras to Nova Scotia).

See: Tyler *et al.* (1990); Clark & Downey (1992); Howell *et al.* (2003); Dilman (2014).

Distribution: North Atlantic, in the west, from the US east coast to the Gulf of Mexico; in the east it is reported from the Porcupine Abyssal Plain (SW of Ireland) and the Bay of Biscay to SW Africa, along the Mid-Atlantic Ridge from the Charlie-Gibbs Fracture Zone to the Azores. The subspecies *D. grandis nobilis* Sladen, 1889 is restricted to the Southwest Atlantic.

Depth: 1,000–5,124 m (AZO: 2,954–5,005 m).

Habitat: soft sediments, from mud to ooze; predator (*e.g.,* on other echinoderms) and scavenger, ingesting sediment.

Development: planktotrophic.

Remarks: when revising *Dytaster* from the Atlantic, Clark & Downey (1992) reunite the following records from the Azores under the name *Dytaster grandis grandis*: *D. biserialis* described by Sladen (1889) on the basis of material collected by RV 'H.M.S. Challenger' (sta 79: N36°21' W23°31', 3,706 m), *D. agassizi* and *D. rigidus* both reported by Koehler (1909) based on specimens collected by RV 'Princesse Alice'.

Dytaster insignis (Perrier, 1884)

$1972. *Dytaster exilis* Sladen; Cherbonnier & Sibuet: 376–377.

Type locality: Gulf of Mexico.

See: Downey (1973: 35–36, pl. 9, figs. C–D); Gage *et al.* (1983: 274); Clark & Downey (1992: 54, pl. 16, figs. G–H); Dilman (2013: 566; 2014: 26).

Distribution: Atlantic deep-waters, reported to the Gulf of Mexico and the Caribbean, eastwards to the Rockall Trough and the Charlie-Gibbs Fracture Zone, south to the Azores; also occurring off Tristan da Cunha.

Depth: 2,515–3,670 m (AZO: 2,844–3,670 m).

Habitat: soft deep sea ooze; omnivorous scavenger.

Development: planktotrophic.

Remarks: the geographic distribution of the relatively poorly known asteroid *Dytaster insignis* is based on a few isolated reports. Cherbonnier & Sibuet (1972) recorded the species *Dytaster exilis* in the Azores (RV 'Jean Charcot', 'Noratlante' cruise: sta P62C03: N36°47'4" W27°11'7", 3,670 m; sta P65B10: N36°58'2" W26°20', 2,871 m), remarking that the specimens were close to the variety *carinata*. Clark & Downey (1992) listed this variety as a synonym of *D. grandis grandis*, a subspecies already known from the Azores. However, Cherbonnier & Sibuet (1972) concluded that though close to the variety '*carinata*', the total absence of pedicellaria on the dorsal surface of the disc and arms placed the specimens close as well to the *D*. *exilis* type, a species presently accepted as *D*. *insignis* (Downey 1973). Using the presence/absence of pedicellaria on dorsal surface as diagnosing character alone and comparing with the descriptions by Clark & Downey (1992) of both D. *grandis grandis* and *D*. *insignis*, we are inclined to include the Azorean specimens under the latter species. Furthermore, Dilman (2014) seems to agree with our conclusions, and listed Cherbonnier & Sibuet (1972) Azorean record under this species. Overall, the record from the Azores together with the reports to the Rockall Trough (Gage *et al*. 1983) and to the Charlie-Gibbs Fracture Zone, on the Mid-Atlantic Ridge north of the Azores (Dilman 2013) further substantiate the presence of this species in the East Atlantic.

***Dytaster intermedius* Perrier, 1891**

$^{\$}$1896a. *Dytaster intermedius* E. Perrier; Perrier: 48, pl. 3, figs. 2, 2a, 2b.

1927. *Dytaster intermedius* Perrier; Mortensen: 55.

1992. *Dytaster intermedius* Perrier; Clark & Downey: 54–55.

2005. *Dytaster intermedius* Perrier, 1891; García–Diez *et al*.: 46.

Type locality: Azores (N41°40'41" W29°04'23").

See: Perrier (1891: 271; 1896a); Clark & Downey (1992: 54–55).

Distribution: known only from the Azores.

Depth: 2,870 m (AZO).

Habitat: soft sediments (muddy sand).

Remarks: *Dytaster intermedius* is known only from the type material collected in the Azores by RV 'Hirondelle' (sta 248: N41°40'41" W29°4'23", 2,870 m; three specimens). Clark & Downey (1992) believed that this species might represent a juvenile of another *Dytaster* species. The question is still pending and the type material of *D. intermedius* has not been revised to date.

Dytaster mollis **(Perrier, 1885c)**

$^{\$}$1894. *Crenaster mollis*, E. Perrier; Perrier: 310–312, pl. 18, fig. 3.

1927a. *Dytaster* (*Crenaster*) *mollis* Perrier; Mortensen: 55.

$^{\$}$1949. *Dytaster mollis* (E. Perrier); Clark: 372–373.

$^{\$}$1992. *Dytaster mollis* (Perrier); Clark & Downey: 55, pl. 16, figs. E–F.

2014. *Dytaster mollis* (Perrier, 1885); Dilman: 26.

Type locality: Azores (N38°38'00" W25°05'46").

See: Perrier (1894); Clark & Downey (1992).

Distribution: known only from the Azores.

Depth: 2,560–2,995 m (AZO).

Habitat: soft mud.

Remarks: *Dytaster mollis* is known only from a few specimens, all less than 45 mm in length, collected by the RVs 'Talisman' and 'Atlantis' in Azorean deep waters. Clark & Downey (1992) believed that this species might represent juveniles of another *Dytaster* species.

Genus *Persephonaster* Wood-Mason & Alcock, 1891

Persephonaster patagiatus **(Sladen, 1889)**

$^{\$}$1896a. *Psilaster Andromeda*, Düben et Karen; Perrier: 51.

$^{\$}$1909. *Psilasteropsis patagiatus*, (Sladen); Koehler: 62–63, pl. 3, fig. 2, pl. 4, fig. 3, pl. 19, fig. 1.

$^{\$}$1921a. *Psilasteropsis patagiatus* (Sladen); Koehler: 2.

1913. *Psilasteropsis patagiatus* (Sladen); Farran: 7.

1927a. *Persephonaster patagiatus* (Sladen); Mortensen: 65–66, fig. 37.

1932. *Psilasteropsis patagiatus* Sladen; Grieg: 19.

1983. *Psilaster patagiatus* Sladen, 1889; Gage *et al*.: 275.

1992. *Persephonaster patagiatus* (Sladen); Clark & Downey: 63–64, figs. 14d, 15f–g, pl. 19, figs. A–C.

2005. *Persephonaster patagiatus* (Sladen, 1889); García-Diez *et al*.: 46.

2006. *Persephonaster patagiatus* (Sladen, 1889); Dilman: 180.

2014. *Persephonaster patagiatus* (Sladen, 1889); Dilman: 27.

Type locality: off Cabo Verde.

See: Harvey *et al.* (1988: 159–160); Clark & Downey (1992); Benavides-Serrato *et al.* (2011: 127).

Distribution: North Atlantic, from the Denmark Strait SW of Iceland, south of the Rockall Trough to NW Africa, including the Azores, Madeira and Cabo Verde; also reported for the Gulf of Mexico and the Caribbean.

Depth: 730–2,165(?2,970) m (AZO: 1,095–1,919 m).

Habitat: soft sediments.

Development: lecithotrophic.

Remarks: Perrier (1896a) reported *Psilaster andromeda* based on material collected by RV ‘Hirondelle’ in the Azores. Later, Koehler (1909) re-examined the material and concluded that Perrier confused *P. andromeda* with *Persephonaster patagiatus* (= *Psilasteropsis patagiatus*), and reassigned the specimens to the latter species (see remarks under *P. andromeda andromeda*).

***Persephonaster sphenoplax* (Bell, 1892)**

$^{\$}$1909. *Astropecten sphenoplax*, J. Bell; Koehler: 42, pl. 17, fig. 8.

$^{\$}$1909. *Persephonaster humilis*, Kœhler; Koehler: 61–62, pl. 19, figs. 2–4.

1927a. *Astropecten sphenoplax* Bell; Mortensen: 59.

1927a. *Persephonaster humilis* (Koehler); Mortensen: 64.

1972. *Astropecten sphenoplax* Bell; Cherbonnier & Sibuet: 374.

$^{\$}$1992. *Persephonaster sphenoplax* (Bell); Clark & Downey: 65–66, figs. 14e, f. h–j, I, 15i, j, pl. 20, figs. A–C.

2005. *Persephonaster sphenoplax* (Bell, 1892); García-Diez *et al*.: 46.

Type locality: NW of Ireland.

See: Clark & Downey (1992).

Distribution: Northeast Atlantic, from the Rockall Trough to the northern part of the Bay of Biscay, in the Azores; possibly also in the SE of Florida.

Depth: (?675)820–1,187 m (AZO: 845–1,187 m).

Habitat: soft to hard substrates.

Remarks: Clark & Downey (1992) remarked that Bell's incomplete original descriptions might have led Koehler (1909) to fail to recognise *Persephonaster sphenoplax* in the Azorean material he used to erect *Persephonaster humilis*. The former authors compared material belonging to both species and concluded them to be conspecific, dismissing morphological differences as size-related.

Genus *Plutonaster* Sladen, 1889

Species *Plutonaster agassizi* Verrill, 1880

Plutonaster agassizi notatus **Sladen, 1889**

$^{\$}$1889. *Plutonaster notatus*, n. sp.; Sladen: 97–99, pl. 14, figs. 6–7, pl. 15, figs. 5–6.

$^{\$}$1889. *Plutonaster abbreviatus*, n. sp.; Sladen: 99–100.

1894. *Plutonaster abbreviatus*; Perrier: 313.

1894. *Plutonaster notatus*; Perrier: 318–319.

$^{\$}$1896a. *Plutonaster inermis*, E. Perrier; Perrier: 49.

$^{\$}$1896a. *Plutonaster notatus*, Sladen; Perrier: 49.

$^{\$}$1896a. *Plutonaster granulosus*, E. Perrier; Perrier: 49–50, pl. 4, figs. 2, 2a–2d.

$^{\$}$1909. *Plutonaster notatus*, Sladen; Koehler: 17–18, pl. 3, fig. 5, pl. 10, figs. 7–12.

$^{\$}$1909. *Plutonaster rigidus*, Sladen; Koehler: 19–22, pl. 4, fig. 6, pl. 10, figs. 5–6.

$^{\$}$1921a. *Plutonaster notatus* Sladen; Koehler: 2.

$^{\$}$1921a. *Plutonaster rigidus* Sladen; Koehler: 2.

1927a. *Plutonaster rigidus* Sladen; Mortensen: 63.

1927a. *Plutonaster notatus* Sladen; Mortensen: 63.

1927a. *Plutonaster abbreviatus* Sladen; Mortensen: 63.

1932. *Plutonaster agassizi* Verrill; Grieg: 14–15, pl. 4, figs. 2–4.

$^{\$}$1992. *Plutonaster agassizi notatus* Sladen; Clark & Downey: 70–71, pl. 17, figs. C–E.

2005. *Plutonaster agassizi notatus* Sladen, 1889; García-Diez *et al.*: 46–47.

$^{\$}$2008. *Plutonaster agassizi notatus* (Sladen, 1889); Dilman: 134–135.

Type locality: Azores (N38°30' W31°14').

See: Clark & Downey (1992); Dilman (2008).

Distribution: Northeast Atlantic, from the Charlie-Gibbs Fracture Zone in the Mid-Atlantic Ridge and off SW Ireland (*c.* N53° W20°) to the Bay of Biscay and the Azores, possibly in the Canaries and Madeira as well; the subspecies *P. agassizi agassizi* Verrill, 1880 is known from south of Newfoundland to the Caribbean and the Gulf of Mexico, as well as the Cabo Verde Archipelago, Ascension Island and South Africa.

Depth: 969–4,252 m (AZO: 1,165–2,178 m).

Habitat: soft substrates, pteropod ooze to muddy sand and rock.

Remarks: through the historical literature, several *Plutonaster* species were described from the Azores, including two species by Sladen (1889) based on specimens collected by RV 'H.M.S. Challenger' in the Azores: *P. notatus* (sta 73: N38°30' W31°14', 1,829 m) and *P. abbreviatus* (sta 78: N37°24' W25°13', 1,829 m). Perrier (1891, 1896a) described *P. granulosus* based on the material collected by RV 'Hirondelle' in the same area. The forms *P. inermis* and *P. rigidus* were also recorded from the Azorean waters respectively by Perrier (1896a) and Koehler (1909, 1921a). Clark & Downey (1992) concluded that all the above were conspecific and included all Azorean records in the subspecies *P. agassizi notatus*.

Genus *Psilaster* Sladen, *in* Thomson & Murray, 1885

Species *Psilaster andromeda* (Müller & Troschel, 1842)

Psilaster andromeda andromeda? (Müller & Troschel, 1842)

?$^{\$}$1894. *Psilaster Andromeda*; Perrier: 195–196.

1896a. *Psilaster Andromeda* Müller et Troschel; Perrier: 17.

1896a. *Psilaster Andromeda*, Düben et Karen; Perrier: 51.

?$^{\$}$1909. *Psilaster andromeda*, (Müller et Troschel); Koehler: 60, pl. 2, fig. 3, pl. 16, figs. 8–9.

1927a. *Psilaster andromeda* (Müller & Troschel 1842); Mortensen: 59–60, fig. 33.

1980. *Psilaster andromeda* (Müller & Troschel, 1842); Marques: 100.

1983. *Psilaster andromeda* (Müller & Troschel, 1842); Gage *et al*.: 274–275.

2005. *Psilaster andromeda andromeda* (J. Müller & Troschel, 1842); García-Diez *et al*.: 47.

Type locality: Kattegat (probably off Bohuslan, western Sweden).

See: Harvey *et al.* (1988: 159); Clark & Downey (1992: 77–78, figs. 14a, 15a–c, k, l, pl. 21, figs. D–G); Dilman (2006: 180).

Distribution: Northeast Atlantic cold waters, from the Arctic south to the SE of Greenland, the Reykjanes Ridge, Iceland-Faeroe Rise and from Scandinavia to the Bay of Biscay and the ?Azores; the subspecies *P. andromeda florae* (Verrill 1889) is known from south of Newfoundland to SE of Cape May, New Jersey (*c.* N38°30').

Depth: 70–2,965 m (?AZO: 140–1,440 m).

Habitat: soft sediments (mud or ooze); predates on molluscs, echinoderms (young spatangoids), foraminifera, etc.

Remarks: Clark & Downey (1992) reviewed the bathymetrical and geographical distributions of *Psilaster andromeda* and concluded that it could not be established with certainty. One of the main contributing factors is that this highly variable species has been frequently confused with other similar species, such as *Persephonaster patagiatus* and *P. sphenoplax*, both overlapping the geographic distribution of *Psilaster andromeda andromeda*. They further suggest that records south of the Bay of Biscay are zoogeographically unlikely, thus implying that the only known Azorean records by Perrier (1894, 1896a) are misidentifications. Historically, Koehler (1909) had already questioned the validity of the determinations made by Perrier on the material from the RVs 'Talisman' and 'Hirondelle' stating that the later author confused *P. andromeda* with *P. patagiatus*. On re-examination of the material taken by RV 'Hirondelle' Koehler confirmed his suspicions and remarked that all specimens belonged to the latter species. As for the material collected by RV 'Talisman', Koehler commented that both species were present. However, Clark & Downey (1992) suspected that Koehler himself confused *P. andromeda* with *P. sphenoplax*. Additionally, on finding a great variability of the diagnostic characters for *P. andromeda* subspecies Dilman (2006) showed some concerns on their subspecific value.

Family Luidiidae Sladen, 1889
Genus *Luidia* Forbes, 1839

Luidia ciliaris (Philippi, 1837)

$^{\$}$1920. *Luidia ciliaris* Philippi*;* Döderlein: 287–288, figs. 8, 17, 34.
1950. *Luidia ciliaris* (Philippi 1837); Madsen: 205–206, fig. 8.
1982a. *Luidia ciliaris* (Philippi); Clark: 170, fig. 3k.
1983. *Luidia ciliaris* (Philippi, 1837); Gage *et al*.: 272.
1992. *Luidia ciliaris* (Philippi); Clark & Downey: 11–12, figs. 7k, 8h, pl. 2, fig. E.
1999. *Luidia ciliaris* (Philippi, 1837); Sneli: 233.
?$^{\$}$2009. *Luidia ciliaris* (Philippi, 1837); Wirtz: 46–47.
2012. *Luidia ciliaris* (Philippi, 1837); Micael *et al*.: 5.

Type locality: Sicily, Mediterranean Sea.
See: Clark (1982a); Clark & Downey (1992); Picton (1993: 23).

Distribution: Mediterranean Sea and Northeast Atlantic; from Scandinavia, the Faeroe Channel and the Shetland Islands, south to Morocco and ?Cabo Verde, including the Azores, Madeira and Canaries.

Depth: 1–650(?805) m, typically from 25 to 200 m (AZO: ?littoral).

Habitat: hard to soft sediments, often found partly buried in gravel.

Development: planktotrophic.

Remarks: the first record of *Luidia ciliaris* in the Azores can be trace back to Döderlein’s (1920) review of the genus, which included a specimen collected in the archipelago from the Simroth collection, though the later author never included any material belonging to this species or genus in his 1888’s report. More recently, Wirtz (2009) reported an animal of *Luidia ciliaris* in a large tide-pool at Faial Island (not collected). The latter author claimed that a picture could be found in Wirtz & Debelius (2003), however, the photographed specimen in the 2003 work is from Madeira. The absence of documented specimens in the archipelago in over 80 years places the presence of this species in the Azores in a somewhat precarious position and thus, should be dealt with caution.

Species *Luidia sarsii* Düben & Koren, *in* Düben, 1844

Luidia sarsii sarsii **Düben & Koren, *in* Düben, 1844**

$^{\$}$1909. *Luidia Sarsi*, (Düben et Koren); Koehler: 59.

$^{\$}$1932. *Luidia sarsii* Düben & Koren; Grieg: 24.

$^{\$}$1965. *Luidia sarsi* Düb. Kor.; Tortonese: 150–152, fig. 69.

1982a. *Luidia sarsi* Düben & Koren; Clark: 175–180, figs. 1c, 2c, g, 3m–o, v, 6.

1983. *Luidia sarsi sarsi* Düben & Koren, 1845; Gage *et al*.: 272.

1992. *Luidia sarsi sarsi* Düben and Koren; Clark & Downey: 18–20, figs. 7m, n, v, 8i, pl. 2, fig. B.

1997. *Luidia sarsi sarsi* Düben & Koren, 1845; Pereira: 336.

1999. *Luidia sarsi* Düben and Koren, 1845; Sneli: 233–234.

2005. *Luidia sarsii sarsii* Düben & Koren, in Düben 1845; García-Diez *et al*.: 47.

2010. *Luidia sarsi sarsi* Düben & Koren, in Düben 1845; Micael & Costa: 322.

2012. *Luidia sarsi sarsi* Düben & Koren, 1845; Micael *et al*.: 5.

Type locality: Norway (lectotype).

See: Clark (1982a); Domanski (1984); Clark & Downey (1992); Picton (1993: 20).

Distribution: Mediterranean Sea and Northeast Atlantic, from Norway and the Faeroe Bank south to Cape Blanc, Mauritania, including the Azores; the subspecies *L. sarsii* *africana* Sladen, 1889 is restricted to Namibian and South African waters, whereas the subspecies *L. sarsii elegans* Perrier, 1875 is known from the western Atlantic waters.

Depth: 9–1,300 m; tends to live in deeper cold waters at its southern geographical range (AZO: ?100–200 m).

Habitat: mud, shell-sand, gravel and stones; night-active, burying itself in the sand during the day.

Development: planktotrophic.

Remarks: the presence of *Luidia sarsii* in the Azores is based solely on three historical records. Koehler (1909) identified a small damaged specimen (R ≈ 50 mm) among the material retrieved by a bottom trawl at Princesse Alice Seabank (sta 899: N37°57’00” W29°14’45”, 200 m). Interestingly, the second known record is from Grieg (1932) who identified a juvenile (with adhering remnants from the larval stage; R=4.5 mm) in a pelagic haul at a depth of just 100 m, 3,139 m above the reported bottom depth. This animal may well represent a late stage in what has been designated in the literature as ‘giant larvae’. *Luidia sarsii* is characterized by an abnormal large bipinnaria larva capable of maintaining planktotrophic activity in the water column long after the development of the post-larval sea star rudiment (see Domanski 1984). Tortonese (1965) is responsible for the most recent record of this species in the Azores, though he listed material from the archipelago without giving further details on the source of the material. Regardless, the scarcity of documented records could be a result of the apparent bathymetrical distribution of this species in the archipelago, which coincides with the least studied depth range in the area (>50 and <200 m).

Family Porcellanasteridae Sladen, 1883
Genus *Hyphalaster* Sladen, 1883

Hyphalaster inermis Sladen, 1883

$^{\$}$1885c. *Hyphalaster antonii*, E. Perrier; Perrier: 61–64.

$^{\$}$1894. *Hyphalaster Antonii*, Edm. Perrier; Perrier: 232–235, pl. 16, fig. 1.

1909. *Hyphalaster Antonii*, Perrier; Koehler: 29–30.

1927a. *Hyphalaster Parfaiti* Perrier; Mortensen: 52.

$^{\$}$1935. *Hyphalaster parfaiti* Ed. Perrier; Lieberkind: 19–25, figs. 6–8, pl. 1, figs. 7–9, pl. 3, figs. 1–2, pl. 4, figs. 11–14.

$^{\$}$1948. *Hyphalaster parfaiti* E. Perrier; Clark: 75.

$^{\$}$1961. *Hyphalaster inermis* Sladen, 1883; Madsen: 58–71, figs. 6–7, pl. 1, figs. 1–14, pl. 2, figs. 1–4, pl. 3, figs. 1–4, pl. 13, figs. 3–4.

Type locality: off Japan (N34°37′ E140°32′), Pacific Ocean.

See: Madsen (1961); Sibuet (1975: 101); Clark & Downey (1992: 98–99, figs. 18g–i, 19a–b, j, pls. 26, figs. A–C); Ramirez-Llodra *et al.* (2002); Dilman (2013: 568).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian deep waters; from the Davis Strait and SW of Greenland, south to Caribbean waters, eastwards in the Mid-Atlantic Ridge and from the Rockall Trough to Angola, including the Azores and Cabo Verde archipelagos; recorded also from the Meteor seamounts.

Depth: 1,444–5,430 m (AZO: 2,995–3,200 m).

Habitat: soft substrates, *Globigerina* ooze, mud to clay.

Development: lecithotrophic.

Remarks: Perrier (1885c, 1894) described *Hyphalaster antonii* based on a single animal collected by RV 'Talisman' in the Azores (sta 131, 1883: N38°28′00″ W25°05′46″, 2,995 m). In the report on the porcellanasterids collected by 'Danish-Ingolf' expedition, Lieberkind (1935) reviewed the type material of *H. antonii* and established its synonymy with *H. parfaiti*, thus confirming previous suppositions that the Azorean species might represent a juvenile of the later species (*e.g.,* Ludwig 1907). Later, Clark (1948) reported seven specimens *Hyphalaster parfaiti* from the archipelago collected by RV 'Atlantis' (sta 15: N35°37′ W30°51′, 3,200 m). In a review of the family Porcellanasteridae, Madsen (1961) placed both *Hyphalaster* species reported in the Azores in the synonymy of the cosmopolitan *Hyphalaster inermis*.

Genus *Porcellanaster* Thomson, 1877

Porcellanaster ceruleus Thomson, 1877

$^{\$}$1885c. *Porcellanaster inermis*, E. Perrier; Perrier: 50–53.

$^{\$}$1894. *Porcellanaster inermis*, Edm. Perrier; Perrier: 212–215, pl. 15, fig. 3.

1927a. *Porcellanaster inermis* Perrier; Mortensen: 52.

$^{\$}$1935. *Porcellanaster coeruleus* Wyville Thomson; Lieberkind: 5–19, figs. 1–5, pl. 2, figs. 1–8, pl. 3, fig. 12, pl. 5, figs. 16–17.

1961. *Porcellanaster cæruleus* Wyville Thomson, 1877; Madsen: 126–142, figs. 22–24.

2006. *Porcellanaster ceruleus* W. Thomson, 1877; Dilman: 179–180.

2008. *Porcellanaster ceruleus* Wyville Thomson, 1877; Dilman: 137.

2013. *Porcellanaster ceruleus* Wyville Thomson, 1877; Dilman: 568.

2014. *Porcellanaster ceruleus* Thomson, 1877; Dilman: 29.

Type locality: off Delaware, USA (N38°34’ W72°10’).

See: Lieberkind (1935); Madsen (1961); Clark & Downey (1992: 100–101, figs. 18a–c, 19d, f, i, pl. 27A–Q); Sumida *et al.* (2001: 19–21, fig. 6); Dilman (2006; 2008).

Distribution: deep-water cosmopolitan, except in the Antarctic; from the Davis Strait south to off Cape Cod, eastwards from south of Iceland along the European and African continental slopes to South Africa, and in the Azores and the Charlie-Gibbs Fracture Zone, in the Mid-Atlantic Ridge.

Depth: 1,158–6,035 m, mostly between 1,600–3,000 m (AZO: 2,995 m).

Habitat: soft substrates, mud, *Globigerina* ooze to clay; juveniles prey on foraminiferans and adults are deposit-feeders, burrowing in the sediment.

Development: lecithotrophic.

Remarks: Perrier (1885b,c, 1894) described *Porcellanaster inermis*, to house the specimens collected by RV ‘Talisman’ at waters between Cabo Verde and NE Africa (sta 101, 1883: N16°38’00” W18°23’46”, 3200 m) and in the Azores (sta 131, 1883: N38°38’ W25°05’46”, 2,995 m). On his report on the porcellanasterids from the Danish-Ingolf expedition, Lieberkind (1935) established the synonymy of *P. inermis* with *P. ceruleus*. With the exception of the three specimens collected by RV ‘Talisman’ no other animals belonging to this species were ever reported from Azorean waters.

Genus *Styracaster* Sladen, 1883

Styracaster armatus **Sladen, 1883**

$^{\$}$1885c. *Styracaster spinosus*, sp. nov.; Perrier: 55–59.

1889. *Styracaster spinosus* Perrier; Sladen: 728.

$^{\$}$1894. *Styracaster spinosus*, sp. nov.; Perrier: 223–226, pl. 17, fig. 2.

$^{\$}$1909. *Styracaster spinosus*, Perrier; Koehler: 39–40.

$^{\$}$1961. *Styracaster spinosus* E. Perrier, 1885; Madsen: 121–123, fig. 37.

1992. *Styracaster armatus* Sladen; Clark & Downey: 102–103, pl. 27, figs. G–H.

2005. *Styracaster armatus* Sladen, 1883; García-Diez *et al*.: 47.

2008. *Styracaster armatus* Sladen, 1883; Dilman: 137.

2013. *Styracaster armatus* Sladen, 1883; Dilman: 568–569.

Type locality: off the Caroline Islands (Pacific, N7°45’ E144°20’).

See: Madsen (1961); Clark & Downey (1992).

Distribution: cosmopolitan, known from the Atlantic, Indian and West Pacific deep waters; in the Atlantic from the Guyana Basin eastwards in the waters between NW Africa and the Cap Verde Archipelago and in the Canary Basin north to the Porcupine Seabight (SW of Ireland; in the Mid-Atlantic Ridge, from the Charlie-Gibbs Fracture Zone south to the Azores.

Depth: 2,700–5,422 m (AZO: 2,995–4,020 m).

Habitat: soft substrates, *Globigerina* ooze, mud or muddy sand.

Remarks: Perrier (1885b, c, 1894) erected the species *Styracaster spinosus* based on two specimens collected by RV 'Talisman' in the Azores (sta 131, 1883: N38°38'00" W25°05'46", 2,995 m). Koehler (1909) also reported this species from the Azores based on animals collected by RV 'Princesse Alice' at two stations (sta 527: N38°09'00" W23°15'45", 4,020 m; sta 745: N38°05'00" W23°50'15", 3,465 m). The material from both cruises was later reviewed by Madsen (1961) in his review of the family Porcellanasteridae as it was the only material known to belong with certainty to this species. Regardless, this species is now considered conspecific with the cosmopolitan *S. armatus* (Clark & Downey 1992).

Styracaster elongatus **Koehler, 1907a**

$1909. *Styracaster elongatus*, Kœhler; Koehler: 33–38, pl. 19, figs. 5–6, pl. 20, figs. 1, 3–4, pl. 21, figs. 3–5.

1961. *Styracaster elongatus* Koehler, 1907; Madsen: 110–113, fig. 19, pl. 10, figs. 1–2.

1975. *Styracaster elongatus* Koehler; Sibuet: 101.

2005. *Styracaster elongatus* Koehler, 1907; García-Diez *et al*.: 47.

Type locality: East of the Azores (N37°17' W20°14').

See: Madsen (1961); Clark & Downey (1992: 103–104, fig. 19k, pl. 27, fig. I); Howell *et al.* (2002: 1906).

Distribution: Indian and Atlantic oceans; from the Gulf of Mexico and Caribbean deep-waters, eastwards to the Azores, the Porcupine Abyssal Plain (SW Ireland) and the Bay of Biscay southwards to the Angola Basin.

Depth: 3,310–6,600 m (AZO: 4,020 m).

Habitat: soft sediments, *Globigerina* ooze and sandy mud.

Remarks: *Styracaster elongatus* is known from the Azores based on a single specimen reported by Koehler (1909; RV 'Princesse Alice', sta 527: N38°09'00" W23°15'45", 4,020 m). The scarcity of local records can be explained by the species' known depth range both in the Azores (>4,000 m) and through its geographical range (>3,000 m).

Family Pseudarchasteridae Sladen, 1889

Genus *Paragonaster* Sladen, *in* Thomson & Murray, 1885

Paragonaster subtilis **(Perrier, 1881)**

$1885c. *Pentagonaster elongatus*, E. Perrier; Perrier: 38.
$1885c. *Goniopecten subtilis* E. Perrier; Perrier: 41.
$1894. *Paragonaster subtilis*; Perrier: 358–362 pl. 23, fig. 5, pl. 24, fig. 3.
$1894. *Paragonaster elongatus*; Perrier: 362–363 pl. 21, fig. 3, pl. 24, fig. 4.
1899. *Paragonaster elongatus* (Per.); Verrill: 196.
$1909. *Paragonaster subtilis*, (Perrier); Koehler: 86–87, pl. 4, fig. 2.
1927a. *Paragonaster subtilis* Perrier; Mortensen: 79.
$1972. *Paragonaster subtilis* (Perrier, 1881); Halpern: 374–378, figs. 5–6.
1973. *Paragonaster subtilis* (Perrier); Downey: 57, pl. 22, figs. A, B.
1975. *Paragonaster subtilis* (Perrier); Sibuet: 108.
1983. *Paragonaster subtilis* (Perrier, 1881); Gage *et al*.: 280.
1992. *Paragonaster subtilis* (Perrier); Clark & Downey: 256–257, pl. 62, fig. C, D.
2005. *Paragonaster subtilis* (Perrier, 1881); García-Diez *et al*.: 47.
$2008. *Paragonaster subtilis* (Perrier, 1881); Dilman: 140.
2014. *Paragonaster subtilis* (Perrier, 1881); Dilman: 33.

Type locality: Gulf of Mexico (N24°33' W84°23').

See: Halpern (1972); Clark & Downey (1992).

Distribution: Atlantic, in the west from off New York, south to the Gulf of Mexico; in the east from the Rockall Trough to the Gulf of Guinea, including the Azores and Cabo Verde archipelagos.

Depth: 1,058–4,825 m (AZO: 2,954–4,261 m).

Habitat: soft substrates (ooze).

Development: lecithotrophic.

Remarks: *Paragonaster subtilis* is a highly variably species and was described in the literature under several names (see Clark & Downey 1992). For example, Perrier (1885c, 1894) described *Paragonaster elongatus* (= *Pentagonaster elongatus*) based on material collected by RV 'Talisman' at the same station in the Azores (sta 131, 1883: N38°38'00" W25°05'46", 2,995 m) where the same author recorded also *P. subtilis*. At the time, Perrier remarked that the former might represent just a variety of later species. Halpern (1972) re-examined the type material including that of *P. elongatus* from the Azores and synonymized the two species.

Genus *Pseudarchaster* Sladen, 1889

Species *Pseudarchaster gracilis* (Sladen, 1889)

Pseudarchaster gracilis gracilis **(Sladen, 1889)**

(Fig. 5.16)

$^{\$}$1889. *Aphroditaster gracilis* n. sp.; Sladen: 117–120, pl. 17, figs. 1–2, pl. 18, figs. 7–8.

1894. *Astrogonium gracile*; Perrier: 342.

$^{\$}$1894. *Astrogonium necator*, Ed. P.; Perrier: 350–355, pl. 23, fig. 1.

1899. *Pseudarchaster necator* (Per.); Verrill: 195.

1899. *Aphroditaster gracilis* Sla.; Verrill: 195.

$^{\$}$1909. *Astrogonium æquabile*, Kœhler; Koehler: 66–68, pl. 11, figs. 1–4.

$^{\$}$1909. *Astrogonium eminens*, Kœhler; Koehler: 68–71, pl. 16, figs. 3–6.

$^{\$}$1909. *Astrogonium marginatum*, sp. nov.; Koehler: 71–73, pl. 14, figs. 1–4.

$^{\$}$1909. *Astrogonium necator*, Perrier; Koehler: 74–75.

$^{\$}$1921a. *Astrogonium marginatum* Kœhler; Koehler: 2.

1927a. *Pseudarchaster* (*Astrogonium*) *necator* (Perrier); Mortensen: 86.

1927a. *Pseudarchaster* (*Astrogonium*) *æquabile* (Koehler); Mortensen: 86.

1927a. *Pseudarchaster* (*Astrogonium*) *eminens* (Koehler); Mortensen: 86.

1927a. *Pseudarchaster* (*Astrogonium*) *marginatus* (Koehler); Mortensen: 86.

1927a. *Pseudarchaster* (*Astrogonium*) *gracilis* (Sladen); Mortensen: 86.

$^{\$}$1972. *Pseudarchaster gracilis* (Sladen, 1889); Halpern: 360–366, figs. 1–2.

1973. *Pseudarchaster gracilis* (Sladen); Downey: 59–60, pl. 23, figs. C, D.

1979. *Pseudarchaster gracilis* (Sladen, 1889); Walenkamp: 44–47, figs. 16, 19, pl. 10, figs. 1–4.

1983. *Pseudarchaster gracilis* (Sladen, 1889); Gage *et al*.: 279–280.

$^{\$}$1992. *Pseudarchaster gracilis gracilis* (Sladen); Clark & Downey: 262–263, pl. 62, figs. E–F.

2005. *Pseudarchaster gracilis gracilis* (Sladen, 1889); García-Diez *et al*.: 47.

2011. *Pseudarchaster gracilis gracilis* (Sladen, 1889); Benavides-Serrato *et al*.: 170–171.

Type locality: Azores (N37°24’ W25°13’).

See: Halpern (1972); Walenkamp (1979); Clark & Downey (1992); Sneli (1999: 242); Dilman (2008: 140); Benavides-Serrato *et al.* (2011); Murillo *et al.* (2015: 16).

Distribution: North Atlantic, from Flemish Cap, off Cape Cod, and from Faeroe waters (Lousy Bank), south to the Equator on the both sides of the Atlantic and, in the Charlie-

Gibbs Fracture Zone and the Azores Archipelago in the Mid-Atlantic Ridge; the subspecies *P. gracilis tessellatus* Sladen, 1889 is restricted to southern Africa.

Depth: 270–2,940 m (AZO: 903–1,940 m).

Habitat: soft substrates, mud or *Globigerina* ooze to fine sand and stones.

Development: direct or lecithotrophic.

Material examined: EMEPC-LUSO L09D18B1 (N of SJG, AZO, N38°42'18" W28°01'18", 2009.10.02, 903 m; 1 spm, R=102 mm, r=31 mm).

Description: stellate and flat body form (R/r=3.3) with narrow, tapering arms terminating in an acute point; wide, rounded interbrachial arcs. Abactinal plates paxillose, extending to terminal plates. Paxillae proximally hexagonal becoming more square-shaped distally, covered with rounded, flattened central granules and one peripheral row of short, slender spinelets. Madreporite rhombic, small, about one and one-half times the size of the adjacent abactinals, located about three quarters from the centre of the disc and to middle of the interbrachial arc. Anus small, located more or less at the centre of the disc. Superomarginal and inferomarginal plates corresponding; 36 in each side of the arm. Lateral angle of superomarginals compressed so that plates are broad and mainly in the vertical plane; superomarginals closely covered by large, rounded, and flattened granules. Inferomarginals covered by short triangular spinules interspersed by conical spines which are about three times larger. Each actinal plate covered by short spinules and one, rarely two or three larger spines. Actinal spines and spinules similar to those on inferomarginals. One pectinate pedicellariae between every two adjacent actinal plates along row contiguous to adambulacrals, particularly conspicuous in the proximal region; pedicellaria along entire width of plate. Adambulacral plates with angular furrow margin bearing six up to nine somewhat flattened furrow spines with blunt tips. Subambulacral spines irregularly arranged in two rows of intermediate shape and size between the actinal and the furrow spines. Each mouth plates bearing ten furrow spines similar to the adambulacral furrow spines, with a large, thick, unpaired median spine at apex of each mouth plate pair. Rest of each plate covered by spines grading progressively into actinal spinules distally.

Remarks: the highly variable *Pseudarchaster gracilis gracilis* was described for the Azores under five different names (Sladen 1889; Perrier 1894; Koehler 1909, 1921a).

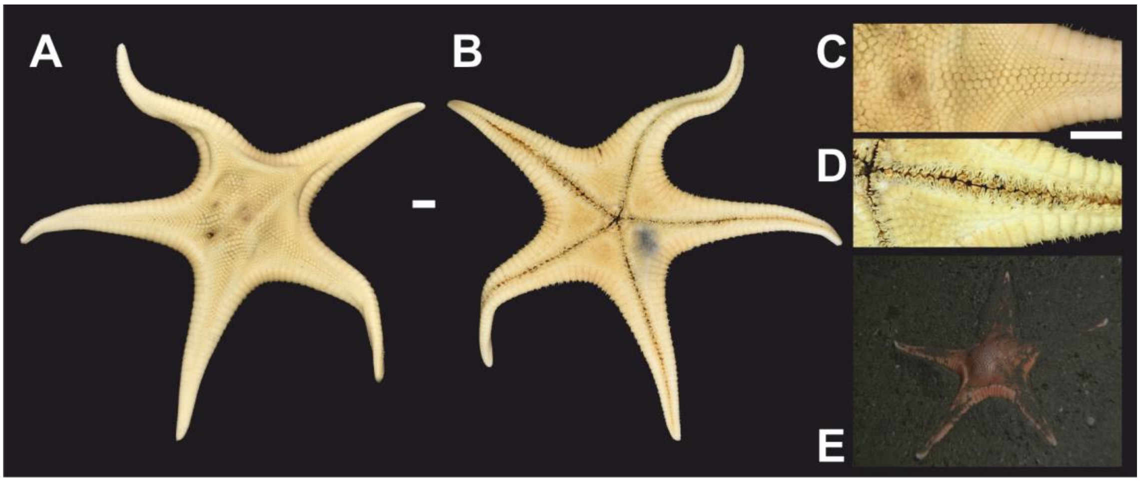


Figure 5.16. *Pseudarchaster gracilis gracilis* (Sladen, 1889) (EMEPC-LUSO L9D18B1). Dorsal view (A); ventral view (B); detail of the disc and arm, dorsal view (C) and ventral view (D); animal *in situ* (N38°42'18" W28°01'18", 2009.10.02, 903 m; E); scale bars are 5 mm (A, B) and 10 mm (C, D).

Halpern (1972) re-examined the type material from the archipelago and established the synonymy. Clark & Downey (1992) also analysed the type material of *P. gracilis* described by Sladen (1889; as *Aphroditaster gracilis*) based on specimens collected in Azores by RV 'H.M.S. Challenger' and demoted *P. tessellatus* to a subspecies of *P. gracilis*.

The North Atlantic subspecies *P. gracilis gracilis* can be distinguished from *P. parelii* also occurring in the Azores (see below) by the conical shape and larger size of the actinal and inferomarginal spines. Additionally, *P. parelii* generally has poorly developed pedicellaria and fewer adambulacral and mouth furrow spines (Halpern 1972). This present record substantiates the historical records.

***Pseudarchaster parelii* (Düben & Koren, 1846)**

$^{\$}$1885c. *Astrogonium fallax*, E. Perrier; Perrier: 37.

$^{\$}$1894. *Astrogonium fallax*, E. Perrier; Perrier: 347–350, pl. 23, fig. 4, pl. 25, fig. 4.

$^{\$}$1896a. *Astrogonium annectens*, E. Perrier; Perrier: 45.

$^{\$}$1909. *Astrogonium annectens*, Perrier; Koehler: 65.

$^{\$}$1909. *Astrogonium fallax*, Perrier; Koehler: 71, pl. 18, fig. 2.

$^{\$}$1921a. *Pseudarchaster* (*Astrogonium*) *fallax* (Perrier); Koehler: 2.

1927a. *Pseudarchaster* (*Astrogonium*) *fallax* (Perrier); Mortensen: 86.

1927a. *Pseudarchaster* (*Astrogonium*) *annectens* (Perrier); Mortensen: 86.

1932. *Astrogonium fallax* Ed. Perrier; Grieg: 21, pl. 5, fig. 1.

$^{\$}$1972. *Pseudarchaster parelii* (Düben and Koren, 1846); Halpern: 366–370, fig. 5.

1983. *Pseudarchaster parelii* (Düben & Koren, 1846); Gage *et al*.: 279.

2005. *Pseudarchaster parelii* (Düben & Koren, 1846); García-Diez *et al*.: 47.

Type locality: Off Kristiansund, Norway.

See: Halpern (1972); Sneli (1999: 242–243);Dilman (2006: 181).

Distribution: North Atlantic, from the Barents Sea, Newfoundland, and southern Greenland, southwards to Florida; and from Iceland and Norway to Mauritania including the Azores.

Depth: 75–3,540 m (AZO: 1,165–1,900 m).

Habitat: soft sediments, such as ooze, sand, gravel and stones.

Development: lecithotrophic.

Remarks: Halpern (1972) re-examined the material described by Perrier (1885c, 1894) as *Pseudarchaster fallax* (= *Astrogonium fallax*) and *P. annectens* (= *Astrogonium annectens*) from the Azores waters and established their synonymy with *P. parelii*.

Superorder Spinulosacea Blake, 1987

Order Spinulosida Perrier, 1884

Family Echinasteridae Verrill, 1867

Genus *Henricia* Gray, 1840

Henricia cylindrella? (Sladen, 1883)

?$^{\$}$1909. *Cribrella abyssalis*, Perrier; Koehler: 102.

1913. *Henricia abyssalis* (Perrier); Farran: 26.

1927a. *Henricia abyssalis* (Perrier); Mortensen: 118.

? $^{\$}$1987. *Henricia cylindrella* (Sladen), n.stat.; Madsen: 231–235, figs. 2g, 21–23.

? $^{\$}$1992. *Henricia cylindrella* (Sladen); Clark & Downey: 390–391, figs. 60a(?), f–g, pl. 93, fig. B, pl. 94, fig. G.

2005. *Henricia cylindrella* (Sladen 1883); García-Diez *et al*.: 47.

Type locality: NW Scotland (N59°29’ W07°13’) (lectotype).

See: Grieg (1932: 30, as *Cribrella abyssalis*); Madsen (1987); Clark & Downey (1992).

Distribution: Northeast Atlantic, from the northern Rockall Trough south to the Porcupine Seabight (SW Ireland) and the Charlie-Gibbs Fracture Zone; probably also extending to the Azores and to waters between Canaries and Morocco.

Depth: 1,015—2,620 m (?AZO: 1,482—1,805 m).

Habitat: soft substrates (?AZO: *Globigerina* ooze).

Remarks: in a preliminary report, Perrier (1885c) described a new species *Cribrella abyssicola,* which in his 1894 report was renamed *Cribrella abyssalis* based on material collected by RV 'Talisman' from Morocco. Following the previous author, Koehler (1909) reported the same species from RV 'Princesse Alice' material collected in the Azores, Portugal and NW Africa. In a review of the genus *Henricia* in the NE Atlantic, Madsen (1987) examined a single specimen (R=43 mm, r=6 mm) identified as *Cribrella abyssalis*, collected by RV 'Talisman' in the Azores at a depth 1,257 m. Though Perrier (1885c, 1894) did not list any material from the Azores under his newly described species, the material examined by Madsen could represent an unreported specimen (RV 'Talisman', sta 127: N38°38'00" W28°20'46", 1,257 m). Madsen proposed that Perrier's species should be synonymized with Sladen's *Henricia cylindrella*. Nevertheless, this author noted that the specimen from the Azores presented slight differences (*i.e*. shorter arms) than the typical *H*. *cylindrella*. Madsen also listed Koehler's (1909) record of *Cribrella abyssalis* followed tentatively in the synonymy of *Henricia cylindrella*. Clark & Downey (1992) agreed with Madsen (1987) as they also found RV 'Talisman' specimen from Azores very close to the lectotype of *Henricia cylindrella*. However, these authors were unable to confirm the conspecificity using the Moroccan type material of *H. abyssalis*. New material is needed to better understand the variability and relationship of *H. abyssalis/cylindrella* (see also remarks below under *H*. *oculata*).

***Henricia oculata*? (Pennant, 1777)**

?$^{\$}$1896a. *Cribrella oculata* (Linck) Forbes; Perrier: 39.

1909. *Cribrella oculata*, (Linck); Koehler: 102–103.

1921b. *Henricia sanguinolenta* (O.F. Müller); Koehler: 31, fig. 23.

1927a. *Henricia sanguinolenta* (O.F. Müller); Mortensen: 118–121.

1938. *Henricia sanguinolenta* (O.F. Müller); Nobre: 39–40, fig. 14.

2005. *Henricia oculata* (Pennant, 1777); García-Diez *et al*.: 47.

2010. *Henricia oculata* (Pennant, 1777); Micael & Costa: 322.

2012. *Henricia oculata* (Pennant, 1777); Micael *et al*.: 5–6.

Type locality: Anglesey, N. Wales (British Isles).

See: Madsen (1987: 254–257, figs. 3c, 44–45); Clark & Downey (1992: 393–394, figs. 60q, r, pl. 93, fig. E, pl. 95, figs. F–G); Picton (1993: 32).

Distribution: Northeast Atlantic, known with certainty from the Shetland Islands south to Portugal; possibly extending west to Nova Scotia and New England north of Cape Cod and to the Azores.

Depth: 0–?180 m (?AZO: 1,266–1,557 m).

Habitat: hard substrates to shell gravel, found as well in sublittoral habitats with considerable hydrodynamics, from kelp forests, tidal streams and on vertical cliffs.

Development: lecithotrophic.

Remarks: the highly polymorphic nature of *Henricia* (= *Cribrella*) species makes this genus as whole particularly difficult with a problematic historical synonymy (Madsen 1987; Clark & Downey 1992; Sneli 1999). For example, the species names *Henricia oculata* (Pennant, 1777) and *H. sanguinolenta* (Müller, 1776) are intermingled and considered synonymous by the time the great oceanographic expeditions reached the Azores Archipelago. In the report of the asteroids collected by RV 'Hirondelle', Perrier (1896a) identified material under the name '*Cribrella oculata* (Linck) Forbes' collected at four stations, the first located east of Newfoundland at about 155 m and the remaining three within the Azorean waters between 1,266–1,557 m. Koehler (1909) in his report on the echinoderms collected by RV 'Princesse Alice' also listed the name '*Cribrella oculata*, (Linck)' for specimens from the British Isles and Scandinavia. However, Koehler added also the name '*Cribrella sanguinolenta* (Müller)', remarking that these species were synonymous with *C. oculata* being the oldest. Later, however, the majority of the authors (*e.g.,* Koehler 1921b; Mortensen 1927a; Nobre 1938) adopted the name *H. sanguinolenta*, as Linck's name did not follow the binominal rules (Madsen 1987). It was only in the late 1970's that Pennant's *Henricia oculata* was again accepted as a distinct species (Madsen 1987). As a consequence, the true geographical and bathymetric range of *H. oculata* is still uncertain. The name as presented by Perrier is generally accepted under the synonymy of this species (*e.g.,* Madsen 1987; Clark & Downey 1992). On the other hand, the Azorean material was retrieved from depths that appear far too deep for *H. oculata* or even for *H. sanguinolenta*, both known from waters no deeper than 200 m. The matter is still pending.

Superorder Valvatacea Blake, 1987

Order Valvatida Perrier, 1884

Family Asterinidae Gray, 1840

Genus *Asterina* Nardo, 1834

Asterina gibbosa (Pennant, 1777)

(Fig. 5.17)

$^{\$}$1888. *Asterina gibbosa* Forbes; Barrois: 70.

?1888. *Asteriscus* sp.; Simroth: 231.

1921b. *Asterina gibbosa* (Pennant); Koehler: 32–33, fig. 34.

1927a. *Asterina gibbosa* (Pennant); Mortensen: 98–99, fig. 56.

1965. *Asterina gibbosa* (Penn.); Tortonese: 169–172, figs. 80–82.

$^{\$}$1992. *Asterina gibbosa* (Pennant); Clark & Downey: 184–185, figs. 30a, 31a, 32a–b, pl. 41, figs. H–J.

1995. *Asterina gibbosa* (Pennant); Moyse & Tyler: 667, fig. 12.3.

$^{\$}$1998. *Asterina gibbosa*; Morton *et al*.: 143, fig. 7.4.

1997. *Asterina gibbosa* (Pennant, 1777); Pereira: 335.

2010. *Asterina gibbosa* (Pennant, 1777); Micael & Costa: 322.

2012. *Asterina gibbosa* (Pennant, 1777); Micael *et al.*: 6.

See: Crump & Emson (1983); Clark & Downey (1992); Haesaerts *et al.* (2006); Koukouras *et al*. (2007: 69). **Distribution:** Mediterranean Sea and Northeast Atlantic; from Scotland to the Azores and Canaries.

Depth: 0–125 m (AZO: low intertidal to subtidal waters).

Habitat: rocky shores, under stones and crevices during the day; also found among algae, sponges and in meadows of Zostera and Posidonia.

Development: lecithotrophic larva.

Remarks: *Asterina gibbosa* was reported for the first time from the archipelago by Barrois (1888), who remarked that they were quite common under boulders in the littoral of Faial and São Miguel islands (specimens presumably lost). Later, Clark & Downey (1992) found seven specimens belonging to this species among the zoological collection of the British Museum that reportedly came from the archipelago (no further data). Morton *et al*. (1998) recorded this small sea star from the low intertidal and subtidal of the Azores. Frias Martins one of the co-authors informed us that he frequently found *A*. *gibbosa* among the boulders in the shallow waters of São Miguel (Fig. 5.17). More recently, Micael *et al*. (2012) remarked that neither Nobre (1938), Marques (1983) nor themselves found this species in the Azorean shallow waters.

Micael and co-authors (2012) suggested that *A. gibbosa* could have disappeared locally from the Azores. Overall, neither the cryptic behaviour nor the small size of *Asterina gibbosa* can explain its almost complete absence in the literature (*e.g.,* Drouët 1861; Chapman 1955; Marques 1983) and in the zoological collections (*e.g.,* DBUA-ECH, DOP, MB–NMHN) covering more than 150 years of zoological studies on the shallow-water fauna of the archipelago. Thus, *Asterina gibbosa* must be considered as a rare species in the Azores, the population density of which appears to vary significantly through time.

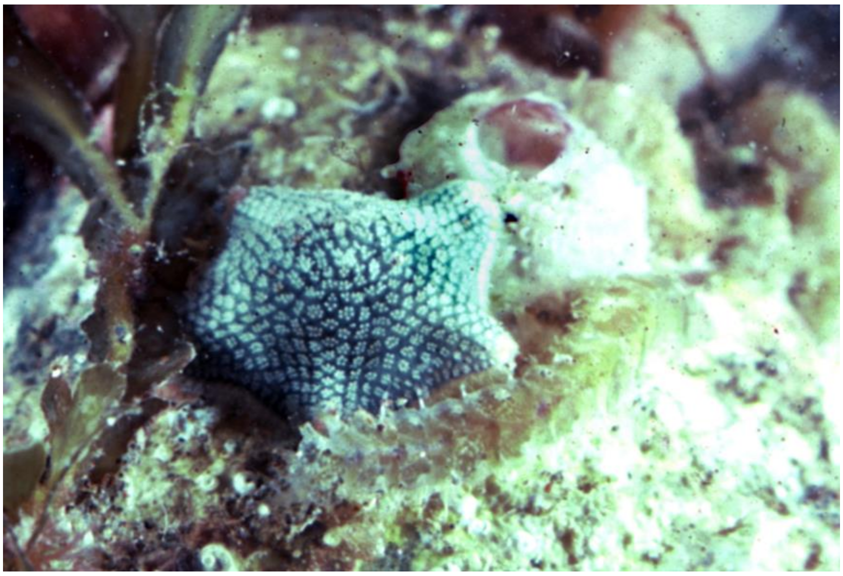


Figure 5.17. *Asterina gibbosa* (Pennant, 1777) *in situ* (São Miguel Island, Azores, *c.* N37°44’53” W25°37’56”, 1985.06, intertidal).

Family Chaetasteridae Sladen, 1889

Genus *Chaetaster* Müller & Troschel, 1840b

Chaetaster longipes (Bruzelius, 1805)

$^{\$}$1889. *Chætaster longipes* (Retzius), Sars; Sladen: 399–400.

1909. *Chætaster longipes*, Bruzelius; Koehler: 88–89.

1914b. *Chaetaster longipes*; Koehler: 274.

1921b. *Chætaster longipes* (Retzius); Koehler: 37–38, fig. 27.

1927a. *Chætaster longipes* (Retzius); Mortensen: 95.

1965. *Chaetaster longipes* (Retz.); Tortonese: 154–155, fig. 71.

1978. *Chaetaster longipes* (Retzius); Pawson: 9–10.

1992. *Chaetaster longipes* (Retzius); Clark & Downey: 145, pl. 35, figs. A–B.

$2003. *Chaetaster longipes* (Retzius); Wirtz & Debelius: 274.

2004. *Chaetaster longipes* (Retzius); Garrido *et al*.: 87–88.

2006. *Chaetaster longipes* Retzius, 1805; Wirtz: 77

$2009. *Chaetaster longipes* (Retzius, 1805); Wirtz: 47–48.

2010. *Chaetaster longipes* (Retzius, 1805); Micael & Costa: 322.

2012. *Chaetaster longipes* (Retzius, 1805); Micael *et al*.: 6.

Type locality: ?Mediterranean Sea.

See: Pawson (1978); Tortonese (1965); Nataf & Cherbonnier (1975: 815); Clark & Downey (1992); Garrido *et al.* (2004).

Distribution: Mediterranean Sea and East Atlantic; from Bay of Biscay to Annobón Island in Gulf of Guinea, including the archipelagos of the Azores, Madeira, Canaries, Cabo Verde, St Helena and Ascension; reported also from the Bay of Biscay.

Depth: 30–1,140 m [AZO: 30–165(?823) m].

Habitat: hard to soft substrates.

Remarks: Sladen (1889) identified *Chaetaster longipes* among the material dredged by RV 'H.M.S. Challenger' in the Azores (sta 75: N38°38'00" W28°28'30") at a depth of 823 m. It is likely that this material came from much shallower depths than reported, possibly between 91–165 m (see remarks under *Astropecten hermatophilus*).

Family Goniasteridae Forbes, 1841

Genus *Ceramaster* Verrill, 1899

Species *Ceramaster granularis* (Retzius, 1783)

Ceramaster granularis granularis **(Retzius, 1783)**

$1896a. *Pentagonaster granularis*, E. Perrier; Perrier: 45.

1909. *Pentagonaster granularis*, Retzius; Koehler: 84–85, pl. 2, fig. 2, pl. 18, figs. 3–4.

1927a. *Ceramaster granularis* (O.F. Müller); Mortensen: 81–82, fig. 44.

1992. *Ceramaster granularis granularis* Retzius; Clark & Downey: 233–234, figs. 39a–b, pl. 55, figs. A–B.

1999. *Ceramaster granularis* (O.F. Müller, 1776); Sneli: 242.

2005. *Ceramaster granularis granularis* (Müller, 1776); García-Diez *et al*.: 47.

Type locality: St. Croix (?Canada).

See: Mortensen (1927a); Clark & Downey (1992); Dilman (2006: 182).

Distribution: North Atlantic, from Newfoundland and South Greenland to Long Island (*c.* N41°) in the west and to the British Isles in the east including the Reykjanes Ridge south to the Azores; the subspecies *C. granularis trispinosus* Clark, 1923a is known only from SW of Vasco da Gama Peak (South Africa).

Depth: 40–2,185 m (AZO: 1,384 m).

Habitat: soft to hard substrates, from mud, sand, gravel and stone.

Development: the large yolky egg of this species could indicate that it may have direct development or a non-feeding larval stage.

Remarks: *Ceramaster granularis* is known from the Azores from a single record by Perrier (1896a) based on three specimens collected by RV 'Hirondelle' (sta 213: N39°22'48" W31°25'16", 1,384 m) (see also remarks under *C. grenadensis grenadensis*).

Species *Ceramaster grenadensis* (Perrier, 1881)

Ceramaster grenadensis grenadensis (Perrier, 1881)

$^{\$}$1885c. *Pentagonaster gosselini*, E. Perrier; Perrier: 35.

$^{\$}$1894. *Pentagonaster Gosselini*, sp. nov.; Perrier: 399–401, pl. 26, fig. 4.

$^{\$}$1896a. *Pentagonaster Gosselini*, E. Perrier; Perrier: 45.

$^{\$}$1909. *Pentagonaster Gosselini*, Perrier; Koehler: 84, pl. 1, fig. 9.

1913. *Pentagonaster balteatus*, Sladen; Farran: 9–10.

1927a. *Ceramaster balteatus* (Sladen); Mortensen: 82, fig. 45.

$^{\$}$1955. *Ceramaster balteatus* (Slad.); Tortonese: 676–677.

1973. *Ceramaster grenadensis* (Perrier); Downey: 49–50, pl. 17, figs. C–D.

1992. *Ceramaster grenadensis grenadensis* (Perrier); Clark & Downey: 234–235, figs. 39c–d, pl. 55, figs. C–D.

2005. *Ceramaster grenadensis grenadensis* (Perrier, 1881); García-Diez *et al.*: 47.

2014. *Ceramaster grenadensis* (Perrier, 1881); Dilman: 32.

Type locality: Grenada, Caribbean (N12°04' W61°50").

See: Clark & Downey (1992); Dilman (2014); Mecho *et al.* (2014: 285, figs. 3A–C; 2015).

Distribution: Mediterranean Sea and Atlantic, in the west from Florida to Brazil and in the east from SW Ireland to the Gulf of Guinea, including the Azores, Canaries and Cabo Verde. The subspecies *Ceramaster grenadensis euryplax* (Clark, 1923a) is restricted to South Africa and *C. grenadensis patagonicus* (Sladen, 1889) is known from the Falkland Islands, Burdwood Bank, Gulf of California and southern Alaska to the Bering Sea. Both *C. grenadensis fisheri* Bernasconi, 1963 and *C. grenadensis productus* Djakonov, 1950 are known only from the Pacific Ocean.

Depth: 200–2,845 m (AZO: 1,095–1,557 m).

Habitat: soft substrates, sand, mud to *Globigerina* ooze.

Development: lecithotrophic.

Remarks: *Ceramaster grenadensis* is a highly variable species, a feature reflected by its long list of synonyms, subspecies and varieties. Perrier (1885c, 1894) described *Pentagonaster gosselini* based on material collected by RV 'Talisman', which included specimens from the Azores. Later, Perrier (1896a) and Koehler (1909) reported the same species among the material collected by RVs 'Hirondelle' and 'Princesse Alice', respectively. Farran (1913) synonymized Perrier's species with *Ceramaster balteatus* (= *Pentagonaster balteatus*) described by Sladen (1891) from the southwest of Ireland. Previously, Verrill (1899) had proposed to synonymise *C. balteatus* with *C. granularis* (= *Tosia granularis*), a decision that did not reunited consensus among contemporaneous authors. John & Clark (1954) accepted Verrill's proposal and placed *P. gosselini* in the synonymy of *Ceramaster granularis* forma *balteatus*. However, Tortonese (1955) argued that *C. balteatus* was morphological distinct from *C. granularis* and only partially sympatric with the latter species, though he could not agree whether the observed differences could be supported at specific or subspecific level. Currently both *C. balteatus* and *P. gosselini* are considered conspecific with *C. grenadensis*.

Genus *Plinthaster* Verrill, 1899

***Plinthaster dentatus* (Perrier, 1884)**

$^{\$}$1885c. *Pentagonaster grandis*, E. Perrier; Perrier: 35–36.

1889. *Pentagonaster perrieri*; Sladen: 265.

$^{\$}$1894. *Pentagonaster Perrieri*, Sladen; Perrier: 391–396.

$^{\$}$1909. *Pentagonaster Perrieri*, Sladen; Koehler: 85–86, pl. 2, fig. 7.

$^{\$}$1921a. *Plinthaster (Pentagonaster) Perrieri* (Sladen); Koehler: 2.

1927a. *Plinthaster Perrieri* (Sladen); Mortensen: 83–84, figs. 46, 47.

1970. *Plinthaster dentatus* (Perrier, 1884); Halpern: 244–252, figs. 17–19

1973. *Plinthaster dentatus* (Perrier); Downey: 52–53, pl. 19, figs. A–B.

1983. *Plinthaster dentatus* (Perrier, 1884); Gage *et al*.: 280.

1992. *Plinthaster dentatus* (Perrier); Clark & Downey: 260, pl. 61, figs. D–E.

2005. *Plinthaster dentatus* (Perrier, 1884); García-Diez *et al*.: 47.

2011. *Plinthaster dentatus* (Perrier, 1884); Benavides-Serrato *et al*.: 168–169.

2014. *Plinthaster dentatus* (Perrier, 1884); Dilman: 33.

Type locality: off Grenada, Caribbean (N12°03’ W61°49’).

See: Grieg (1932: 21–23); Gray *et al.* (1968: 151); Halpern (1970); Sumida *et al.* (2001: 26–28, figs. 9a–E); Benavides-Serrato *et al.* (2011).

Distribution: Atlantic, in the west from North Carolina southwards to Northern Brazil and in the east from the Rockall Trough south to the Gulf of Guinea, including the archipelagos of the Azores, Canaries and Cabo Verde.

Depth: 229–2,910 m (AZO: 1,095–1,740 m).

Habitat: muddy to sandy substrates; found also on *Lophelia* coral reefs.

Remarks: the highly variable *Plinthaster dentatus* was described under several different names through the years (see Halpern 1970). For example, Perrier (1885c) described *Pentagonaster grandis* based on specimens collected by RV ‘Talisman’ in NW Africa and the Azores. Soon after, Sladen (1889) change the name of this species to *Pentagonaster perrieri*, as it could be confused with another goniasterid from the Australian waters known at the time as *Tosia grandis*. Farran (1913) based on his own observations and on Koehler (1909) established the synonymy with *P*. *concinnus*, a species described by Sladen (1891) for the southwest of Ireland. Farran (1913) also synonymised those two species with the West Atlantic species *P*. *dentatus*. Grieg (1932) based on the material collected by RV ‘Michael Sars’ in NW Africa, the Canaries and Rockall Trough (SW Ireland) supported Farran’s decision to reunite the East and West Atlantic species. However, the synonymy was only formally accepted in 1970, after the extensive review by Halpern.

Genus *Sphaeriodiscus* Fisher, 1910

Sphaeriodiscus bourgeti **(Perrier, 1885c)**

$ ^{\$} $1885c. *Stephanaster Bourgeti*, E. Perrier; Perrier: 31–34.
$ ^{\$} $1894. *Stephanaster Bourgeti*, sp. nov.; Perrier: 403–406, pl. 26, fig. 1.
1927a. *Sphœriodiscus* (*Stephanaster*) *Bourgeti* Perrier; Mortensen: 79.
1956. *Sphaeriodiscus bourgeti* (Perrier); Tortonese & Clark: 347, 349, 350.

Type locality: Cabo Verde.

See: Perrier (1894); Cherbonnier (1970: 1266); Tortonese & Clark (1956); Clark & Downey (1992: 266, pl. 65, figs. C–E).

Distribution: Northeast Atlantic, from the Bay of Biscay south to the Northwest of Africa, Cabo Verde and the Azores; reported also from Natal (South Africa).

Depth: 285–760 m (AZO: 560 m).

Habitat: soft substrates (sand and gravel).

Remarks: Perrier (1885c, 1894) described *Stephanaster bourgeti* for the first time based on the material collected by RV 'Talisman' in Cabo Verde. However, apparently Perrier did not notice that among the listed material there were three individuals from the Azores (sta 123, 1883: N38°23'00" W28°49'46", 560 m). Fisher (1910, 1911) designated Perrier' species as the type of the new genus *Sphaeriodiscus*. Except for some authors (*e.g.,* Mortensen 1927a; Tortonese & Clark 1956), most of the subsequent references ignored the Azorean record and *S. bourgeti* was considered solely an African species (*e.g.,* Clark & Downey 1992). Another record that appears to have been ignored in the related bibliography was made by Cherbonnier (1970), who reported this species from the Bay of Biscay, based on material collected by RV 'Thalassa'. Regardless, the distribution of this species seems remarkably discontinuous with reported localities quite remote from each other.

Family Odontasteridae Verrill, 1899

Genus *Hoplaster* Perrier, *in* Milne-Edwards, 1882

Hoplaster spinosus **Perrier, *in* Milne-Edwards, 1882**

$1889. *Pentagonaster lepidus*, n. sp.; Sladen: 275–277, pl. 57, figs. 1–4.

$1894. *Hoplaster spinosus*, E. Perrier; Perrier: 324–325, pl. 14, fig. 2.

1894. *Pentagonaster lepidus*; Perrier: 390.

1899. *Hoplaster spinosus* Perrier 1882; Verrill: 197.

1899. *Hoplaster lepidus* (Sladen); Verrill: 198.

1927a. *Pentagonaster lepidus* Sladen; Mortensen: 77.

1983. *Hoplasler spinosus* Perrier, 1882; Gage *et al*.: 278.

$1992. *Hoplaster spinosus* Perrier; Clark & Downey: 151–152, pl. 36, figs. E, F.

2014. *Hoplaster spinosus* Perrier, 1882; Dilman: 31–32.

Type locality: near the Porcupine Seabight (N49°47'50" W12°41'46"), SW Ireland.

See: Perrier (*in* Milne-Edwards 1882: 48; 1894); Clark & Downey (1992).

Distribution: East Atlantic, from the Rockall Trough and the Porcupine Seabight to off Morocco, including the Azores; reported also south off Cape Town, South Africa.

Depth: 1,795–3,310 m (AZO: 1,829–2,595 m).

Habitat: soft substrates, sand with pumice stones, ooze or mud.

Remarks: Sladen (1889) described a new species, *Pentagonaster lepidus* based on material collected by RV 'H.M.S. Challenger' in the Azores (sta 78: N37°24' W25°13', 1,829 m). However, Sladen remarked that this species was an immature form of what could prove to be conspecific to any of the *Pentagonaster* species described by Perrier (1885c) from the same area before. Perrier (1894) added material collected by RV 'Talisman' in the Azores (sta 131: N38°38' W27°26', 2,595 m) to the type material of *Hoplaster spinosus* collected by RV 'Travailleur' in Irish waters. Though, Perrier acknowledge Sladen' species, only after Verrill (1899) *P. lepidus* was synonymized with *H. spinosus*, a decision followed by subsequent authors (*e.g.,* Gage *et al*. 1983; Clark & Downey 1992).

Family Ophidiasteridae Verrill, 1870

Genus *Hacelia* Gray, 1840

Hacelia attenuata **Gray, 1840**

(Fig. 5.18)

?$^{\$}$1861. Asterias lœvigata Lam.; Drouët: 211.

?$^{\$}$1888. *Ophidiaster* sp.; Simroth: 231.

$^{\$}$1889. *Ophidiaster attenuatus* Gray; Sladen: 403.

$^{\$}$1909. *Hacelia attenuata* (Gray); Koehler: 89, pl. 2, fig. 1, pl. 20, fig. 5.

1914b. *Hacelia attenuata*; Koehler: 274.

1921a. *Hacelia attenuata*; Clark: 87.

1921b. *Hacelia attenuata* Gray; Koehler: 40, fig. 29.

$^{\$}$1965. *Hacelia attenuata* (Gray); Tortonese: 164–166, fig. 78.

$^{\$}$1983. *Hacelia attenuata* (Gray, 1840); Marques: 2, fig. 1.

1992. *Hacelia attenuata* (Gray); Clark & Downey: 272–273.

$^{\$}$1996. *Hacelia attenuata* (Gray, 1814); Wirtz & Vader: 17–22.

1997. *Hacelia attenuata* (Gray, 1840); Pereira: 335.

$^{\$}$1998. *Hacelia attenuata*; Morton *et al.*: 66, 76, figs. 3.6O, 4.2A.

2005. *Hacelia attenuata* Gray, 1840; García-Diez *et al*.: 47.

2010. *Hacelia attenuata* Gray, 1840; Micael & Costa: 322.

2012. *Hacelia attenuata* Gray, 1840; Micael *et al*.: 6.

See: Clark & Downey (1992); Bacallado *et al.* (1985: 150); Koukouras *et al.* (2007: 70).

Distribution: Mediterranean Sea and Northeast Atlantic, in the Gulf of Guinea, the Azores, Canaries and Cabo Verde.

Depth: 1–190 m (AZO: 1–165(?823) m); in the Azores this species tends to be particularly abundant at depths deeper than 40 m.

Habitat: hard substrates to biogenic detritus, gravel, sand and shells to sandy silt; also associated with deep-water coral communities of *Dendrophyllia ramea* (Linnaeus, 1758).

Material examined: DBUA-ECH 074 (Baixa do Ouro, Caloura, SMG, AZO, *c*. N37°43'32" W25°32'47", 1996.12.05, 15 m; 3 spms, R=75–99 mm, r=13–17 mm).

Description: disc of moderate size, five arms, long, rounded abactinally and flattened actinally, tapering gently to rather acute tip. Body covered with densely packed granules. Abactinal plates small, flat, arranged in regular longitudinal rows. Each of the ten pore areas containing up to 32 papular pores; Lowermost row nearest adambulacrals with double pore areas but each containing less than half the number of pores. Both marginal series more distinct distally; last few plates in each series enlarged, tumid and bare (as are the last few carinal plates). Three rows of actinal plates proximally, the outermost one not extending to end of arm. Adambulacral plates with two blunt, flattened, parallel furrow spines, proximal one larger; one large, blunt, slightly flattened subambulacral spine. No pedicellaria. Colour (in ethanol) white.

Remarks: *Hacelia attenuata* can be easily distinguished from the only other ophidiasterids known from the shallow-waters of the Azores (≤50 m), *Ophidiaster ophidianus* (Lamarck, 1816) by the overall shape of the body whereas in the first species the arms tend to be flattened ventrally and in the second species tubular. Also in *H. attenuata* the number of papular areas longitudinal rows tends to be higher than in *O. ophidianus*, 10 and 8 respectively. Regardless, these two sea stars tend to be bathymetrically separate as *O. ophidianus* occurs typically in the first few meters and *H. attenuata* becomes abundant in waters below 40 m. Also, *H. attenuata* can be easily distinguished from *H. superba* the only other species of genus *Hacelia* known to occur in the Atlantic, as the latter has typically less pores in each of the papular areas (8–22), thicker broad- based arms and an ridged abactinal surface due to its the tumid plates and sunken popular areas (Clark & Downey 1992). See below remarks under *O. ophidianus*.

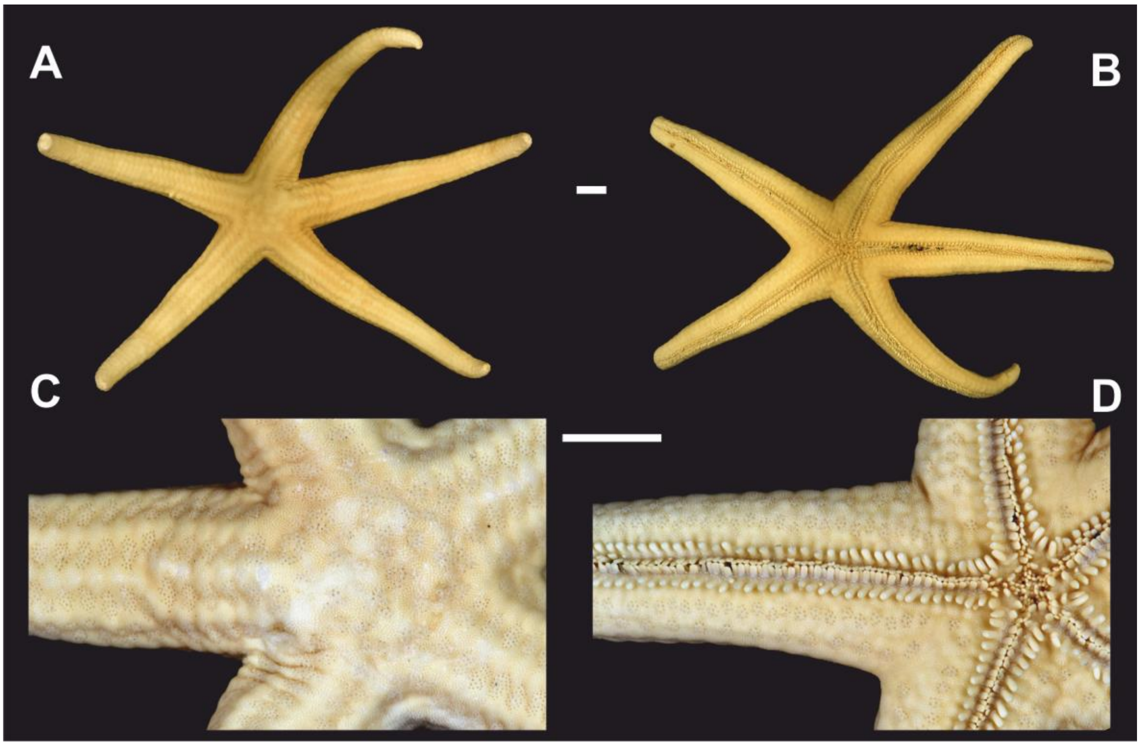


Figure 5.18. *Hacelia attenuata* Gray, 1840 (DBUA-ECH 074). Dorsal view (A); ventral view (B); detail of the arm and disc, dorsal view (C), ventral view (D); scale bars are 10 mm.

The first report of this species to the archipelago was made by Drouët (1861). Later, Simroth (1888) commented that he also found at Ponta Delgada Museum an individual identified as *Ophidiaster ophidianus*, but he believed that it was equivalent to the Drouët's *Asterias laevigata*. However, Barrois (1888) contested Drouët's identification, claiming that the later confused with *O. ophidianus*, one of the most common sea stars of the shallow water of the Azores. Sladen (1889) reported *Hacelia attenuata* (= *Ophidiaster attenuatus*) among the material collected by RV 'H.M.S. Challenger' in the Azores, presumably at a depth of 823 m (sta 75: N38°38'00" W28°28'30"), which is notably deep for a shallow-water species. Moreover, this species was identified together with other species that are generally found at depths lower than 150 m, suggesting a misprint in the dredge depth. It is very likely that the maximum reported depth lay somewhere between 92–165 m (see remarks under *Astropecten hermatophilus*).

Genus *Ophidiaster* Agassiz, 1836

***Ophidiaster ophidianus* (Lamarck, 1816)**
(Fig. 5.19)

?$^{\$}$1861. *Asterias lœvigata* Lam.; Drouët: 93, 211.

$^{\$}$1888. *Ophidiaster ophidianus* L. Agassiz; Barrois: 71.

?$^{\$}$1888. *Ophidiaster* sp.; Simroth: 231.

$^{\$}$1889. *Ophidiaster ophidianus* (Lamarck), Agassiz; Sladen: 403.

$^{\$}$1894. *Ophidiaster ophidianus*, Lamarck; Perrier: 330.

$^{\$}$1896a. *Ophidiaster ophidianus*, Lamarck; Perrier: 44.

$^{\$}$1909. *Ophidiaster ophidianus*, (Lamarck); Koehler: 92.

1914b. *Ophidiaster ophidianus*; Koehler: 274.

1921a. *Ophidiaster ophidianus*; Clark: 79.

1924. *Ophidiaster ophidianus* (Lamk.); Nobre: 89.

$^{\$}$1930. *Ophidiaster ophidianus* (Lamk.); Nobre: 68–69.

$^{\$}$1938. *Ophidiaster ophidianus* Lamarck, 1816; Cadenat: 351, 373.

$^{\$}$1938. *Ophidiaster ophidianus* (Lamk.); Nobre: 46, fig. 20.

$^{\$}$1965. *Ophidiaster ophidianus* (Lam.); Tortonese: 160–164, figs. 75–77.

$^{\$}$1978. *Ophidiaster ophidianus* (Lamarck); Pawson: 10, fig. 3.

$^{\$}$1983. *Ophidiaster ophidianus* (Lamarck, 1816); Marques: 2.

1992. *Ophidiaster ophidianus* (Lamarck); Clark & Downey: 281–282, figs. 44e, f, pl. 69, fig. F.

$^{\$}$1996. *Ophidiaster ophidianus* (Lamarck, 1816); Wirtz & Vader: 17–22.

1997. *Ophidiaster ophidianus* (Lamarck, 1816); Pereira: 335.

$^{\$}$1998. *Ophidiaster ophidianus;* Morton *et al*.: 63, figs. 2.5Y, 3.4Z, 3.5T, 5.2L, 8.1N.

1999. *Ophidiaster ophidianus* (Lamark, 1816); Pérez-Ruzafa *et al*.: 47–48.

2002. *Ophidiaster ophidianus* (Lamark, 1816); Pérez-Ruzafa *et al.*: 280.

$^{\$}$2005. *Ophidiaster ophidianus*; Cardigos *et al*.: 165.

2005. *Ophidiaster ophidianus* (Lamarck, 1816); García-Diez *et al*.: 47.

$^{\$}$2006. *Ophidiaster ophidianus* (Lamarck, 1816); Micael *et al*.: 5.

2010. *Ophidiaster ophidianus* (Lamarck, 1816); Micael & Costa: 322.

$^{\$}$2011. *Ophidiaster ophidianus* (Lamarck, 1816); Micael *et al*.: 205–216, figs. 2–7.

2012. *Ophidiaster ophidianus* (Lamarck, 1816); Micael *et al*.: 6.

$^{\$}$2013. *Ophidiaster ophidianus* (Lamarck, 1816); Micael *et al*.: 1087–1095.

$^{\$}$2014. *Ophidiaster ophidianus* (Lamarck, 1816); Micael *et al*.: 1–10, figs. 2–3.

Type locality: Western Mediterranean Sea.

See: Tortonese (1965); Clark & Downey (1992); Koukouras *et al.* (2007: 71).

Distribution: Mediterranean Sea and Northeast Atlantic; from the North African coasts south to the Gulf of Guinea, including the archipelagos of the Azores, Madeira, Selvagens, Canaries, Cabo Verde, São Tomé and Saint Helena.

Depth: 0–105 m (AZO: 0–165(?823) m).

Habitat: rocky and coralligenous habitats, occasionally found on soft sediments; in Azores common among rocks at low-tide and also in rock pools.

Development: lecithotrophic.

Material: DBUA-ECH 075 (Baixa do Cerco, Caloura, SMG, AZO, *c.* N37°42’20” W25°30’30”, 2010.08.13, 20 m; 1 spm, R=67 mm, r=7 mm); DBUA-ECH 076 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06; 1 spm, r=10 mm); DBUA-ECH 080 (Poços, São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.20, 30 m; 2 spms, R=79–93 mm, r=10–12 mm); DBUA-ECH 081 (Poços, São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.17, 12 m; 3 spms, R=110–122 mm, r=10–13 mm); DBUA-ECH 082 (Banco João de Castro, AZO, *c.* N38°13’18” W26°36’12”, 1996.07.27, 30 m; 1 spms, R=120 m, r=15 mm); DBUA-ECH 112 (Vila do Porto, SMA, AZO, *c.* N36°56’42” W25°08’50”, 1990.06; 1 spm, R=122 mm, r=13 mm); DBUA-ECH 409 (Poças de Santa Cruz, GRA, AZO, *c.* N39°05’16” W28°00’25”, 2010.08.5, 1–2 m; 2 spm, R=126–138 mm, r=10–15 mm); DBUA-ECH 410 (Santa Cruz, GRA, AZO, *c.* N39°05’16” W28°00’25”, 2010.08.6, intertidal; 1 spm, R=130 mm, r=20 mm).

Description: disc small with five relatively long, cylindrical arms slightly constricted at the insertion with the disc and a blunt distal extremity; many specimens with missing distal part of the arms or arms with different degrees of regrowth. Body densely covered by granulation, with larger flattened granules intermingled by finer granules. Papular areas in 8 regular longitudinal rows. Maximum number of papular pores per area from 8–10 in the smallest specimen (DBUA-ECH 075, R=67) increasing progressively with the size of the animals to more than 20. Abactinal plates cruciform. Adambulacral plates bearing two blunt, rounded furrow spines, distal one smaller than proximal one. One large, thick, blunt subambulacral spine; no pedicellaria. Colour (when alive) orange to bright red with or without darker blotches. Colour (in ethanol): whitish with some traces of the original orange colouration.

Remarks: on redescribing *Ophidianus guildingii* Gray, 1840, Clark (1921a) concluded that this Western Atlantic species can be distinguished from the Eastern Atlantic *O. ophidianus* primarily by the relative shape of the spines in the adambulacral armature, but also by its colour pattern, slender rays, coarser granulation and larger and fewer papulae. Mortensen (1933c) commented that the colour pattern could not be used as a diagnostic character, since animals of *O. ophidianus* from Santa Helena and the Canaries can also present a molted pattern, a character considered to be characteristic of *O. guildingii*. Madsen (1950) believed that both forms were the same species, and suggested to demote *O. guildingii* to a subspecies of *O. ophidianus*. Tortonese (1965)

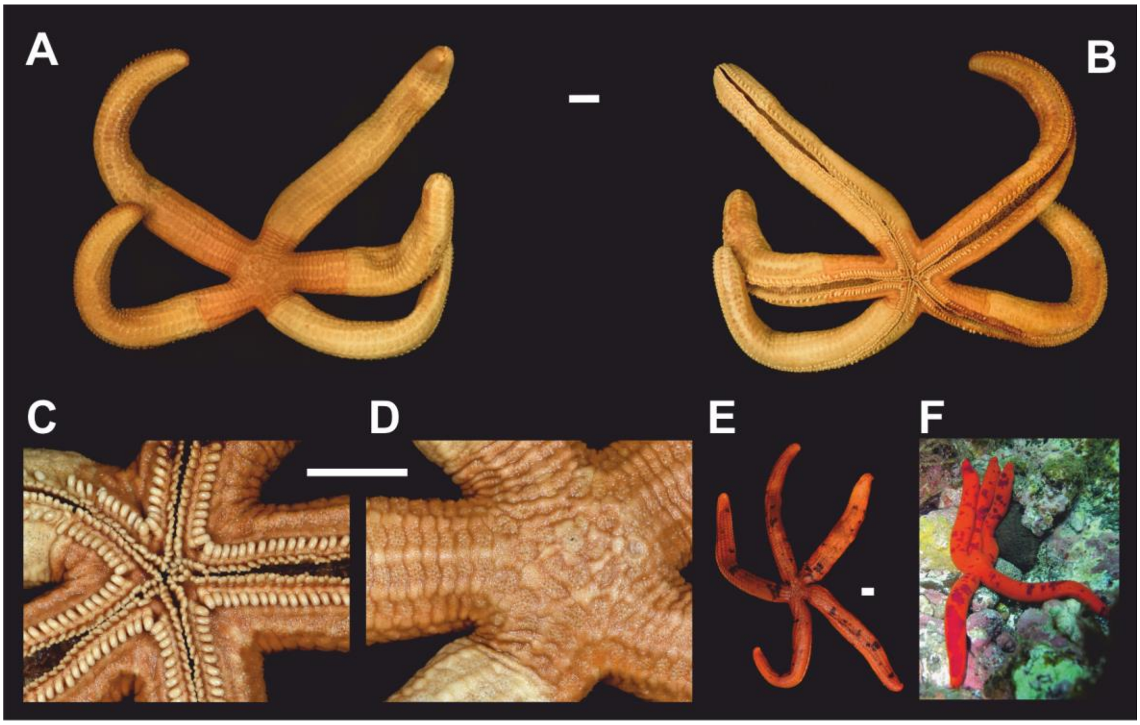


Figure 5.19. *Ophidiaster ophidianus* (Lamarck, 1816) (DBUA-ECH 081: A–D; DBUA-ECH 409: E). Dorsal view (A); ventral view (B); detail of the arm and disc, dorsal view (C), ventral view (D); molted colour pattern (E); animal *in situ* (Pico Island, Azores, ca. N38°23'22" W28°15'04", 2010.08.20, 1 m; F); all scale bars are 10 mm.

commented on the high variability in colour patterns presented by Mediterranean specimens, from bright orange, red, pink to violet, with or without spots of variable number and size. Nataf & Cherbonnier (1975) noted that the number of papillae is highly variable too, depending on the size of the animals. Our own observations on Azorean specimens are in accordance with the data presented by these authors.

Nataf & Cherbonnier (1975) also observed that the granulation is also variable, a trait as well observed by us. Pawson (1978) recommended that the limits of variation, particularly of the colour patterns should be further studied. Most of the individuals housed in the DBUA-ECH collection showed no presence of conspicuous blotches, however little or nothing of the original colour survived in the preservation medium. In Wirtz & Debellius (2003: 276) a photograph taken in Faial Island (Azores) of two specimens side by side can be found: one uniform bright red and the other bright red with small dark blotches. Sympatric occurrence of these two colour morphs was observed in the field us (Figs. 5.19E, F). In a phylogeographic study by Micael *et al.*

(2014) on *O. ophidianus* populations from the Azores, Madeira and Mediterranean, no evidence of significant differences were found, suggesting a recent range expansion.

Drouët (1861) published the first possible report of this species in the archipelago under the name *Asterias lævigata*. Simroth (1888) found a specimen identified as *Ophidiaster ophidianus* at Ponta Delgada Museum, which he believed to be equivalent to Drouët's *Asterias lævigata*. Barrois (1888) contested Drouët identification and place it under the name *O. ophidianus*, one of the most common sea stars of the present-day Azorean shallow-water (Morton *et al*. 1998; Micael *et al*. 2010). The closest name to the original identification is *A. laevigata* (Linnaeus, 1758), now accepted as *Linckia laevigata* (Linnaeus, 1758), a sea star of similar shape but restricted to the Indo-Pacific, which makes it an unlikely candidate. However, the *subspecies Asterias laevigata varietas* Lamarck, 1816 is considered a synonym of *Hacelia attenuata* a species present in the Azores (Clark & Downey, 1992; see above). The only descriptions provided by Drouët (1861) and by Simroth (1888) are the bright red and orange red colour of the specimens, respectively. Unfortunately, in the Azores both species *O. ophidianus* and *H. attenuata* can have bright red and orange colours.

In the historical collection of the Museum Carlos Machado (Ponta Delgada, São Miguel Island) houses some animals belonging to *O. ophidianus*. However, it is not possible to ascertain if those specimens were the same as the ones referred by Simroth. Thus, without the original material it is impossible to further discuss the original identification, and considering the conspicuous presence of *O. ophidianus* in the Azorean shallow waters, one is inclined to accept Barrois (1888) rectification, a view also accepted by Pereira (1997). In any case, Nobre (1924, 1930) place Simroth's record under *O. ophidianus*, but it is not certain if Nobre saw Simroth's original animals.

Sladen (1883, 1889) reported this strictly shallow-water species to the Azores from a depth of 823 m (RV 'H.M.S. Challenger', sta 75: N38°38'00" W28°28'30"), though showing some concerns due to the size of the specimen since in his opinion it was almost too small for an accurate determination, an opinion later joined by Clark (1921a). Nevertheless, the station depth was in all probability much shallower than the one reported (see remarks under *Astropecten hermatophilus*), about 91–165 m, which falls in the maximum depth limit for *O. ophidianus*. Additionally, DBUA-ECH collection houses an animal collected in the area of Don João de Castro Seamount (between Terceira and São Miguel islands), one of the rare examples in Azores of a shallow-water hydrothermal-active volcanic seamount. This species was also recorded by Cardigos *et al*. (2005) in the same area.

The deep-water *O*. *reyssi* (see below) the only other known *Ophidiaster* species in the Azores can be easily distinguished from *O*. *ophidianus* by the presence of pedicellaria and by the overall shape of the body with arms tapering from a broad base. Additionally, *O*. *reyssi* can also be distinguished from all other *Ophidiaster* species by the isolated small bead-like subambulacral spines and a very fine body granulation (Clark & Downey 1992).

Ophidiaster reyssi **Sibuet, 1977**

$1977. *Ophidiaster reyssi* n. sp.; Sibuet: 1085–1090, figs. 1A–C.

$1992. *Ophidiaster reyssi* Sibuet; Clark & Downey: 282, pl. 69, figs. G, H.

Type locality: Azores (N39°33’00” W31°17’30”).

See: Sibuet (1977); Clark & Downey (1992).

Distribution: known only from the Azores and the Mediterranean Sea.

Depth: 128–350 m (AZO: 350 m).

Habitat: hard substrate.

Remarks: *Ophidiaster reyssi* was described by Sibuet (1977) based on an individual collected in Azores by the oceanographic mission ‘Biacores’ (RV ‘Jean Charcot’). Clark & Downey (1992) reported a second specimen from the Mediterranean Sea (near Sicily), expanding the geographical distribution of *Ophidiaster reyssi*, which was otherwise known only from the holotype.

Subphylum Echinozoa Haeckel, 1896

Class Echinoidea Leske, 1778

Subclass Cidaroidea Smith, 1984

Order Cidaroida Claus, 1880

Superfamily Cidaridea Gray, 1825

Family Cidaridae Gray, 1825

Subfamily Cidarinae Mortensen, 1928

Genus *Cidaris* Leske, 1778

Cidaris cidaris (Linnaeus, 1758)
(Fig. 5.20)

$^{\$}$1895a. *Dorocidaris papillata* Leske; Koehler: 224.

$^{\$}$1898. *Dorocidaris papillata*, (Leske); Koehler: 8.

$^{\$}$1909. *Dorocidaris papillata*, (Leske); Koehler: 214–215.

$^{\$}$1921a. *Dorocidaris papillata* Leske; Koehler: 3.

1927a. *Cidaris cidaris* (Linnæus); Mortensen: 272–273, figs. 149, 150–152.

1928. *Cidaris cidaris* (Linn.); Mortensen: 289–298, pl. 30, figs. 3–4, pl. 31, figs. 1–10, pl. 67, fig. 5, pl. 72, figs. 20–22.

$^{\$}$1938. *Cidaris cidaris* Linnâ, 1758; Cadenat: 363.

1938. *Dorocidaris papillata* (Leske); Nobre: 104–105, figs. 45, 55.

1956. *Cidaris cidaris* (Linné); Harvey: 63.

1980. *Cidaris cidaris* (Linné, 1758); Marques: 104.

$^{\$}$1992. *Cidaris cidaris;* Pérès: 253.

?$^{\$}$1992. *Porocidaris purpurata*; Pérès: 252.

?$^{\$}$1992. *Stereocidaris ingolfiana*; Pérès: 254, 258.

2005. *Cidaris cidaris* (Linnaeus, 1758); García-Diez *et al.*: 50.

2006. *Cidaris cidaris* (Linnaeus, 1758); Mironov: 98–99.

2006. *Cidaris cidaris* (Linné, 1758); Schultz: 32, fig. 53–55.

See: Mortensen (1928); Mironov (2006); Schultz (2006); Koukouras *et al.* (2007: 81); Stevenson & Rocha (2012).

Distribution: East Atlantic and the Mediterranean Sea, from south of Iceland and Norway south to equatorial West Africa, including the Azores, Madeira, Canaries, Cabo Verde and Santa Helena; also in Gorringe, Josephine and the Meteor seamounts.

Depth: 20–2,010 (?4,275) m (AZO: 165–1,385 m).

Habitat: mud, fine sand, gravel to hard substrates; an opportunistic scavenger; feeds also on deep sea reef building corals such as *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* (Linnaeus, 1758).

Type of Development: planktotrophic.

Material examined: DOP–2976 (Banco Cavala, AZO, N38°16’12” W30°39’00”, 2008.07.08, 723 m; 1 spm, D=20 mm); DOP–2977 (Banco Cavala, AZO, N38°16’12” W30°39’00”, 2008.07.08, 723 m; 1 spm, D=12 mm); DOP–4335 (Banco Princesa Alice, off SW PIX, AZO, N38°00’10.80” W29°19’04.80”, 2010.09.03, 165–219 m; 1 spm, D=10 mm); DOP–7933 (Banco Princesa Alice, off SW PIX, AZO, N37°58’51.60” W29°31’22.80”, 2011.28.05, 384 m; 1 spm, D=5 mm); EMEPC-LUSO L09D18B2 (N of SJG, AZO, N38°42’14” W28°01’25”, 2009.10.02, 869 m; 1 spm, D=52 mm).

Description: test circular, flattened to almost spherical (test height between 55–70%D). Ambulacra distinctly sinuate, about 20% of the interambulacra in width. Marginal series of tubercles regular. The largest specimen (EMEPC-LUSO L09D18B2; D = 52 mm) presented a regular double series of inner tubercles with a distinct naked median line, becoming a single series just near the apical disc. Pore zones sunken; pores of equal size, each pair separated by a narrow wall. Primary tubercles perforated, not crenulate; areoles are rather large and deep, not confluent; subambital areoles distinctly transverse-oval; mamelon rather large, with the boss rather low. Scrobicular tubercles not very conspicuous. Interradial and adradial zones distinct and naked, both conspicuously sunken. Apical disc covered with small tubercles of uniform size in larger individuals (D ≥20 mm), leaving a fairly conspicuous bare edge between the plates. Apical disc large, dicyclic; genital pores closed in the smaller specimens (D ≤11 mm); Periproct quite flat, covered by moderate number of plates. Peristome smaller than the apical disc, circular to sub-pentagonal. Primary spines rather long, about 2–2.5 times the diameter of the test, cylindrical, thick at the base, tapering very gently, and covered with a fine, spongy coat of anastomosing hairs; oral primaries spines relatively short and flattened with finely serrate edges; scrobicular spines flattened, tapering to a rounded point; marginal ambulacral spines slender, pointed, slightly flattened in the basal part and about half the length of the scrobicular spines. Both large and small globiferous pedicellariae usually present in fair numbers; globiferous pedicellaria with a distinct terminal teeth; large tridentate pedicellaria present on both oral and apical sides. Colour (in ethanol): generally of a uniform light brown to white; spines white or cream; occasionally some of the primary spines are pinkish to dark brown red colour (*e.g.,* DOP 2976); some of the larger spines of the largest individuals (EMEPC-LUSO L09D18B2) are encrusted with serpulids and cirripeds.

Remarks: among the five cidaroids reported from the Azores, *Cidaris cidaris* is the only species known to occur with certainty in the extant waters of the archipelago. Though highly variable this species is easily distinguished from the remaining species by the presence of a coat of hairs covering the primary spines and by the presence of enlarged terminal teeth in the globiferous pedicellaria.

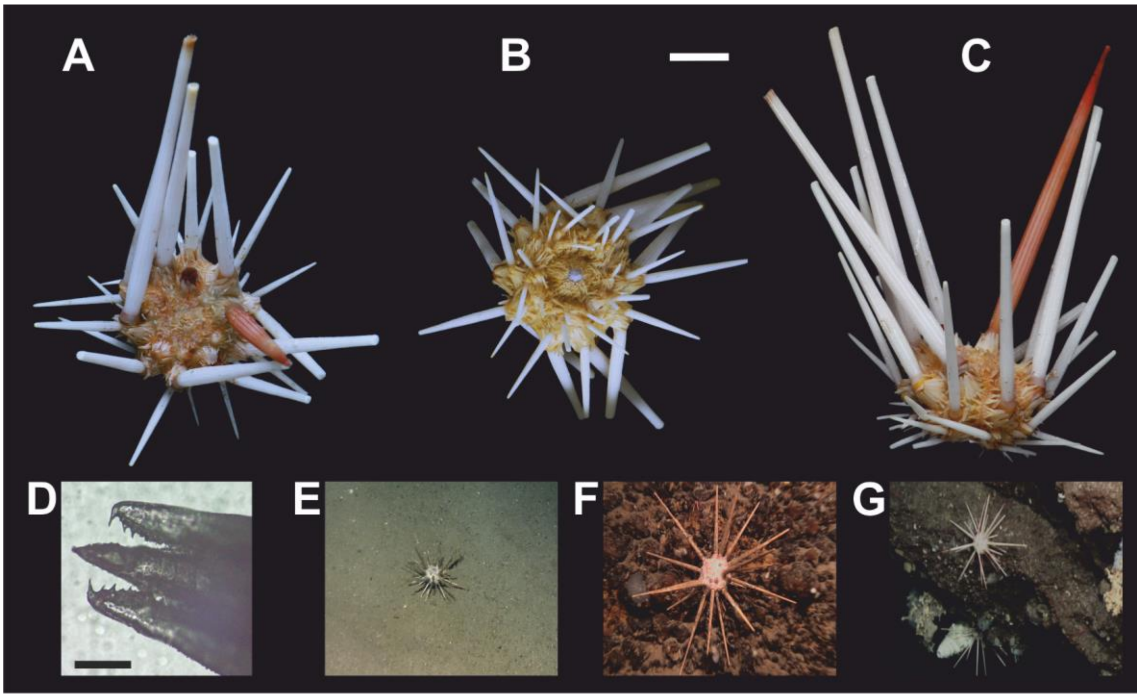


Figure 5.20. *Cidaris cidaris* (Linnaeus, 1758) (DOP 2976: A–D; EMEPC-LUSO L09D18B2: E). Aboral view (A); oral view (B); lateral view (C); globiferous pedicellaria (D); animal *in situ* (N38°42'14" W28°01'25", 2009.10.02, 869 m; E); Cidarids possible belonging to *C. cidaris in situ* in the Azores deep-waters (EMEPC-LUSO, N38°31'45" W27°56'16", 2009.10.04, 869 m, F; N38°14'07" W26°33'27", 2009.10.09, 815 m, G); scale bars are 10 mm (A–C) and 200 µm (D).

Historically, abundant material from the Azores identified as *C. cidaris* (as *Dorocidaris papillata*) is listed in the cruises reports of RVs 'Princesse Alice' and 'Hirondelle' (Koehler 1898, 1909, 1921a), from depths of 500 and 1,200 m. Cadenat (1938) in his report of the expedition of the RV 'Président Théodore-Tissier' also recorded this species in the archipelago from a similar depth. This species appears to be quite common in the Azores at this depth range as the footage by ROV LUSO (EMEPC, 2009 expedition) seems to exemplify. They show cidaroids most likely belonging to *C. cidaris* in practically any kind of environment from sediment to vertical walls (Figs. 3.20D–F).

Genus *Eucidaris* Pomel, 1883

Eucidaris tribuloides? (Lamarck, 1816)

$1895a. *Cidaris tribuloides* Lamarck; Koehler: 224.

$1898. *Cidaris tribuloides*, Lamarck; Koehler: 8—10.

1928. *Eucidaris tribuloides* (Lamarck); Mortensen: 400–408, pl. 41, figs. 9–16, pl. 48, fig. 1, pl. 73, fig. 1, pl. 86, fig. 16.

1956. *Eucidaris tribuloides* (Lamarck); Harvey: 63.

1997. *Cidaris tribuloides* Lamarck, 1816; Pereira: 333.

1999. *Eucidaris tribuloides* (Lamarck, 1816); Pérez-Ruzafa *et al*.: 50–51.

2005. *Cidaris tribuloides* Lamarck, 1816; García-Diez *et al*.: 50.

2010. *Cidaris tribuloides* de Lamarck, 1816; Micael & Costa: 322.

2012. *Eucidaris tribuloides* (Lamarck, 1816); Micael *et al*.: 3.

See: Clark (1925: 21–22); Mortensen (1928); Lares & McClintock (1991); Schultz (2006: 38–39, figs. 65–67); Lessios *et al.* (1999); Madeira *et al.* (2011: 245–248).

Distribution: restricted to the tropical areas of the Atlantic; in the west from South Carolina and Bermuda to Brazil; in the west, present in the Gulf of Guinea, Cabo Verde, the ?Azores, Ascension and St Helena.

Depth: 0–450 m (?AZO: 130 m).

Habitat: mainly a littoral form, occurring under stones and crevices and among corals.

Type of Development: planktotrophic.

Fossil record: *Eucidaris tribuloides* is a common presence in the Miocene-Pliocene fossiliferous outcrops in Santa Maria Island (Azores).

Remarks: Koehler (1895a, 1898) identified a small individual of *E. tribuloides* among the material collected by RV 'Hirondelle' in the Azores (sta 226: N38°31'19" W28°34'31", 130 m). The specimen may represent a vagrant that managed to arrive in the Azores, *i.e.* it does not represent a real self-sustained population (for discussion see Madeira *et al.* 2011). Thus, until new material is collected in this area, the presence of this species in the archipelago should be treated with caution.

Subfamily Stereocidarinae Lambert, 1900

Genus *Stereocidaris* Pomel, 1883

***Stereocidaris ingolfiana*? Mortensen, 1903**

?$^{\$}$1992. *Stereocidaris ingolfiana*; Pérès: 254, 258.

Type locality: Denmark Strait.

See: Koehler (1909: 216); Mortensen (1903: 38–41, pl. 6, figs. 1–5, pl. 8, figs. 4,10–11, 16, 19–21, 23, 26, 28, 30, 36, pl. 11, figs. 12, 16–17, 23, 28, 30, 32–33; 1928: 267–268, pl. 27, figs. 1–3, pl. 70, fig. 6).

Distribution: North Atlantic, from the Denmark Strait south to the Caribbean in the west and to Cabo Verde in the east.

Depth: 300–1,745 m (?AZO: 2,050–3,300 m).

Habitat: soft sediments.

Type of Development: lecithotrophic.

Remarks: Pérès (1992) claimed to have observed *Stereocidaris ingolfiana* during a dive made by the bathyscaphe 'Archimède' north of São Miguel Island (2,050 m depth) and east of Santa Maria Island (3,150–3,300 m depth). No specimen was collected and the identification seems to have rested solely on the long size of the spines of the observed animals. Pérès observations could represent an intermediary record between the east and West Atlantic populations, though *S. ingolfiana* known depth range is slightly shallower than the depth reported by this author. In the other hand, *Cidaris cidaris* is the only cidaroid confirmed species to occur in the archipelago with abundant documented material (see above). At macroscopic level these two species are almost identical, and in many instances the diagnose rests on the observation of pedicellaria (see Mortensen 1927a, 1928). Thus, until material belonging to *S. ingolfiana* is documented in the archipelago, Pérès observation must be placed as a dubious record (see also remarks under *Histocidaris purpurata*).

Superfamily Histocidaroidea Lambert, 1900

Family Histocidaridae Lambert, 1900

Genus *Histocidaris* Mortensen, 1903

***Histocidaris purpurata*? (Thomson, 1872b)**

?$^{\$}$1992. *Porocidaris purpurata*; Pérès: 252.

Type locality: about 100 miles to the north of the Hebrides.

See: Mortensen (1927b: 24; 1928: 104–107, pl. 1, fig. 6, pl. 3, figs. 3–5, as *Poriocidaris purpurata*); Gage *et al.* (1985: 179 as *Poriocidaris purpurata*); Filander *et al*. (2019: 72–73, figs. 1A, B).

Distribution: North Atlantic; in the East from southern Iceland, south to Canaries and Western Sahara; in the west known only from the Caribbean; reported elsewhere in South African waters.

Depth: 300–1,800 m (AZO: ?800 m)

Habitat: soft sediments, from sandy mud to muddy bottoms; gut contents revealed bottom material and fragments of crustaceans.

Type of Development: lecithotrophic.

Remarks: on a dive made by the bathyscaphe 'Archimède' in the Azores, Pérès (1992) reported to have observed animals of *Histocidaris purpurata* with their typical long spines with alternating bands of purple and violet. This cidaroid species has a wide distribution in the Atlantic, thus its report in the Azores could be easily considered as an intermediate location between its distribution in the Caribbean and the European or NW Africa records. However, no specimen was collected in the Azores that on a close examination in the laboratory could substantiate Pérès observations. Another cidaroid species known to occur in area *Cidaris cidaris* is characterised by high morphological variability, including the colour of its spines (primary or secondary) which can vary from the typical white or pinkish to brownish-purplish spines (Fig. 5.20; see also Mortensen 1928). Historically, the Azores was extensively dredged at depths similar to the observations by Pérès (*e.g.,* Koehler 1898, 1909). As a result, abundant material of *Cidaris cidaris* became available, but remarkable none of the oceanographic cruises managed to secure a single specimen of *H. purpurata*. Thus, until animals collected in the area prove to belong to this species, the record of this species in the archipelago should be treated with caution.

Subclass Euechinoidea Bronn, 1860
Infraclass Acroechinoidea Smith, 1981
Order Diadematoida Duncan, 1889
Family Diadematidae Gray, 1855a
Genus *Diadema* Gray, 1825

Diadema africanum? Rodríguez *et al.*, 2013

1940a. *Diadema antillarum* Philippi; Mortensen: 269–275, figs. 144, 145, pl. 47, fig. 8, pl. 49, fig. 5, pl. 57, figs. 1–8, pl. 58, figs. 1–6, pl. 73, fig. 21, pl. 74, figs. 4–8.
1956. *Centrechinus* (*Diadema*) *antillarum* (Philippi); Harvey: 63.
1978. *Diadema antillarum antillarum*; Pawson: 17.
1999. *Diadema antillarum* (Philippi, 1845); Pérez-Ruzafa *et al.*: 51–52.
2002. *Diadema antillarum* (Philippi, 1845); Pérez-Ruzafa *et al.*: 283–284.
$^{\$}$2014. *Diadema africanum* Rodriguez *et al.* 2013; Minderlein & Wirtz: 2, fig. 2.

Type locality: Tenerife, Canary Islands.

See: Alves *et al.* (2001, as *Diadema antillarum*); Lessios *et al.* (2001, as *Diadema antillarum*); Rodrigues *et al.* (2013); Hernández *et al.* (2013: 495–499, fig. 15.6e).

Distribution: East Atlantic, from Senegal to Gulf of Guinea and also in the Azores, Madeira, Selvagens, Canaries, Cabo Verde and São Tomé.

Depth: strictly a littoral form (AZO: 8 m).

Habitat: hard substrates.

Type of Development: probably planktotrophic (inferred from the genus).

Remarks: the inclusion of the Azores in the geographical distribution of *Diadema antillarum* by Mortensen (1940a) at the time appears to be a product of a misprint since no specimen belonging to this species was reported from the archipelago (see below remarks under *Centrostephanus longispinus*). Recently, however, Minderlein & Wirtz (2014) have identified *Diadema africanum* in Santa Maria Island, making the Azores the northernmost limit for this species. Nevertheless, considering its known gregarious behaviour and conspicuous presence on shallow rocky shores throughout this species distribution (Alves *et al*. 2001; Schultz 2006; Hernández *et al*. 2008), it is hard to believe that *D*. *africanum* could represent a case of an overlooked shallow-water element of the Azores in over 150 years of echinoderm studies in the area. In the future, it will be interesting to understand if the specimen found in the southernmost island of the Azores represent a solitary vagrant or a recent established population, as a result of a recent range expansion of this tropical East Atlantic form to the northern waters of the Azores. Minderlein & Wirtz (2014) remarked that since its collection in 2010 no other sightings have been reported, indicating that the presence of this species in the archipelago could be a direct result of the global warming, as occasional propagules find the increasingly warmer waters in the Azores suitable for establishment. Its rare occurrence could be the result of lag times between the initial invasion event(s) to population outbreaks, which are a common phenomenon in the invasion process of many marine species. For example, after its initial discovery more than a decade ago, the alien invasive *Diadema setosum* still is exceptionally rare in the Mediterranean (Bronstein *et al*. 2017).

Genus *Centrostephanus* Peters, 1855

Centrostephanus longispinus (Philippi, 1845)

(Fig. 5.21)

$^{\$}$1888. *Centrostephanus longispinus* Peters; Barrois: 74.

1909. *Centrostephanus longispinus*, (Peters); Koehler: 220, pl. 31, fig. 20.

1914b. *Centrostephanus longispinus*; Koehler: 277.

1921b. *Centrostephanus longispinus* Peters; Koehler: 113, fig. 74.

1927a. *Centrostephanus longispinus* (Philippi); Mortensen: 277.

1940a. *Centrostephanus longispinus* (Philippi); Mortensen: 300–307, figs. 95c, 154–156, pl. 34, figs. 1–11, pl. 35, figs. 11–12, pl. 75, figs. 5–24.

$1955. *Centrostephanus longispinus* Peters; Chapman: 399.

1956. *Centrostephanus longispinus* (Philippi); Harvey: 63.

1965. *Centrostephanus longispinus* (Phil.); Tortonese: 311–312, figs. 143–145.

$1983. *Centrostephanus longispinus* (Philippi, 1845); Marques: 4, fig. 5.

1983. *Centrostephanus longispinus longispinus* (Philippi); Pawson & Miller: 4, fig. 1.

$1993. *Centrostephanus longispinis* (Philippi, 1845); Wirtz & Martins: 59.

$1998. *Centrostephanus longispinus*; Morton *et al*.: 76, fig. 4.2H.

1997. *Centrostephanus longispinus* Philippi, 1845; Pereira: 333.

$2003. *Centrostephanus longispinus*; Wirtz & Debelius: 257.

$2006. *Centrostephanus longispinus* (Philippi, 1845); Micael *et al*.: 5.

$2006. *Centrostephanus longispinus* (Philippi, 1845); Mironov: 104–106.

2006. *Centrostephanus longispinus* (Philippi, 1845); Schultz: 91–93, figs. 164–168.

2008. *Centrostephanus longispinus*; Haddad & Barreiros: 9.

2010. *Centrostephanus longispinus* (Philippi, 1845); Micael & Costa: 323.

2012. *Centrostephanus longispinus* (Philippi, 1845); Micael *et al*.: 4.

Type locality: Sicily, Mediterranean Sea.

See: Mortensen (1940a; 1951a: 296–297); Pawson & Miller (1983); Mironov (2006); Schultz (2006).

Distribution: Mediterranean Sea and Atlantic, in the East Atlantic from Morocco south to Angola, including the Azores, Madeira, Canaries and Cabo Verde archipelagos and Ampere, Gorringe, Josephine, Seine, Great Meteor, Dacia and Conception seamounts, in the western Atlantic, reported from the Gulf of Mexico and the Caribbean to Brazil, including the Brazilian island of Trindade.

Depth: 12–360 m (AZO: 6–468 m).

Habitat: detritic and rocky substrates; feeds on bottom detritic material and algae.

Type of Development: probably planktotrophic (inferred from the genus.

Material examined: DBUA-ECH 001 (Piscina da Lagoa, SMG, AZO, *c.* N37°44’29” W25°34’27”, 1996.07.25, 15 m; 2 spms, D=59 mm); DOP 5467 (Condor Seamount, AZO, N38°32’13” W28°59’06”, 2010.08.06, 468 m; 1 spm, D=10 mm); EMEPC-LUSO L09D9B03S01 (Gorringe Bank, NE Atlantic, N36°42’49” W11°09’54”, 2009.09.13, 130 m; 1 spm, D=25 mm); MB-NMHN 382–20758 (Caloura, SMG, AZO, *c.* N37°42’46” W25°29’44”, 1977, 8 m; 1 spm, D=53 mm); MB-NMHN 388–20764 [Varadouro (submarine cave), FAY, AZO, *c.* N38°33’49” W28°46’28”, 1979.08.02, 6 m; 1 spm, D=30 mm]; MB-NMHN

422–20798 (Ponta da Galera, SMG, AZO, *c.* N37°42’20” W25°30’33”, 1979, 18 m; 1 spm, D=57 mm); MB-NMHN 435–20811 (Ponta Delgada harbour, SMG, AZO, *c.* N37°44’13” W25°39’26”, 1982; 1 spm, D=6 mm).

Description: test circular, flattened above and below, about to 50%D, though in most of larger specimens the test tends to be somewhat inflated adapically, reaching as much as 72%D. Ambulacra tuberculation typically composed of a single primary tubercle about the same size as the primary tubercles in the corresponding interambulacra (absent in the area above the ambitus), and one conspicuous smaller secondary tubercle located in the perradial median zone; pore pairs in a straight line adapically, changing to arcs of three closer to the ambitus and crowded at the peristomial edge; ambulacral area about 65 to 75% of the interambulacral area at the ambitus. In interambulacra, large primary tubercle occupying most of the plate; the small interradial space occupied by small secondary tubercles; the adradial area occupied by a larger secondary tubercle reaching a considerable size at the ambitus of larger specimens. Apical disc about 33 to 40%D; in larger specimens the ocular plates are insert; in the smallest specimen (MB-NMHN 435–20811; D=6 mm) some of the plates are still exsert and no periproctal scales exist. In the second smallest specimen

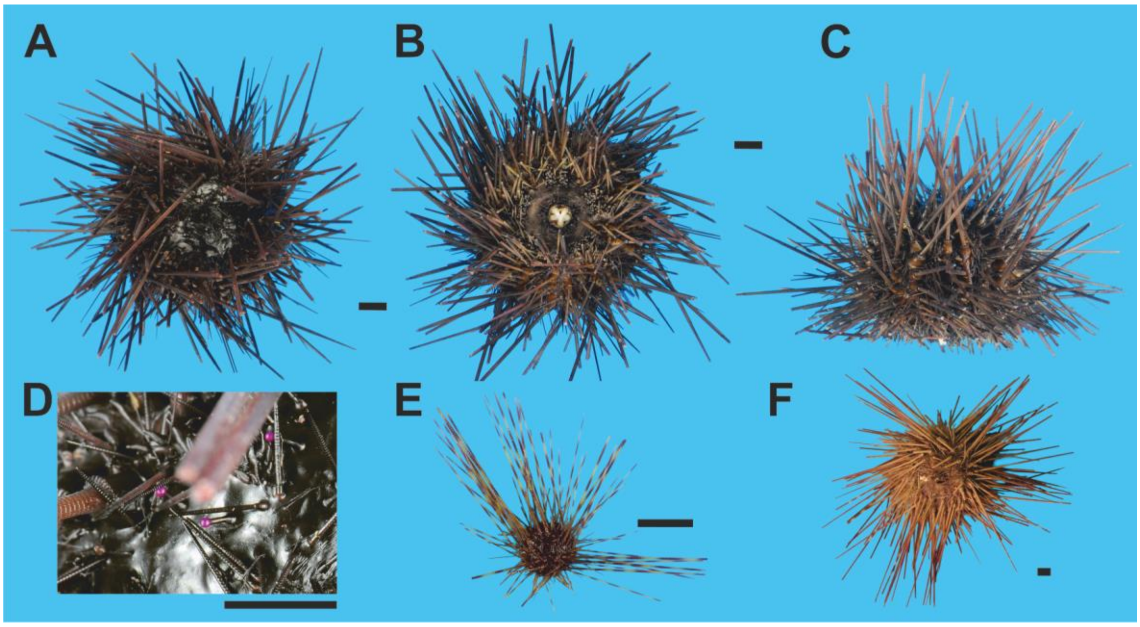


Figure 5.21. *Centrostephanus longispinus* (Philippi, 1845) (DBUA-ECH 001: A–D; DOP 5467: E; MB-NMHN 422–20798: F). Aboral view (A); oral view (B); lateral view (C); detail of the apical area showing claviform spines (D); aboral view of a juvenile (E); aboral view of a dry specimen (F); scale bars are 5 mm (D) and 10 mm (A–C, E–F).

(DOP–5467; D=10 mm) some plates are already present in the periproctal membrane and ocular plates I, IV, and V are insert; ocular plates naked or with one spine in the smallest specimens to up to two spines in the largest specimens; genital plates (madreporite inflated) bear up to three spines, with the exception of the smallest specimens in which the plates are naked or bear a single spine; the periproct is covered with small naked scales in the two smaller specimens; all other specimens have scales with spines, especially in the area surrounding the anal opening; gonopores not open in the two smallest individuals (≤10 mm D). Peristome larger in the smaller individuals, about 50%D diminishing proportionally in larger specimens to about 37%D; buccal membrane with plates particularly numerous in the ambulacral areas; paired buccal plates bear pedicellariae. Most of the spines were broken in all specimens, particularly in the ambital area; primary spines hollow, verticilate, and very fragile; spines on the oral side terminate in a crown shaped tip; on the apical side, the uppermost spines small club-shaped (claviform spines) with bright purple to pink tips (with the exception of the smallest specimen in which such spines are not yet present). Larger specimens black to dark brown or light brown in the case of the dry specimens from Museu Bocage; specimens of intermediate sizes (DOP–5467, EMEPC-LUSO L09D9B03) with the same pattern as the larger specimens, with the exception of the presence of a white line in the median area of both ambulacra and interambulacra; the smallest specimen (MB-NMHN 435–20811) almost white coloured, with the primary tubercles and the apical plating of a darker pinkish colour; spine colouration highly variable; the largest individuals (DBUA-ECH 001) with conspicuous dark coloured spines, though some of the spines presented a weak lighter red banding; spines of the largest dry specimens (MB-NMHN 422–20798 and MB-NMHN 382–20758) of a light brown colour at the basis, progressively changing to a more purplish tone or interchanging distally between the two colours, forming a banded pattern in many spines; all specimens of intermediate to smaller sizes with conspicuous yellow and purple to pinkish banded spines.

Remarks: until recently, the occasional reports of *Diadema antillarum* from the Azores were most likely a result of confusions with *Centrostephanus longispinus*. As was one time noted by Wirtz & Martins (1993: 59), ‘at least those along the coasts of Faial seen by us are a black colour morph of *Centrostephanus longispinus* and not *Diadema* *antillarum*'. Nevertheless, and aside from morphological similarity between the two species, another possible source for such misidentifications is the unusual depth at which *C. longispinus* can occur in the Azores, as low as 5 m in sheltered areas such as ports or underwater cave-like habitats (Chapman 1955; Wirtz & Martins 1993; Morton *et al*. 1998; Micael *et al*. 2006; *personal observation*).

The unusual black colour shown by some of the Azorean individuals in opposition to the typical lighter colours, as described for the type specimens from the Mediterranean Sea [Philippi 1845, as *Cidaris* (*Diadema*) *longispina*] another reason for confusion. Clark (1921b) described a closely resembling species, *C. rubricingulus*, from the Caribbean, which according to Mortensen (1940a) could only be distinguished from *C. longispinus* by the interambulacral tuberculation, spine structure and pedicellaria morphology. The later author considered the colour pattern in *C. longispinus* far too variable to be considered as a diagnostic character. However, Clark's and Mortensen's descriptions were based on very few specimens available at the time. Later, Pawson & Miller (1983) based on new material agreed with Fell (1975) to treat the East Atlantic species as a subspecies of *C. longispinus* since they could not support any of the diagnostic characters pointed out by Mortensen (1940a). In addition, they concluded that the colour of the spines is a diagnostic character that can distinguish the western solid dark colour spines from the lighter banded colour spines of the eastern subspecies. Nevertheless, Pawson & Miller (1983) alerted that the absence of banding could only be expected in individuals larger than 25 mm in total diameter.

In the Azores, *C. longispinus* can adopt a large spectrum of colours from purplish with whitish-banded spines to solid black colour pattern, with no conspicuous banding of spines (see Marques 1983; Wirtz & Debelius 2003). Unfortunately, due to the very fragile nature of the spines in this species, the specimens herein examined were lacking most of the spines. Nevertheless, it was possible to confirm the presence of banding pattern in the spines of all but one specimen (DBUA-ECH 001; D=59 mm). However, understanding that in larger specimens banding is not a constant trait of all spines in one individual and that frequently banding is present in the distal part of the spine only, it was impossible to determine whether this specimen could have any banded pattern present if all its spines had survived intact. The colour in the eastern form of *C. longispinus* is known to change under exposure to different light conditions, and the activity of black chromatophores is well studied in this species (*e.g.,* Dambach 1969; Weber & Dambach 1974; Gras & Weber 1977). Additionally, Pawson & Miller (1983) mentioned that bleaching spines (*i.e*. removal of black pigment) from western Atlantic *C. longispinus* specimens uncover the presence of a banding pattern, in otherwise solid dark individuals.

The material herein examined reveals yet another source of colour variation, the method of preservation. Marques (1983) described the specimens collected at the Azores during a 1979's expedition as solid black with no banding pattern. On figure 5 presented by Marques one can clearly recognize specimen MB-NMHN 422–20798, the same specimen that now can be characterized by spines possessing a clear banding pattern (Fig. 5.21F). Thus, methods of preservation such as dehydration seems to mimic the effects of bleaching, possible due to the shrinkage or destruction of the black pigment chromatophores and tissue degradation, turning once black specimen into a 'banded' animal. Mironov (2006) studied the variation of reported diagnostic characters reported by Mortensen (1940a) and Pawson & Miller (1983) in specimens of *C. longispinus* throughout its geographical range. Although he did find some indication for a geographical gradient from east to west in the primary spines colouration of adult specimens, he regarded it as far too inconsistent to retain the subspecies. Our results agree with Mironov and we thus refrain from assigning the Azorean specimens to either subspecies. In contrast to Mironov (2006) who noted that the minimum total diameter at which the genital pores were developed was of 9 mm, the specimen of 10 mm D examined by us had no gonopores yet.

The long spinned *C. longispinus* can be easily distinguished from other sea urchin species inhabiting the Azorean coastal waters by its very long spines and the presence of conspicuous bright purple to pink claviform spines around the apical disc.

Order Pedinoida Mortensen, 1939

Family Pedinidae Pomel, 1883

Genus *Caenopedina* Agassiz, 1869

Caenopedina cubensis Agassiz, 1869

$^{\$}$1909. *Hemipedina cubensis* Agassiz; Koehler: 221–226, pl. 1, fig. 1, pl. 30, figs. 8–17, pl. 31, fig. 21.

1927a. *Cænopedina cubensis* Agassiz; Mortensen: 277.

1940a. *Cænopedina cubensis* Agassiz; Mortensen: 96–99, pl. 2, figs. 19–20, pl. 66, figs. 1–9.

1985. *Caenopedina cubensis* A. Agassiz 1869; Serafy & Fell: 20, fig. 11.

2005. *Caenopedina cubensis* Agassiz, 1869; García-Diez *et al*.: 50.

Type locality: off Havana, Cuba.

See: Koehler (1909); Mortensen (1940a); Downey (1968: 11).

Distribution: North Atlantic; in the west, in USA coast from northern Nova Scotia to the Caribbean and the Gulf of Mexico; in the East recorded from the Azores and Canaries.

Depth: 250–1,187 m (AZO: 1,187 m).

Habitat: soft substrates: feeds on bottom detritus.

Type of Development: planktotrophic.

Remarks: *Caenopedina cubensis* is known from the Azores by two specimens reported by Koehler (1909) on the material collected by RV ‘Princesse Alice’ (sta 1311: N37°37’00” W25°20’45”, 1,187 m).

Infraclass Carinacea Kroh & Smith, 2010

Superorder Calycina Gregory, 1900

Order Salenioida Delage & Hérouard, 1903

Family Saleniidae Agassiz, 1838

Genus *Salenocidaris* Agassiz, 1869

Salenocidaris hastigera (Agassiz, 1879)

$^{\$}$1895a. *Salenia hastigera* Agassiz; Koehler: 224.

p.p.$^{\$}$1895b. *Salenia hastigera* Agassiz; Koehler: 228.

$^{\$}$1898. *Salenia hastigera*, Agassiz; Koehler: 9.

p.p.$^{\$}$1909. *Salenia hastigera*, A. Agassiz; Koehler: 219–220.

$^{\$}$1921a. *Salenia hastigera* A.Agassiz; Koehler: 3.

1927a. *Salenia profundi* (Duncan); Mortensen: 289.

1935. *Salenocidaris profundi* (Duncan); Mortensen: 354–357, pl. 85, figs. 1, 2, 29, 30, 35, 36, pl. 86, figs. 1, 2.

1938. *Salenia hastigera* A. Agassiz; Nobre: 109–110.

$^{\$}$1972. *Salenocidaris hastigera* (A. Agassiz 1879); Sibuet: 122–123.

2005. *Salenocidaris profundi profundi* (Duncan, 1877); García-Diez *et al*.: 50.

2014. *Salenocidaris profundi profundi* Duncan, 1877; Mironov: 123.

$ 2014. *Salenocidaris hastigera* (Agassiz, 1879); Mironov: 122.

Type locality: Pacific (Banda Sea).

See: Agassiz (1879:198–199, as *Salenia hastigera*); Mironov (2014).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian oceans; in the Atlantic confirmed from the Azores and Atlantis Seamount (Meteor).

Depth: 370–2,605 m (AZO: 793–2,440 m).

Remarks: historically, *S. hastigera* was confused with two closely resembling species, *S. varispina* Agassiz, 1869 and *S. profundi* (Duncan, 1877). Following Agassiz's (1879, 1881) descriptions, Koehler (1895a, 1895b, 1898, 1909, 1921a) recorded this species from the Azores. Later, Mortensen (1927a,b, 1935, 1940b) considered all the records of this species in the Atlantic as misidentifications of *S. profundi*, retaining the name *S. hastigera* to the form from the Indo-Malayan region. Sibuet (1972) ignored Mortensen's decision and place the identification of a small specimen collected by the bathyscaphe 'Archimède' in the Azores (1,730 m depth) under the later species. More recently, Mironov (2006, 2014) confirmed the presence of this species in the Azorean waters, at a maximum depth of 2,440 m. The true geographical distribution and depth range in the Atlantic of *S. hastigera* is still pending on a future review (Mironov 2006, 2014). Regardless, if all reports for the archipelago are returned back to the original determination of *S. hastigera* by Koehler (1895a, 1895b, 1898, 1909) it leaves no record of *S. profundi* in the archipelago. Additionally, Mortensen (1935) assumed that among the material of *S. hastigera* reported by Koehler there were specimens belonging to *S. varispina*, and on the re-examination of a specimen from RV 'Princesse Alice' collected within the Azorean waters (sta 578: N38°26' W26°30'45", 1,732 m) confirmed his suspicions (see below).

Salenocidaris varispina **Agassiz, 1869**

(Fig. 5.22)

$ 1881. *Salenia varispina*; Agassiz: 55–56, pl. 4, figs. 1–2.

p.p.$ 1895b. *Salenia hastigera* Agassiz; Koehler: 228.

p.p.$ 1909. *Salenia hastigera*, A. Agassiz; Koehler: 219–220.

1927a. *Salenocidaris varispina* (A. Agassiz); Mortensen: 289.

$^{\$}$1935. *Salenocidaris varispina* A. Agassiz; Mortensen: 350–354, fig. 193a, pl. 66, fig. 9, pl. 84, fig. 4, pl. 85, figs. 3–4, 8, 16–17, 37.

$^{\$}$2006. *Salenocidaris varispina* Agassiz, 1869; Mironov: 106.

2014. *Salenocidaris varispina* Agassiz, 1869; Mironov: 122–123.

Type locality: Off Double Head Shot Key, Cuba.

See: Agassiz (1869: 254–256); Mortensen (1935); Serafy & Fell (1985: 4, 11, 21, fig. 19); Mironov (2006, 2014).

Distribution: cosmopolitan, known from the Atlantic and Pacific Oceans; in the West Atlantic from south of Cape Cod to Brazil, and in the east Atlantic from Bay of Biscay to off Ascension Island, including the archipelago of the Azores, and the Atlantis, Tropic and Antialtair seamounts.

Depth: (?290) 610–2,600 m (AZO: (?718)1,165–1,830 m).

Habitat: typically found on fine-grained sediments, feeds on bottom material, including foraminifera.

Type of Development: planktonic.

Material examined: EMEPC-LUSO L09D22S1 (D. João de Castro Bank, AZO, *c.* N38°14'02" W26°33'37", 2009.10.09, 718-825 m; 1 bt, D=2 mm); EMEPC-LUSO L09D25ARB21 (between São Jorge and Pico Island, *c.* N38°36'19" W28°06'47", 2009.10.21, 1,179 m; 1 spm, D=3 mm).

Description: test small, low and hemispherical with a flattened oral side. Apical disc dicyclic, relatively large (about 80%D), occupying much of the aboral side; Plates of the apical disc densely ornamented with rough papillae arranged somewhat concentrically. Periproct off centre and angular, larger than the suranal plate. No genital pores open. Ambulacral plating simple except for plates adjacent to the peristome, which are bigeminate. Pores small; pore areas slightly widened at the peristome. One primary tubercle per ambulacral plate, slightly smaller than the corresponding one in the interambulacra. A pair of sphaeridia at the peristomial edge of each ambulacrum. Interambulacral plates each with a single, large, primary crenulated and non-perforated primary tubercle. Primary spines long, slender and verticillated, more than twice the size of the test (broken off at the tips); milled ring prominent; thorns developed primarily on upper (aboral spines) or lateral sides (oral spines). Secondary spines spatulated and rather broad. Periproctal spines short, thick and club-shaped to almost globular. Tridentate pedicellariae could not be found. Triphyllous and ophicephalus pedicellariae common, including the distal area of the apical disc.

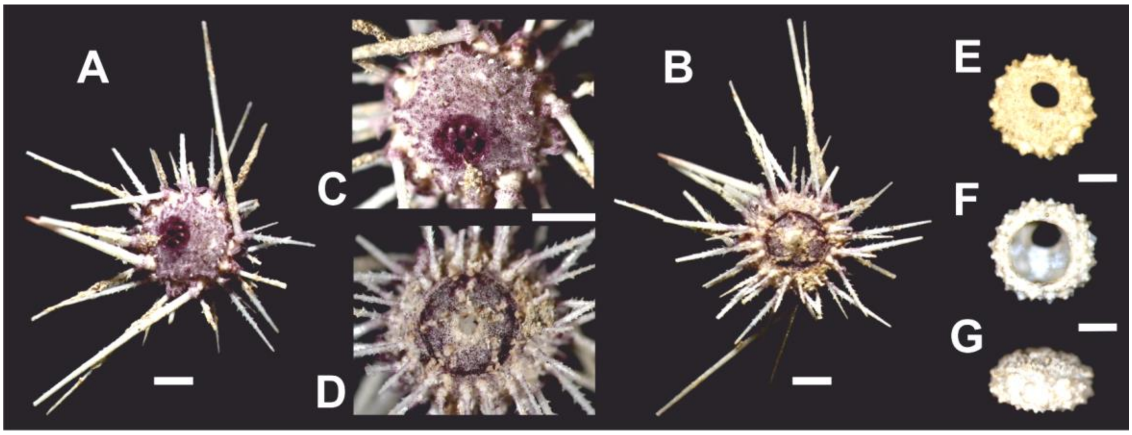


Figure 5.22. *Salenocidaris varispina* Agassiz, 1869 (EMEPC-LUSO L09D25ARB21: A–D; EMEPC-LUSO L09D22S1: E–G). Aboral view (A, E); oral view (B, F); lateral view (G); detail of the aboral surface (C) and oral surface (D); scale bars are 1 mm.

Colour (in ethanol): periproct deep purple; apical disc, peristome and secondary spines purple; tube feet cream white; primary spines uniform white with a purple base.

Remarks: as with other *Salenocidaris* recorded from the archipelago, *S. varispina* was frequently misidentified, confused with the close resembling species, *S. profundi* and *S. hastigera*. For example, Mortensen (1935) re-examined a small specimen from RV 'Princesse Alice' collected in Azorean waters (sta 578: N38°26'00" W26°30'45", 1,732 m) previously identified by Koehler (1909) as *S. hastigera*, and reassigned it to *S. varispina*. Nevertheless, more recently, Mironov (2006) found 4 specimens of *S. varispina* collected north of São Miguel Island by the RV 'Jean Charcot' ('Biacores' cruise, sta 179: N38°05'30" W25°46'30", 1,590–1,665 m), further substantiating the presence of this species in the archipelago.

The main diagnostic character of *S. varispina* is the relative short and wider valves of its tridentate pedicellariae (Mironov 2006). Other characters are also used to distinguish this species from *S. profundi* or *S. hastigera* are: broader interambulacral areas, broader secondary spines, thick and short periproctal spines and shorter and less thorny spines with the thorns only well developed in the adapical side (Mortensen 1935; Mironov 2006). In spite of the colour variability presented by *S. varispina* the presence of a dark purple periproct is also considered characteristic of this species (Mortensen 1935; Mironov 2006). The specimens herein examined were small (D <3 mm) and not fully developed. Also, both lack important diagnostic characters as no tridentate pedicellaria were present. However, we feel confident that they belong to *S*. *varispina*. The complete specimen (EMEPC-LUSO L09D25ARB21) presented many of the typical features of *S*. *varispina*, particularly the deep purple periproct. The ornament of the primary spines varied slightly from typical *S*. *varispina*. This deviation could be dismissed as age dependent based on previous observations by Mortensen (1935). The identification of the naked test (EMEPC-LUSO L09D22S1) was less safe as most of diagnostic characters in this genus rely on external appendages, none of which were present. However, comparing the test of both specimens they are nearly identical with comparable arrangement and ornamentation of the apical disc and the plating and tuberculation of the ambulacral and interambulacral areas. The known depth ranges of *S*. *hastigera* (370–2,605 m) and *S*. *varispina* are similar (650–2,600 m), though the former is also known from shallower depths outside the Atlantic (Mironov 2014). Reports in the Azores appear to follow the same general pattern, though *S*. *varispina* (1,165–1,830 m) is known locally from a narrower depth range than *S*. *hastigera* (793–2,440 m). The naked test herein reported (EMEPC-LUSO L09D22S1) was collected at shallower depth (718–825 m) than previous records of this species from the archipelago. Regardless, Mironov (2014) concluded that in the Northeast Atlantic *S*. *varispina* typically occurs in depths shallower than 2,000 m, whereas *S*. *hastigera* usually occurs deeper (>1,900 m).

Superorder Echinacea Claus, 1876
Order Arbacioida Gregory, 1900
Family Arbaciidae Gray, 1855a
Genus *Arbacia* Gray, 1835

Arbacia lixula **(Linnaeus, 1758)**
(Fig. 5.23)

$^{\$}$1861. *Echinus aequituberculatus*; Drouët: 93.
$^{\$}$1861. *Echinocidaris aequituberculatus* Desmoul.; Drouët: 210–211.
$^{\$}$1863. *Arbacia æquituberculata* Gray; Agassiz: 20.
1872. *Arbacia pustulosa* Gray; Agassiz: 232–234, pl. 1g, fig. 5, pl. 2a, figs. 15–33, pl. 5, figs. 19–21, pl. 28, fig. 6, pl. 38, figs. 10a–c.
1888. *Echinocidaris æquituberculatus* Desmoulins; Barrois: 31.
$^{\$}$1888. *Arbacia pustulosa* Gray; Barrois: 74–75.
$^{\$}$1888. *Arbacia pustulosa* (Leske); Simroth: 231.
$^{\$}$1889. *Arbacia pustulosa* (Gray); John: 285.

$1895a. *Arbacia pustulosa* Leske; Koehler: 224.

$1898. *Arbacia pustulosa*, Leske; Koehler: 9.

1912. *Arbacia lixula* (Linné) – Jackson: 158.

1921b. *Arbacia aequituberculata* Blainville; Koehler: 113–114, fig. 75.

$1924. *Arbacia æquituberculata* (Blainville); Nobre: 89.

1927a. *Arbacia lixula* (Linn.); Mortensen: 290.

$1930. *Arbacia æquituberculata* (Blainville); Nobre: 30, 69.

1935. *Arbacia lixula* (Linnæus); Mortensen: 566–572, pl. 70, fig. 13, pl. 87, figs. 11, 12.

$1938. *Arbacia æquituberculata* Blainville 1825; Cadenat: 366, 373.

1956. Arbacia lixula (Linné); Harvey: 51, 63.

$1955. *Arbacia aequituberculata* (Blainville); Chapman: 399.

$1983. *Arbacia lixula* (Linné, 1758); Marques: 4–5.

$1983. *Arbaciella elegans* Mortensen, 1910; Marques: 5. [juvenile of *A*. *lixula*]

$1984. *Arbacia lixula* (L.); Marques: 103–108, fig. 1.

1997. *Arbacia lixula* (Linnaeus, 1758); Pereira: 333–334.

1997. *Arbaciella elegans* Mortensen, 1910; Pereira: 334. [based on Marques 1983]

$1998. *Arbacia lixula*; Morton *et al*.: 92–93, figs. 3–3H1, 3–4X, 5–1R, 5–2T1, 8–1M.

2002. *Arbacia lixula* (Linneo, 1758); Pérez-Ruzafa *et al*.: 284–285.

$2003. *Arbacia lixula*; Wirtz & Debelius: 259.

2005. *Arbacia lixula*; Cardigos *et al*.: 165.

2005. *Arbacia lixula* (Linnaeus, 1758); García-Diez *et al*.: 50.

2006. *Arbacia lixula* (Linné, 1758); Schultz: 118–119, figs. 211–215.

$2008. *Arbacia lixula*; Haddad & Barreiros: 9, fig. 3c.

2008. *Arbaciella elegans*; Haddad & Barreiros: 9. [based on Marques 1983]

2010. *Arbacia lixula* (Linnaeus, 1758); Micael & Costa: 322.

2010. *Arbaciella elegans* Mortensen, 1910; Micael & Costa: 322. [based on Marques 1983]

$2010. *Arbacia lixula* (Linnaeus, 1758); Micael *et al*.: 329.

$2011. *Arbacia lixula* (Linnaeus, 1758); Kroh *et al*.: 99–105, figs. 2–4.

2011. *Arbacia lixula* Linnaeus, 1758; Madeira *et al*.: 248–249, figs. 4,5A, 6A.

2012. *Arbacia lixula* (Linnaeus, 1758); Micael *et al*.: 3

2012. *Arbaciella elegans* Mortensen, 1910; Micael *et al*.: 3. [based on Marques 1983]

$2012. *Arbacia lixula* (Linnaeus, 1758); Wangensteen *et al*.: 1–16.

See: Mortensen (1935); Cherbonnier (1959: 43, pl. 3, figs. G–P, pl. 4, fig. A, as *Arbacia lixula* var. *africana*); George (1990); Alves *et al.* (2001); Schultz (2006); Kroh *et al.* (2011); Madeira *et al.* (2011); Wangensteen *et al.* (2012).

Distribution: East Atlantic and Mediterranean Sea; present along the Atlantic warmer waters of Africa to the Gulf of Guinea and Angola, including the Azores, Madeira, Selvagens, Canaries and Cabo Verde; it is present as well in Brazil.

Depth: 0–55 m, common on the first few meters in the Azores (<15–18 m), but can occur at depths as great as 55 m.

Habitat: hard substrata, particularly dominant on exposed rocky shores of the Azores; nocturnal omnivorous grazer.

Type of Development: planktotrophic (*c.* 26 days).

Fossil record: spines and test fragments were reported from Pleistocene sediments of Santa Maria Island.

Material examined: DBUA-ECH 013 (Rosto do Cão, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1997.02.07, 13 m; 1 broken bt); DBUA-ECH 014 [Capelas (Morro), SMG, AZO, *c.* N37°50’37” W25°41’18”, 1996.05.26, 9 m; 1 spm, D=36 mm]; DBUA-ECH 015 (São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2006.07.11, intertidal; 1 bt, D=38 mm); DBUA-ECH 016 (Vila Franca do Campo, SMG, AZO, *c.* N37°42’50” W25°25’58”, 2006.07.20, intertidal; 1 bt, D=38 mm); DBUA-ECH 107 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06; 3 spms, D=36–46 mm); DBUA-ECH 235 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2009.12.4, 5 m; 1 bt, D=3 mm); DOP 3014 (Channel PIX–FAY, AZO, N38°34’16” W28°32’31”, 2008.06.16, 55 m; 1 spm, D=10 mm); DOP 3024 (Channel PIX–FAY, AZO, N38°34’16” W28°32’31”, 2008.06.16, 50 m; 1 spm, D=4 mm); MB-NMHN 367–20743 (Ponta Delgada harbour, SMG, AZO, *c.* N37°44’12” W25°39’26”, 1982, collected and identified by Vasco Marques as *Arbaciella elegans*; 11 spms, D=5–8 mm); MB-NMHN 372–20748 (Castelo Branco, FAY, AZO, *c.* N38°31’05” W28°43’23”, collected and identified by Vasco Marques as *Arbaciella elegans*; 3 spms, D=5–13 mm); MB-NMHN 385–20761 (SMG, AZO, 1982; 7 spms, D=24–45 mm); MB-NMHN 385–2076 (SMG, AZO, 1988; 7 spms, D=24–45 mm); MB-NMHN 401–20777 (SMG, AZO, 1982; 3 spms, D=38–40 mm); MB-NMHN 403–20779 (Castelo Branco, FAY, AZO, *c.* N38°31’05” W28°43’23”, 1979; 4 spms, D=30–50 mm); MB-NMHN 412–20788 (SMG, AZO, 1988; 7 spms, D=35–50 mm); MB-NMHN 415–20791 (SMG, AZO, 1982; 7 spms, D=27–52 mm); MB-NMHN 416–20792 (SMG, AZO, 1982; 5 spms, D=43–52 mm); MB-NMHN 548–20924 (Baixinha, GRA, AZO, *c.* N39°05’13” W27°59’09”, 1982.08.10, 15 m; 5 spms, D=50–58 mm).

Description: test circular, hemispherical, flattened on the oral side with a height about of 40–50%D. Epistroma well developed, particularly evident on the aboral side. Apical disc about 50%D in smaller animals changing gradually to about 21%D in larger animals, naked and in most dicyclic, though the Oc V tends to be wedged in between the genital plates. Madreporite enlarged. Periproct oval shaped, with four naked anal plates; Gonopores open at sizes greater than 6 mm, though in some individuals as large as 10 mm are still not developed (*e.g.,* DOP 3014). Ambulacra narrow, about

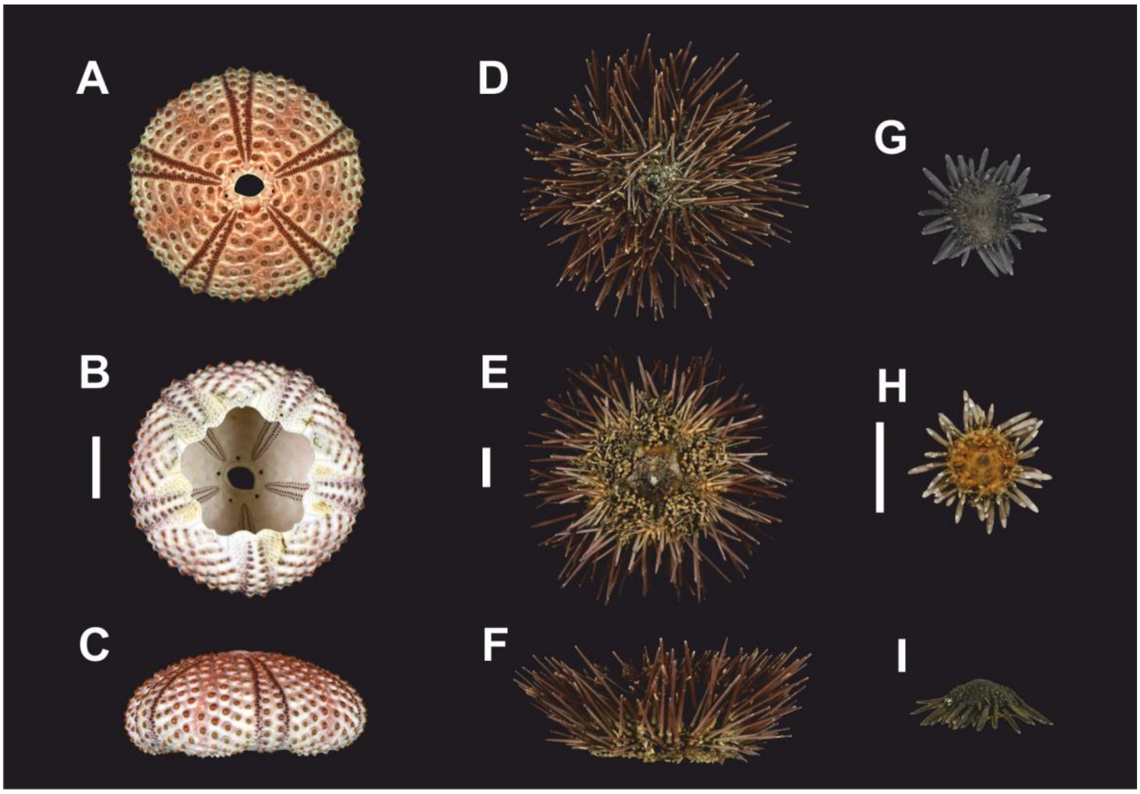


Figure 5.23. *Arbacia lixula* (Linnaeus, 1758) (DBUA-ECH 015: A–C; DBUA-ECH 020: D–F; DOP 3024: G–I). Aboral view (A, D, G); oral view (B, E, H); lateral view (C, F, I); scale bars are 10 mm (A–F) and 5 mm (G–I).

30–40% of the inter-ambulacra at the ambitus, but widening to twice the size of the interambulacra at the peristomal edge; plates trigeminate, bearing a single primary tubercle each. These are arranged in alternating fashion near the apical disc but changing to a double vertical series just above the ambitus. Primary tubercles in the interambulacra reduced to one per plate in the area surrounding the apical disc, becoming numerous towards the ambitus, reaching up to 4 to 5 per plate in the larger specimens, the most interradial of which is usually smaller; in smaller specimens (<13 mm D), the spines only develop at the ambitus, about the third or fourth plate from the apical disc, giving a rather naked appearance of apical side. Peristome relatively large, about half of the D, ambulacral margins protruding and interambulacra terminating in well-defined buccal notches, giving the peristome an overall sinuous pentagonal appearance. Primary spines about 60–70%D; the primary spines in the small individuals (<5 mm D) are dorsoventrally flattened, sword like shaped, changing to the typical tip-pointed spines seen in larger specimens through ontogeny. Colour: solid black to dark brown; in smaller specimens (<5 mm), the spines are rather translucid with a black hue. Colour (naked test): interambulacra and ambulacra pink or reddish, particularly so in pore zones; apical disc can be darker, with a greyish hue.

Remarks: according to the text, Drouët (1861) only found *Arbacia lixula* (=*Echinocidaris aequituberculatus*) in Terceira Island and concluded that it was a rare species in the Azores. Conversely, Barrois (1888, as *Arbacia pustulosa*) commented that this species was quite common in rocky shores of the Azores, where it occurs in association with *Paracentrotus lividus* (as *Strongylocentrotus lividus)*. Marques (1983, 1984) reported densities of *Arbacia lixula* up to 15 individuals/m^2 on São Miguel and Graciosa rocky shores, between 2 and 15 m depth. Marques' observations agree with our observations though no quantitative studies have been made recently. Marques also noted that *P. lividus* and *A. lixula* seldom co-occur in the Azores. Though both species are frequently observed in same low intertidal waters of the archipelago (<2 m), we agree with Marques in the sense that *Arbacia lixula* tends to be more numerous in relatively more exposed shores, such as vertical walls in ports, whereas *P. lividus* seems to prefer areas of low slope and with less direct exposure to the wave action, living inside bore-holes (personal observation). Cardigos *et al*. (2005) recorded this species in the area of Don João de Castro Seamount (between Terceira and São Miguel islands), one of the rare examples in Azores of a shallow-water hydrothermal-active volcanic seamount (the top of the seamount lies 13 m deep). Additionally, small specimens of this species have been misidentified as *Arbaciella elegans* Mortensen, 1910, including the ones re-examined here from Museu Bocage (MB-NMHN 367–20743 and MB-NMHN 372–20748), collected and identified by Marques (1983).

A recent revision showed that records of *Arbaciella* in North Atlantic and Mediterranean waters were misidentifications of juveniles of *Arbacia lixula*, reducing the distribution of this species to the original tropical West African coasts, south of Cap Blanc (for discussion see Kroh *et al*. 2011).

Order Camarodonta Jackson, 1912
Infraorder Echinidea Kroh & Smith, 2010
Family Echinidae Gray, 1825
Genus *Echinus* Linnaeus, 1758

Echinus melo Lamarck, 1816

(Fig. 5.24)

$\$$1909. *Echinus melo*, Lamarck; Koehler: 232.

1921b. *Echinus melo* Lamarck; Koehler: 118–119, fig. 79.

1938. *Echinus melo* (Lamarck); Nobre: 115–116, fig. 52.

1943a. *Echinus melo* Lamarck; Mortensen: 53–57, pl. 9, figs. 2, pl. 13, figs. 2, pl. 17, fig. 1.

1956. *Echinus melo* Lamarck; Harvey: 64.

1965. *Echinus melo* Lam.; Tortonese: 332–333, fig. 157B.

1980. *Echinus melo* Lamarck, 1816; Marques: 105.

1997. *Echinus melo* Lamarck, 1816; Pereira: 334.

2005. *Echinus melo* Lamarck, 1816; García-Diez *et al*.: 50.

2006. *Echinus melo* Lamarck, 1816; Mironov: 110.

2006. *Echinus melo* Lamarck, 1816; Schultz: 190, figs. 252–253.

2010. *Echinus melo* Lamarck, 1816; Micael & Costa: 323.

p.p.?$\$$2010. *Echinus acutus*; Wisshak *et al*.: 2382, fig. 2L.

2012. *Echinus melo* Lamarck, 1816; Micael *et al*.: 4.

See: Mortensen (1943a); Mironov (2006); Schultz (2006); Minin (2012).

Distribution: Mediterranean Sea and Northeast Atlantic, from the British Islands to the northwest African coasts, including the Azores, Madeira, Canaries and Cabo Verde archipelagos and the Josephine, Ampere and Meteor seamounts.

Depth: 25–1,100 m (AZO: 200–475 m).

Habitat: muddy bottoms to hard substrates.

Material examined: EMEPC L09D17B1 (E of TER, AZO, N38°39’52” W26°51’22”, 2009.09.30, 475 m; 1 spm, D=185 mm).

Description: test globular, slightly pentagonal with a height about of 75%D; Apical disc dicyclic, about 12%D. Periproctal plates with none to two spines. Madreporite enlarged. Gonopores open. Ambulacra about half the width of the interambulacra; in general, every ambulacral plate and every second interambulacral plate aborally bearing a primary tubercle; ambulacral plating trigeminate with pore-pairs in arcs of three at a distance from the edge of ambulacra. Peristome slightly larger than the apical disc (17%D). Primary spines short (10%D) and slender; on the oral side primary spines somewhat flattened with blunt tip; each peristomal plate with a small spine. Valves of globiferous pedicellaria with one short lateral tooth on each side below the end tooth; basal part with round angles and as long as the blade. Large form of tridentate pedicellariae (up to 3 mm) with straight, narrow valves (edges with numerous small serrations). Small form with slender, slightly curved valves.

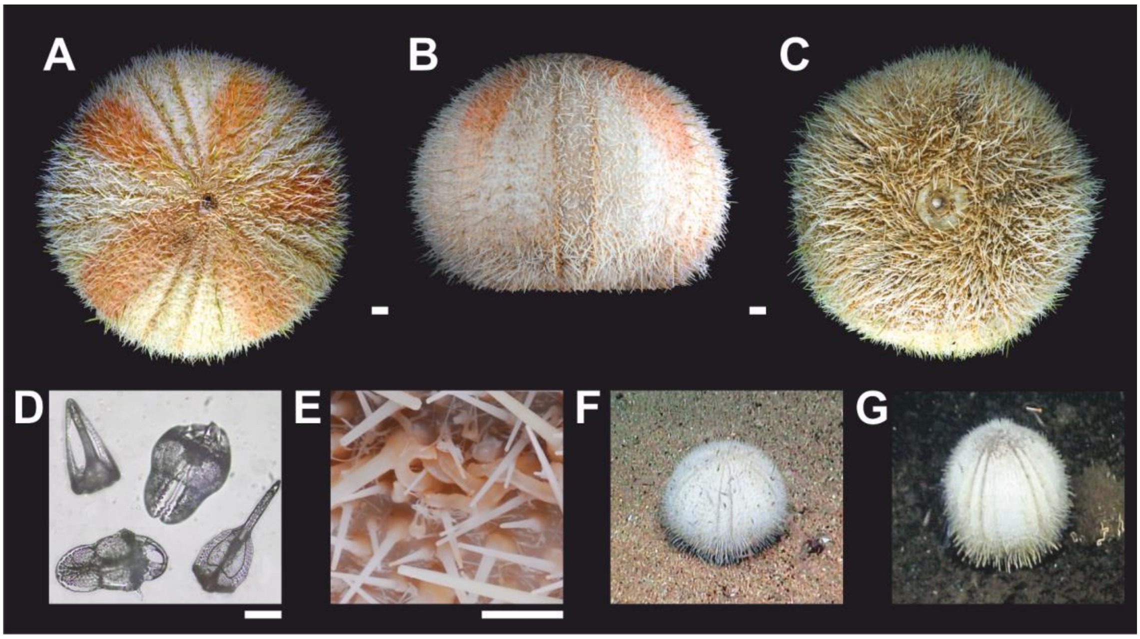


Figure 5.24. *Echinus melo* Lamarck, 1816 (EMEPC-LUSO L09D17B1: A–C, E, G; DOP 3598: D). Aboral view (A); lateral view (B); oral view (C); pedicellariae (D); detail pore area showing large tridentate pedicellariae; animal *in situ* (F); echinoid most possibly belonging to *E*. *melo in situ* in Azorean deep-waters (EMEPC-LUSO, N38°47’50” W27°28’57”, 455 m; G); scale bars 10 mm (A–C), 5 mm (E) and 200 µm (D).

Valves of ophicephalous pedicellariae constricted in the middle and with round edges armed with minute teeth. Colour: test cream white; pore areas brown; primary spines white to green with white tips; secondary spines white; madreporite ochre. For some unknown reason the preserved specimen became tinged by a light pink hue.

Remarks: *Echinus melo* can be easily identified from other echinid species (except *Gracilechinus acutus*) known to occur in the Azores by its spherical large test reaching a maximum diameter of 170 mm (Mironov 2006) to 185 mm. Another easy recognizable character is the large distance between the pore zone and the adradial suture. *Echinus melo* was previously documented for the Azores by a single small specimen reported by Koehler (1909) based on the material collected in the Princesse Alice Bank (RV ‘Princesse Alice’, sta 899: N37°57’00” W29°14’45”; 200 m). The new record further substantiates the presence of this species in the Azorean deep waters. Also, during EMEPC cruise (2009) in the Azores, an animal believed to belong to this species was captured on video east of Terceira Island at similar depths (N38°47'50" W27°28'57", 455 m, Fig. 5.24F). See also remarks below under *Gracilechinus acutus*.

Genus *Gracilechinus* Fell & Pawson, 1966

Gracilechinus acutus? (Lamarck, 1816)

1898. *Echinus acutus*? Lamarck; Koehler: 7, 23.

1938. *Echinus acutus* (Lamarck); Nobre: 114–115, figs. 48, 51.

2005. *Echinus acutus* Lamarck, 1816; García-Diez *et al*.: 50.

p.p.?$^{\$}$2010. *Echinus acutus;* Wisshak *et al*.: 2382, fig. 2L.

2010. *Echinus acutus* de Lamarck, 1816; Micael & Costa: 323.

2012. *Gracilechinus acutus* (Lamarck, 1816); Micael *et al*.: 4.

See: Koehler (1921b: 116–117, figs. 77–78, as *Echinus acutus* Lamarck); Mortensen (1943a: 43–52, pl. 3, fig. 3, pl. 5, figs. 1–5, pl. 6, figs. 1–5, pl. 7, figs. 7–9, pl. 8, figs. 1–10, pl. 10, figs. 1–2, pl. 54, fig. 26, as *Echinus acutus*); Madsen (1957: 481, as *Echinus acutus mediterraneus*).

Distribution: Mediterranean Sea and Northeast Atlantic, in the north from the Denmark Strait, Iceland, the Barents Sea, and Scandinavia [*G. acutus norvegicus* (Düben & Koren, 1846)], southwards along the European and North African coasts to Sierra Leone .

Depth: 20–1,280 m (?AZO: 380–500 m).

Habitat: from detritic bottoms, where it feeds on all kind of bottom living organisms, with preference for crustaceans and foraminifera.

Type of Development: planktotrophic.

Remarks: Koehler (1898) examined young specimens collected by RV ‘Hirondelle’ in Azorean waters between 1,372 and 1,850 m, which he identified as possible *G. acutus* or *G. alexandri* though due to their small sizes (less than 1 cm) he could not identify them without doubt. Later, Koehler (1909) reviewed the material from RV ‘Hirondelle’ and established that the specimens did not belong to *G. acutus*. The author also added it was not possible to identify the material because of their small size and lack of pedicellaria. Recently, Wisshak *et al*. (2010: 2383, fig. 2L) presents a photograph of an echinoid taken at 380 m in the southern Faial Channel, which they identified as *G. acutus* (= *Echinus acutus*). They also observed that this large echinoid was abundant at a depth of 500 m. However, the photograph portraits a large white basketball-shaped animal with relatively short spines. The spherical white test and the short spines points towards *E. melo* (Fig. 5.24) and not to *G. acutus*, which is generally characterized in the Atlantic by a subconical brightly coloured test (Koehler 1921b). However, images provided by M. Wisshak for additional specimens observed at 460 m, suggest that they indeed observed both *G. acutus*, as well as *E. melo*. Unfortunately, no material was collected by Wisshak and co-workers precluding to verify the identification based on images taken by the submersible 'Lula'. Both species are very variable in colour, shape and spine length (see Mortensen 1943a) and thus are difficult to distinguish even in the lab. It is, therefore, usually impossible to confirm their identity based on photographs alone (especially in specimens exhibiting slightly intermediate characteristics). Consequently, unless collected and verified by direct examination, the presence of *G. acutus* in the Azorean EEZ, though likely, remains unconfirmed.

Gracilechinus affinis **(Mortensen, 1903)**

$1909. *Echinus affinis* Mortensen; Koehler: 229–230, pl. 31, figs. 1–2, 19.
1927a. *Echinus affinis* Mrtsn; Mortensen: 305–306, fig. 174.
1943a. *Echinus affinis* Mrtsn; Mortensen: 83–86, pl. 11, figs. 1–7, pl. 55, figs. 15, 17, 19.
1985. *Echinus affinis* Mortensen, 1903; Gage *et al.*: 183–184.
1985. *Echinus affinus* Mortensen 1903; Serafy & Fell: 21, fig. 26.
2014. *Gracilechinus affinis* Mortensen, 1903; Mironov: 123.

Type locality: south of Iceland.

See: Mortensen (1903: 150–152, pl. 5, figs. 4, 8, pl. 15, figs. 3, 10, pl. 16, figs. 6, 20, pl. 18, figs. 4, 16, 28, pl. 19, fig. 27, pl. 20, figs. 17, 21; 1943a); Koehler (1921a: 3, as *Echinus affinis*); Gage *et al.* (1985); Harvey *et al.* (1988: 176–177, as *Echinus affinis*); Young & Tyler (1993).

Distribution: North Atlantic, from the east coast of the USA, the Denmark Strait and Iceland south to the Rockall Trough, Galicia (N Spain) and the Azores.

Depth: 770–2,700 (?5,300) m (AZO: 1,482–2,252 m).

Habitat: soft bottoms, muddy sand to ooze; possibly an opportunistic scavenger.

Type of Development: planktotrophic.

Remarks: *Gracilechinus affinis* is known from the Azores only from Koehler (1909) who reported this species (as *Echinus affinis*) among the material collected by RV 'Princesse Alice' at several stations. This species was the fourth species of the genus *Gracilechinus* reported from the archipelago at one time. The presence in the Azores of *G. acutus* and *G. elegans* were dismissed as unconfirmed and erroneous respectively since the first was based on poorly preserved juveniles (see remarks under *G. alexandri*) and the other is likely to be based on misprint by Mortensen (1927a), reducing the presence of this genus in the Azores to just two species.

Gracilechinus alexandri **(Danielssen & Koren, 1883)**

$^{\$}$1895b. *Echinus Alexandri* Danielssen et Koren; Koehler: 229.

$^{\$}$1909. *Echinus Alexandri*, Düben et Koren; Koehler: 230.

1927a. *Echinus Alexandri* Danielssen and Koren; Mortensen: 304–305, figs. 167.1, 172–173.

1932. *Echinus alexandri* Danielssen & Koren; Grieg: 42.

1943a. *Echinus Alexandri* Dan. & Koren; Mortensen: 65–68, figs. 20a, 21a–b, pl. 11, figs. 8–11.

1985. *Echinus alexandri* Danielssen & Koren, 1883; Gage *et al*.: 184.

1985. *Echinus alexandri* Danielssen and Koren 1883; Serafy & Fell: 4, 20, 21–22, fig. 29.

?$^{\$}$1992. *Echinus alexandri*; Pérès: 255.

2005. *Echinus alexandri*, Danielssen & Koren, 1883; García-Diez *et al*.: 50.

$^{\$}$2006. *Echinus alexandri* Danielssen & Koren, 1883; Desbruyères *et al*.: 479, figs. 1–4.

2014. *Gracilechinus alexandri* Danielssen et Koren, 1883; Mironov: 123–124.

Type locality: off Lofoten (N69°18’ E14°32’), Norway.

See: Danielssen & Koren (1883: 294–296, pl. 3–4, figs. 7–16, as *Echinus alexandri*); Mortensen (1903: 146–150, pl. 5, figs. 2, 3, 5,7, pl. 15, figs. 13, 17, pl. 16, fig. 8, pl. 17, figs. 9, 11, 19, 23, 25, pl. 19, figs. 16, 31, 34, 38, pl. 20, figs. 1, 2, 27, pl. 21, figs. 18–20, 27, as *Echinus alexandri*; 1943a); Desbruyères *et al.* (2006); Stevenson & Rocha (2012).

Distribution: North Atlantic; in the west, along the east side of North America and in the east from Icelandic, Scandinavian and British deep-waters, southwards to the Bay of Biscay and the Azores; possibly also in Tristan da Cunha.

Depth: 230–3,150 m (AZO: 1,165–1,940(?2,560) m.

Habitat: soft substrates, ooze to sand; diet consisting of bottom mud with foraminiferans; feeds also on deep sea reef building corals such as *Lophelia pertusa* and *Madrepora oculata*; it can be found in the vicinity of deep-water hydrothermal vents.

Type of Development: planktotrophic.

Remarks: Koehler (1898) examined young specimens collected by RV ‘Hirondelle’ in Azorean waters between 1,372 and 1,850 m, which he identified as possible *Gracilechinus acutus* (= *Echinus acutus*) or *Gracilechinus alexandri* (= *Echinus alexandri*) but due to the small size of the animals (less than 1 cm) he could not ascertain without doubt. The confirmation of *G. alexandri* presence in the archipelago was made later by Koehler (1895b, 1909) who identified material belonging to this species collected by RV ‘Princesse Alice’ at several stations located inside the Azorean waters. During a dive made by the bathyscaphe ‘Archimède’ north of the São Miguel, Pérès (1992) claimed to observe an animal of this species at a depth of 2,560 m, though no specimen was collected. More recently, a small population of *G. alexandri* was found at one time in the vicinity of the Azorean Mid-Atlantic hydrothermal vent field Lucky Strike, from which a specimen has been figured in the Handbook of Deep-Sea Hydrothermal Vent Fauna by Desbruyères *et al*. (2006).

Family Parechinidae Mortensen, 1903

Genus *Paracentrotus* Mortensen, 1903

Paracentrotus lividus **(Lamarck, 1816)**

(Fig. 5.25)

$1861. *Echinus lividus* Lam.; Drouët: 210.

$1863. *Toxopneustes lividus* Ag. Cat. Rais.; Agassiz: 23.

$1872. *Strongylocentrotus lividus*; Agassiz: 446–447, pl. 5b, fig. 3, pl. 24, fig. 25.

1888. *Echinus lividus* Lamarck; Barrois: 31.

$1888. *Strongylocentrotus lividus* A. Agassiz; Barrois: 75.

$1888. *Toxopneustes lividus* (Lam.); Simroth: 231.

1889. *Strongylocentrotus lividus* (Brandt); John: 285.

$1895a. *Strongylocentrotus lividus* (Lamarck); Koehler: 225.

$1898. *Strongylocentrotus lividus*, (Lamarck); Koehler: 24.

1912. *Strongylocentrotus lividus* (Lamarck); Jackson: 162.

1914b. *Paracentrotus lividus*; Koehler: 278.

1927a. *Paracentrotus lividus* (Lamarck); Mortensen: 306–309, figs. 175–177.

$1838. *Paracentrotus lividus* Lamarck, 1816; Cadenat: 367.

1938. *Paracentrotus lividus* (Lamark); Nobre: 118–119, figs. 48–49, 66.

$1943a. *Paracentrotus lividus* (Lamarck); Mortensen: 157–168, figs. 69–72, pl. 17, figs. 2–3, pl. 22, figs. 1–9, pl. 57, figs. 1–3, 11, 12, 20.

$1955. *Paracentrotus lividus* (Lamark); Chapman: 399.

1956. *Paracentrotus* (*Strongylocentrotus*) *lividus* (Lamarck); Harvey: 51, 65.

$1965. *Paracentrotus lividus* (Lam.); Tortonese: 337–341, figs. 160–162.

$1983. *Paracentrotus lividus* (Lamarck, 1816); Marques: 5–6.

$1983. *Psammechinus microtuberculatus* (Blainville, 1825); Marques: 5. [misidentification]

$1984. *Paracentrotus lividus*; Marques: 105.

1995. *Paracentrotus lividus* (Lamark); Moyse & Tyler: 678–680, 12.8.

1997. *Paracentrotus lividus* (Lamarck, 1816); Pereira: 334.

1999. *Paracentrotus lividus* (Lamark, 1816); Pérez-Ruzafa *et al.*: 52–53.

2002. *Paracentrotus lividus* (Lamarck, 1816); Pérez-Ruzafa *et al.*: 285–286.

$2005. *Paracentrotus lividus*; Cardigos *et al.*: 165.

2005. *Paracentrotus lividus* (Lamarck, 1816); García-Diez *et al.*: 50.

2006. *Paracentrotus lividus* (Lamarck, 1816); Schultz: 194–195, figs. 361–363.

2008. *Paracentrotus lividus*; Haddad & Barreiros: 9, fig. 3a.

2009. *Paracentrotus lividus*; Ávila *et al.*: 27.

2010. *Paracentrotus lividus*; Ávila *et al.*: 56.

2010. *Paracentrotus lividus* (de Lamarck, 1816); Micael & Costa: 323.

$^{\$}$2010. *Paracentrotus lividus* (de Lamarck, 1816); Micael *et al.*: 329.

$^{\$}$2010. *Paracentrotus lividus*; Wisshak *et al.*: 2382.

2011. *Paracentrotus lividus* (de Lamarck, 1816); Madeira *et al.*: 249–250, figs. 5C, 6C, 7C.

2012. *Paracentrotus lividus* (Lamarck, 1816); Micael *et al.*: 3, 5.

See: Mortensen (1943a); Alves *et al.* (2001); Schultz (2006); Ávila *et al.* (2009: 27; 2010: 16, 26, 56, fig. 10).

Distribution: Mediterranean Sea and Northeast Atlantic, from Ireland, along the coast of Europe to Mauritania, including the archipelagos of the Azores, Madeira, Selvagens, Canaries and Cabo Verde.

Depth: 0–80 m [AZO: 0–40(?207) m], rarely below 30 m.

Habitat: preferentially rocky shores where it can bore holes in the rock; diet mainly of algae.

Type of Development: planktotrophic.

Fossil fauna: remains of this species, spines and test fragments were found in Pleistocene sediments of Santa Maria Island. At the Pleistocene outcrop at Prainha, bore-holes were found on a basaltic rock about 5 meters above present sea level, which were attributed to *P. lividus* boring activities.

Commercial value: edible.

Material examined: DBUA-ECH 123 (São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2012.11.16, intertidal; 1 spm, D=5 mm); DBUA-ECH 138 (Poças de Santa Cruz, GRA, AZO, *c.* N39°05’16” W28°00’25”, 2010.08.02, intertidal; 1 spm, D=13 mm); DBUA-ECH 164 (Baia do Rosto do Cão, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1990.07; 14 spms, D=9–14 mm); DBUA-ECH 166 (off Vila Franca do Campo, SMG, AZO, N37°41’17” W25°25’06”, 2006.07.15, 129–207 m; 1 bt, D=7 mm); DBUA-ECH 190 (Vila Franca do Campo, SMG, AZO, *c.* N37°41’39” W25°27’27”, 2006.07.21, 95–121 m; 1 bt, D=3 mm); DBUA-ECH 280 (Ponta Delgada harbour, SMG, AZO, *c.* N37°44’12” W25°39’26”, 1996.12.04; 1 spm, D=34 mm); DBUA-ECH 287 (Rosto do Cão, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1990.05.14, 1 m; 1 spm, D=45 mm); DBUA-ECH 323 (Islet of Mosteiros, SMG, AZO, *c.* N37°53’25” W25°50’06”, 2011.07.07, 26 m; 2 spms, D=8–12 mm); DBUA-ECH 337 (Piscinas de Santa Cruz, FLS, AZO, *c.* N39°27’18” W31°07’30”, 2007.07.22, intertidal; 7 spms, D=15–49 mm); DBUA-ECH 338 (SMG, AZO, *c.* N37°50’06” W25°40’10”, 1997.7, intertidal; 1 spm, D=9 mm); DBUA-ECH 412 (Santa Cruz, GRA, AZO, *c.* N39°05’16.00” W28°00’25”, 2010.08.06, intertidal; 2 spms, D=51–58 mm); MB-NMHN 39–357 (Castelo Branco, FAY, AZO, *c.* N38°31’05” W28°43’23”, 25 m, collected and identified by Vasco Marques as *Paracentrotus* cf. *gaimardi*; 1 bt, D=9 mm); MB-NMHN 39–354 (Horta, FAY, AZO, *c.* N38°31’51” W28°37’23”, 1979, collected and identified by Vasco Marques as *Psammechinus microtuberculatus*; 1 bt, D=7 mm); MB-NMHN 39–355 (Castelo Branco, FAY, AZO, *c.* N38°31’05” W28°43’23”, 1979, collected and identified by Vasco Marques as *Psammechinus microtuberculatus*; 1 bt and 1 dry spm, D=6 mm).

Description: test circular, relatively low with a height of about 40%D in smaller specimens increasing to almost 60% in larger specimens. Apical disc dicyclic. Periproctal plates naked; Small individuals with three naked periproctal plates, one large and two other ones half the size of the large one. Genital pores closed in the smallest individual (D=5 mm; DBUA-ECH 123). Ambulacral plates polygeminate, with four to five pore pares per plate at the ambitus in smaller specimens and five pore pairs throughout in larger specimens; one large primary tubercle per ambulacral plate, with secondary tubercles forming a zigzag series along the midline of the area; primary tubercles in the ambulacral plates of the same size as the ones in the interambulacra. Interambulacra with two regular series of primary tubercles flanked one or two sub-equal secondary tubercles. Peristome somewhat sunken, from 45–60%D in smaller specimens (<9 mm D) to 34-36%D in larger specimens (>33 mm D). Peristomal membrane with small-scattered plates. Primary spines long and robust, about 20–30%D in smaller specimens increasing to more 50–60%D in larger specimens. Globiferous pedicellaria with one large terminal tooth and one lateral tooth on each side. Colour variable, from dark green/purple to lighter green/purple or with primary spines dark coloured at the base and becoming lighter towards the tips.

Remarks: the genus *Paracentrotus* comprises just two extant shallow-water species, *P. lividus* (Europe and NW Africa waters) and *P. gaimardi* (South Atlantic tropical waters: Gulf of Guinea, Angola and Brazil) (Schultz 2006). Mortensen (1943a) compared and discussed several diagnostic characters considered in the previous literature and concluded that none could be considered as reliable due to the high morphological variation demonstrated by both species. Nevertheless, Mortensen considered that the best character was the ornamentation on the apical disc, although he commented that

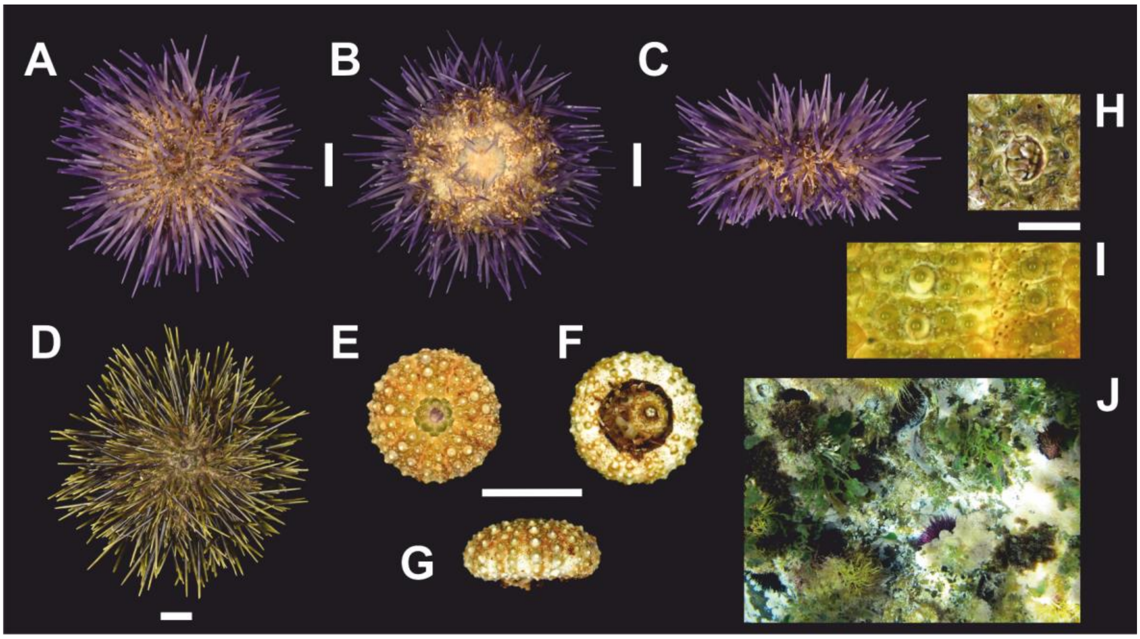


Figure 5.25. *Paracentrotus lividus* (Lamarck, 1816) (DBUA-ECH 280: A–C; DBUA-ECH 337: D; DBUA-ECH 412: H–J; MB-NMHN 39–354: E–F). Aboral view (A, D, E); oral view (B, F); lateral view (C, G); apical disc (H); ambulacral and interambulacral plates (I); *in situ* (Santa Maria Island, Azores, 2010.07.02, intertidal; J); scale bars are 10 mm (A–D) and 5 mm (E–I).

it was also subject to variation as animals from both species could present a rather weak striation.

The number of pore pairs was another character discussed by Mortensen, being almost constantly five in *P. lividus* and usually four in *P. gaimardi*. Again, both species show a degree of overlapping variation with some specimens of *P. gaimardi* having plates bearing five pore pairs and specimens of *P. lividus* presenting four to six pore pairs. The collection of Museu Bocage houses an unreported specimen from the Azores, collected and identified by Marques Vieira as *Paracentrotus* cf. *gaimardi*. The specimen presents only four pore pairs at the ambitus, a character that Marques Vieira may have used to identify the Azorean animal as western *P.* cf. *gaimardi*. However, taking in to account the size of the Azorean specimen (≈9 mm), the lack of ornamentation of the apical disc, and the NE Atlantic origin, we strongly believe that the specimen represents a young *P. lividus*, a common inhabitant of the Azorean rocky shores.

Marques Vieira's echinoderm collection at the Museu Bocage also houses three small animals (D=6 mm) identified as *Psammechinus microtuberculatus*, a species believed to be endemic to the Mediterranean Sea (see below remarks under *P.*

miliaris). Marques (1983) remarked that this species was the least frequent echinoid species in the Azores shallow waters. Thus, it is quite likely that the material housed at the Museum is the sole material used by Marques on which his report of *P. microtuberculatus* from the Azores was based. However, all three specimens possess ambulacral plates with four pore pairs per plate, a feature not found in *Psammechinus*. Furthermore, the valves of globiferous pedicellaria from the only complete specimen were typical of the genus *Paracentrotus*, presenting a single pair of lateral teeth beneath the terminal tooth, not several as would be expected in *Psammechinus* specimens. Apparently, Marques (1983) had misidentified juveniles of *P. lividus* as *P. microtuberculatus*.

Paracentrotus lividus is a typical inhabitant of the first few meters of the Azorean rocky shores, with a maximum reported depth in the Azores of *c.* 40 meters. Specimens dredged from 95–200 m all are slightly abraded naked tests possibly transported after the animals' death to these depths. Additionally, Cardigos *et al.* (2005) recorded this species in the area of Don João de Castro Seamount (between Terceira and São Miguel islands), one of the rare examples in Azores of a shallow-water hydrothermal-active volcanic seamount (the top of the seamount lies 13 m deep). See also remarks under *Arbacia lixula*.

Genus *Psammechinus* Agassiz & Desor, 1846

***Psammechinus miliaris*? (Müller, *in* Knorr, 1771)**

?$1888. *Echinus microtuberculatus* Blainville; Barrois: 109.

1927a. *Psammechinus miliaris* (Gmelin); Mortensen: 294–295.

1938. *Psammechinus miliaris* (Gmelin); Nobre: 110–111, figs. 48–49.

1938. *Psammechinus microtuberculatus* (Blainville); Nobre: 111–112.

?$1943a. *Psammechinus miliaris* (P. L. S. Müller, Gmelin); Mortensen: 127–139, figs. 56a–b, 57, 58a–b, 59a, 60b, 63b, pl. 10, figs. 3–5, pl. 18, figs. 1–7, 20–21, pl. 58, figs. 19, 23–25.

1965. *Psammechinus microtuberculatus* (Blv.); Tortonese: 333–335, fig. 159.

?$1983. *Psammechinus microtuberculatus* (Blainville, 1825); Castro & Viegas: 24.

1995. *Psammechinus miliaris* P.L.S. Müller; Moyse & Tyler: 680, fig. 12.8.

1997. *Psammechinus microtuberculatus* (Blainville, 1825); Pereira: 334.

2006. *Psammechinus miliaris* (P.L.S. Müller, 1771); Schultz: 198–198, figs. 370–372.

2008. *Psammechinus microtuberculatus*; Haddad & Barreiros: 9.

2010. *Psammechinus microtuberculatus* (Blainville, 1825) Heller, 1868; Micael & Costa: 323.

2010. *Psammechinus miliaris* (P.L.S. Müller, 1771); Micael & Costa: 323.

2012. *Psammechinus microtuberculatus* (Blainville, 1825); Micael *et al*.: 4.

2012. *Psammechinus miliaris* (P.L.S. Müller, 1771); Micael *et al*.: 4.

See: Mortensen (1943a); Schultz (2006).

Distribution: Northeast Atlantic, from Iceland and Scandinavia to Cape Blanc, including the ?Azores, ?Madeira, ?Canaries and ?Cabo Verde.

Depth: 0–100 m (?AZO: 10–20 m).

Habitat: live on virtually any kind of bottom (on bouldery sheltered shores, among sea-grass or algae, under stones, on rocks); omnivorous, depending on the bottom on which it lives.

Type of Development: planktotrophic.

Commercial value: edible.

Remarks: *Psammechinus microtuberculatus* (Blainville, 1825) was frequently reported from the Azores, unfortunately without descriptions. Koehler (1921b) showed some concerns about the records for the Atlantic, since he believed that the geographical range of this species did not go further than the Iberian Peninsula. Mortensen (1927b, 1943a) stated that the species *Psammechinus microtuberculatus* was endemic to the Mediterranean Sea and all reports of this species in the NE Atlantic were a result of misidentifications with close related species *Psammechinus miliaris* or *Paracentrotus lividus*. Additionally, on reviewing the material collected by Simroth (unreported) Mortensen (1943a) concluded that the animals were far too small (D=2.5 mm) to allow a reliable identification. Mortensen also added that the material report by Barrois (1888) from the Azores as *P. microtuberculatus* was presumably lost. We have no knowledge on the whereabouts of Castro & Viegas (1983) material or even if any specimens were actually deposited in a collection. The specimens identified by Marques (1983) as *Psammechinus microtuberculatus* (housed in the zoological collections of Museu of Bocage–MNHM) proved to be juveniles of *Paracentrotus lividus*, a common inhabitant of the Azores coastal waters (see remarks under *Paracentrotus lividus*). After critically examining the echinoid extant material in the DBUA-ECH collection we could not find a single specimen belonging to either *P. microtuberculatus* or *P. miliaris* was found. In sum, the only known *Psammechinus* material from the Azores is either lost or too small to allow a reliable identification.

Both *P. miliaris* and *P. microtuberculatus* species have a planktotrophic larval development with a high dispersal potential (Emlet 1995). Thus, it is not entirely unlikely that new recruits from the NE Atlantic or even Mediterranean continental coasts could have reached the insular coasts. Furthermore, it is not unprecedented to have Mediterranean species present in the Azores (*e.g.,* the sea star *Sclerasterias richardi*). Nevertheless, we follow Mortensen (1943a) in assigning the historical reports of *P. microtuberculatus* from the Azores to *P. miliaris*. In the absence of well documented adult specimens, the presence of *P. miliaris* in the Azores, however, needs to remain doubtful until confirmed by new records.

Superfamily Odontophora Kroh & Smith, 2010

Family Toxopneustidae Troschel, 1872

Genus *Sphaerechinus* Desor, 1856

***Sphaerechinus granularis* (Lamarck, 1816)**
(Fig. 5.26)

$^{\$}$1861. *Echinus brevispinosus* Risso; Drouët: 210.

$^{\$}$1863. *Sphærechinus granularis* A. Ag.; Agassiz: 23.

$^{\$}$1872. *Sphaerechinus granularis*; Agassiz: 159–160, 452–453, pl. 5a, fig. 7, pl. 6, figs. 16–17.

p.p.$^{\$}$1881. *Sphærechinus granularis*; Agassiz: 106–107.

1888. *Echinus brevispinosus* Risso; Barrois: 31.

$^{\$}$1888. *Sphœrechinus granularis* A. Agassiz; Barrois: 109–110.

$^{\$}$1888. *Sphaerechinus granularis* (Lam.); Simroth: 231, 233.

1889. *Sphaerechinus granularis* (Ag.); John: 285.

$^{\$}$1895a. *Sphærechinus granularis* Lamarck; Koehler: 225.

$^{\$}$1898. *Sphærechinus granularis*, (Lamarck); Koehler: 23.

1912. *Sphaerechinus granularis* (Lamarck); Jackson: 162.

$^{\$}$1924. *Sphaerechinus granularis* (Lamk.); Nobre: 89.

$^{\$}$1925. *Sphaerechinus granularis*; Clark: 140–141.

1927a. *Spœrechinus granularis* (Lamarck); Mortensen: 309–312, figs. 178–180.

$^{\$}$1930. *Sphaerechinus granularis* (Lamk.); Nobre: 69.

$^{\$}$1938. *Sphaerechinus granularis* Lamarck, 1816; Cadenat: 367–368.

1938. *Sphœrechinus granularis* (Lamarck); Nobre: 119–120, figs. 48, 49, 66.

1943b. *Sphærechinus granularis* (Lamarck); Mortensen: 515–526, figs. 242c, 309–314, pl. 39, figs. 1–4, pl. 40, figs. 1–5, pl. 41, figs. 1–7, pl. 56, figs. 1, 8, 10, pl. 25, fig. 13.

$^{\$}$1955. *Sphaerechinus granularis* (Lamark); Chapman: 399.

1956. *Sphaerechinus granularis* (Lamarck); Harvey: 51, 66.

$1965. *Sphaerechinus granularis* (Lam.); Tortonese: 323–327, figs. 151–154.

$1983. *Sphaerechinus granularis* (Lamarck, 1816); Marques: 5.

1997. *Sphaerechinus granularis* (Lamarck, 1816); Pereira: 334.

$1998. *Sphaerechinus granularis*; Maciel & Gonçalves: 182.

$1998. *Sphaerechinus granularis*; Morton *et al*.: 150–151, figs. 3–3L1, 8–1L.

2002. *Sphaerechinus granularis* (Lamarck, 1816); Pérez-Ruzafa *et al*.: 285.

$2003. *Sphaerechinus granularis*; Wirtz & Debelius: 258.

$2005. *Sphaerechinus granularis*; Cardigos *et al*.: 159.

2005. *Sphaerechinus granularis* (Lamarck, 1816); García-Diez *et al*.: 50.

2006. *Sphaerechinus granularis* (Lamarck, 1816); Mironov: 112.

2006. *Sphaerechinus granularis* (Lamarck 1816); Schultz: 266–267, figs. 509–513.

2008. *Sphaerechinus granularis*; Haddad & Barreiros: 9, fig. 3d.

2010. *Sphaerechinus granularis* (de Lamarck, 1816); Micael & Costa: 323.

$2010. *Sphaerechinus granularis* (Lamarck, 1816); Micael *et al*.: 329.

2011. *Sphaerechinus granularis* (Lamarck, 1816); Madeira *et al*.: 250, figs. 5B, 6B.

2012. *Sphaerechinus granularis* (Lamarck, 1816); Micael *et al*.: 4.

See: Mortensen (1943b); Alves *et al.* (2001); Schultz (2006); Koukouras *et al.* (2007: 83); Madeira *et al.* (2011).

Distribution: Mediterranean Sea and Northeast Atlantic; from Channel Islands to the Gulf of Guinea, including the Azores, Madeira, Selvagens, Canaries, Cabo Verde and Gorringe and Dacia seamounts.

Depth: 0–120 m (AZO: 0–60 m).

Habitat: generally found on hard substrates, but also on *Posidonia* and *Zostera* meadows, silty sand or maërl bottoms.

Type of Development: planktotrophic.

Fossil fauna: remains of this species, spines and test fragments were found in Pleistocene sediments at Santa Maria Island.

Commercial value: edible.

Material examined: DBUA-ECH 025 (São Roque Islet, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2006.11.07, 3 m; 1 bt, D=54 mm); DBUA-ECH 026 (São Roque Islet, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2006.11.07, 3–5 m; 1 bt, D=85 mm); DBUA-ECH 027 (São Roque Islet, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2006.11.07, 3–5 m; 1 bt, D=82 mm); DBUA-ECH 028 (São Roque Islet, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2006.11.07, 3–5 m; 1 bt, D=63 mm); DBUA-ECH 030 (Banco D. João de Castro, AZO, *c.* N38°13’18” W26°36’12”, 2006; 1 spm, D=70 mm); DBUA-ECH 031 (Banco D. João de Castro, AZO, *c.* N38°13’18” W26°36’12”, 1996.07.02, 30 m; 5 spms, D=81–87 mm); DBUA-ECH 032 (Cerco, Caloura, SMG, AZO, *c.* N37°42’26” W25°30’37”, 20 m; bt, D=21 mm); DBUA-ECH 054 (Santa Cruz, GRA, AZO, *c.*

N39°05’16” W28°00’25”, 2010.08.02, intertidal; 1 spm, D=11 mm); DBUA-ECH 140 (Poças de Santa Cruz, GRA, AZO, *c.* N39°05’16” W28°00’25”, 2010.08.07, intertidal; 4 spms, D=37–54 mm); DBUA-ECH 158 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06, 45 m; 2 spms, D=6–11 mm); MB-NMHN 410–20786 (Baixinha, GRA, AZO, *c.* N39°05’13” W27°59’09”, 1979; 2 spms, D=92–100 mm); MB-NMHN 285–18681 [Pópulo (Praia Grande), SMG, AZO, *c.* N37°45’00” W25°37’24”, 1980; 1 spm, D=55 mm]; MB-NMHN 368–20744 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 1979; 2 spms, D=12–18 mm).

Description: test circular, flattened orally, height reaching about 55–65%D, the peristome area is at most only slightly depressed. Apical disc hemicyclic, with Oc. I and V insert, though in the smaller specimens the latter can be exsert (D <11 mm). Periproct nearly ellipsoid, enclosing numerous periproctal plates of various sizes, many of which bear a slender spine; in smaller individuals periproct bearing one larger anal plate. Gonopores closed in the smallest specimens (D ≈ 6 mm; DBUA-ECH 158). Ambulacra with irregular arcs of four or five pore pairs per plate in smaller specimens (D ≤30 mm) up to six pore pairs per plate in larger specimens; in smaller specimens the number of pore pairs drop to 5 (D ≤30 mm) or four (D ≤11 mm). Number of ambulacral primary tubercles at the ambitus from one in small specimens (D ≤11 mm) up to two or three in larger animals; free space of both adradial and perradial zones filled with small secondary tubercles and miliary granulation. The number of primary tubercles in the interambulacra at the ambitus from two in small specimens (D ≤18 mm) up to six in large specimens (D ≥80 mm); adradial and interradial spaces filled by smaller secondary tubercles of various sizes. Peristome from 50–57%D in small specimens (D ≤11 mm) decreasing in relative size in larger animals to about 22–25 %D; buccal membrane with small embedded plates and devoid of spines. Gill slits well developed particularly in larger animals, giving an overall almost pentagonal shape to the peristome. Presence of large globiferous pedicellaria (≈ 3 mm in larger specimens). Primary spines relative short and stout, with blunt tips. Colour: naked test purple or light brown; spines white, brown or bright violet with or without whitish tips; smaller specimens (D ≤11 mm) with green, orange or brown tests and primary spines white, bright pink, orange, reddish-brown or brown with or without whitish tips.

Remarks: Mortensen (1943b) reviewed the intraspecific variation in *S. granularis*, which included some of the Azorean specimens’ particularities, *i.e*. the higher number of pore pairs in the ambulacral plates. He rejected the hypothesis of specimens with six pore pairs per plate as belonging to a different species or a variety.

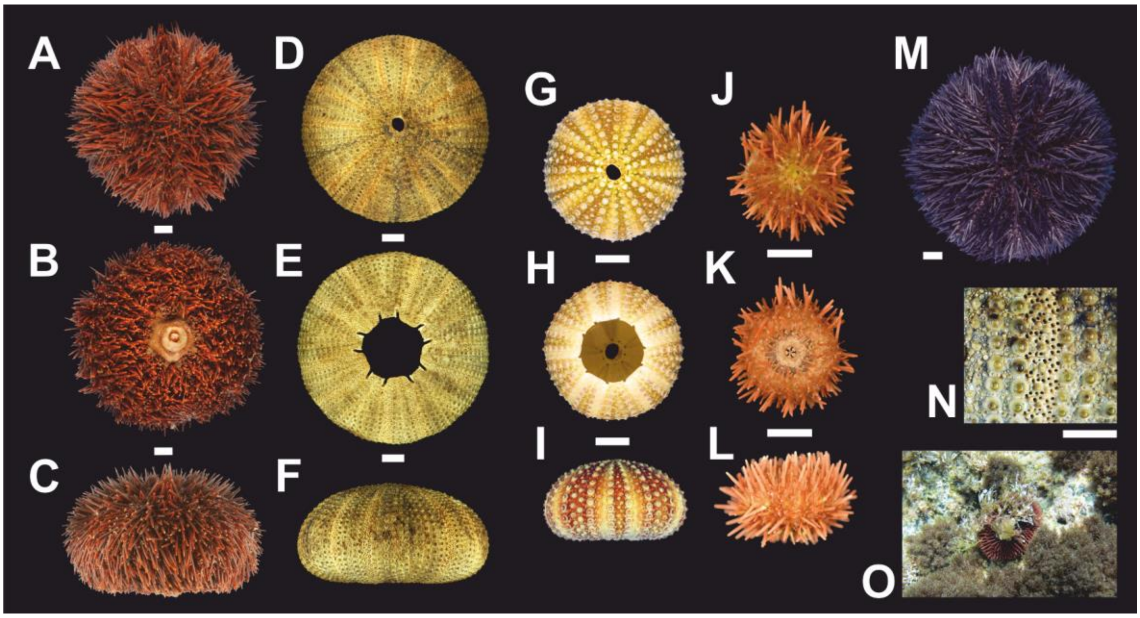


Figure 5.26. *Sphaerechinus granularis* (Lamarck, 1816) (DBUA-ECH 031: A–C, M; DBUA-ECH 027: D–F; DBUA-ECH 032: G–I; DBUA-ECH 158: J–L; DBUA-ECH 028: N). Aboral view (A, D, G, J, M); oral view (B, E, H, K); lateral view (C, F, I, L); detail of the pore areas (N); *in situ* (Santa Maria Island, Azores, 2010.07.02, intertidal; O); scale bars are 10 mm (A–F, M) and 5 mm (G–L, N).

Our results suggest that specimens with different number of pore pairs coexist in the same area. Furthermore, a higher number of pore pairs on the ambulacra is not exclusive for the Azores population. Agassiz (1872) reported specimens with six pore pairs from a batch from the Mediterranean Sea or Canaries (which location he did not specified), dismissing it as an ontological variation. Our observations, in contrast agree with Mortensen (1943b) who showed that such differences are not dependent on the size of the animal. In spite of the intraspecific variation being overall constant throughout the species geographic range, we could not help notice the colour morph presented as 'typical' by several authors for the Mediterranean Sea is the purple/violet colour (*e.g.,* Koehler 1921b; Mortensen 1927a; Tortonese 1965; Schultz 2006). In contrast, in the Azores, the brown colour morph appears very common if not the most common. Nonetheless, the presence of both colour morphs in the same area, or even clutching together to the same rock is not uncommon in the Azorean subtidal (*personal observation*).

The red colour morph of *Genocidaris maculata*, a species also native to the archipelago, have historically been confused with juveniles of *S. granularis* (Figs. 3.26G-I; Koehler 1921b; Mortensen 1943b). For example, Agassiz (1881) recorded *S. granularis* from the Azores ('Challenger' sta 75: N38°37' W28°30'). On re-examination of this material, later authors (*e.g.,* Clark 1925; Mortensen 1943b) realized that Agassiz failed to notice the presence of a reddish colour morph of *Genocidaris maculata* among the batch (see remarks under *Genocidaris maculata*).

Infraorder Temnopleuridea Kroh & Smith, 2010

Family Trigonocidaridae Mortensen, 1903

Genus *Trigonocidaris* Agassiz, 1869

Trigonocidaris albida **Agassiz, 1869**

$^{\$}$1895a. *Trigonocidaris albida* Agassiz; Koehler: 224.

$^{\$}$1895b. *Trigonocidaris albida* Agassiz; Koehler: 228.

$^{\$}$1898. *Trigonocidaris albida*, A. Agassiz; Koehler: 22–23.

$^{\$}$1909. *Trigonocidaris albida*, A. Agassiz; Koehler: 227.

1927a. *Trigonocidaris albida* A. Agass.; Mortensen: 292.

1943b. *Trigonocidaris albida* A. Agassiz; Mortensen: 318–321 pl. 18, figs. 10–13.

2005. *Trigonocidaris albida* Agassiz, 1869; García-Diez *et al*.: 50.

2006. *Trigonocidaris albida* Agassiz, 1869; Mironov: 111.

2012. *Trigonocidaris albida* A. Agassiz, 1869; Benavides-Serrato *et al*.: 71–72.

Type locality: Caribbean.

See: Mortensen (1943b); Mironov (2006); Benavides-Serrato *et al.* (2012).

Distribution: cosmopolitan, in the North Atlantic, Pacific and Indian Oceans; from the Gulf of Mexico and the Caribbean eastwards to the Iberian Peninsula and Morocco, including the archipelagos of the Azores and Canaries, and the Seine, Josephine and Meteor seamounts.

Depth: 70–720 m (AZO: 349–550 m).

Habitat: mud, sand, gravel to hard substrates and in association with azooxanthellate corals; feeds on foraminifera.

Type of Development: planktotrophic.

Remarks: in the Azores*, Trigonocidaris albida* is known only from Koehler's reports (1898, 1909) based on material collected at several stations by the RVs 'Hirondelle' and 'Princesse Alice'. The rarity of records in the archipelago might be explained by the minute size that characterizes this sea urchin, easily overlooked or lost (depending on the sampling method employed) during the rare occasions in which waters from its typical depth ranges (>70 m) were surveyed in the archipelago waters (see also below remarks under *Genocidaris maculata*).

Genus *Genocidaris* Agassiz, 1869

Genocidaris maculata **Agassiz, 1869**

(Fig. 5.27)

1872. *Temnechinus maculatus* A. Ag.; Agassiz: 165, 215, 286–289, pl. 8, figs. 1–18.

p.p.$^{\$}$1881. *Sphærechinus granularis*; Agassiz: 106–107.

$^{\$}$1898. *Temnechinus maculatus*, (A. Agassiz); Koehler: 21–22, pl. 8, figs. 3, 9.

1903. *Genocidaris maculata*; Mortensen: 85.

$^{\$}$1909. *Genocidaris maculata*, (A. Agassiz); Koehler: 226–227, pl. 31, fig. 3.

1914b. *Gonocidaris maculata*; Koehler: 278, 283.

1921b. *Genocidaris maculata* Agassiz; Koehler: 115–116, fig. 76.

$^{\$}$1925. *Genocidaris maculata*; Clark: 76–77.

1927a. *Genocidaris maculata* A. Agass.; Mortensen: 292.

1943b. *Genocidaris maculata* A. Agassiz; Mortensen: 358–362, figs. 219, 220, pl. 18, figs. 37–47.

1943b. *Genocidaris maculata* var. *splendes* Mrtsn.; Mortensen: 362–363, fig. 221a.

1965. *Genocidaris maculata* A. Ag.; Tortonese: 321–322, fig. 150.

1985. *Genocidaris maculata* A. Agassiz 1869; Serafy & Fell: 21.

1997. *Genocidaris maculata* A. Agassiz, 1869; Pereira: 334.

2005. *Genocidaris maculata* Agassiz, 1869; García-Diez *et al.*: 50.

2006. *Genocidaris maculata* A. Agassiz, 1869; Mironov: 211–212.

2010. *Genocidaris maculata* A. Agassiz, 1869; Micael & Costa: 323.

2012. *Genocidaris maculata* A. Agassiz, 1869; Micael *et al.*: 4.

Type locality: Caribbean waters.

See: Agassiz (1869: 262–263); Mortensen (1943b); Tortonese (1965); Mironov (2006); Benavides-Serrato *et al.* (2012: 70).

Distribution: Mediterranean Sea and Atlantic; in the West from Cape Cod, through the Caribbean to North Brazil waters; in the east from the North African coasts to the Gulf of Guinea, including the Azores, Madeira and Canary archipelagos, and Gorringe, Josephine and Seine seamounts.

Depth: 12–500 m [AZO: (?0)20–200(?823) m].

Habitat: sandy to coralligenous substrates; feeds on bottom material, ingesting small benthic animals (*e.g.,* foraminiferans, molluscs and bryozoans).

Type of Development: planktotrophic.

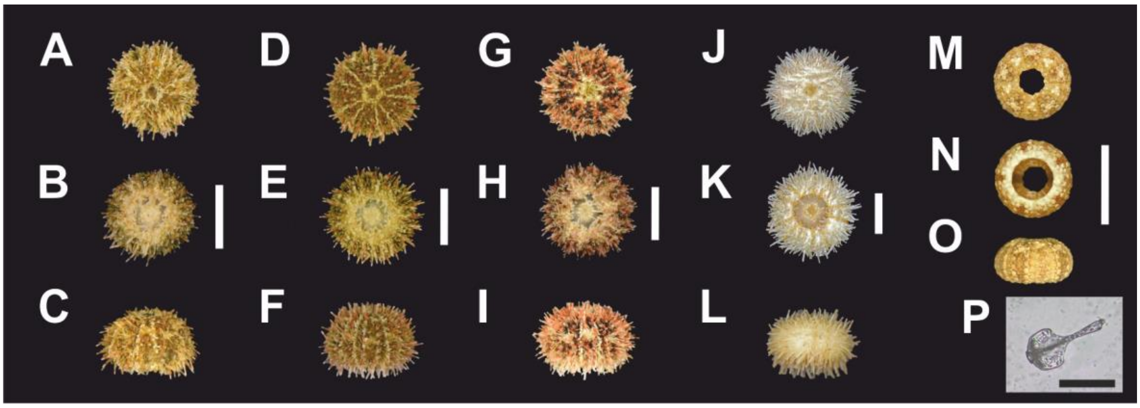


Figure 5.27. *Genocidaris maculata* Agassiz, 1869 (DBUA-ECH 155: A–C; DBUA-ECH 151: D–F; DOP 3015: G–I; DBUA-ECH 327: J–L, P; DBUA-ECH 258: M–O). Aboral view (A, D, G, J, M); oral view (B, E, H, K, N); lateral view (C, F, I, L, O); valve of globiferous pedicellariae (P); scale bars 5 mm (A–O) and 200 µm (P).

Material examined: DBUA-ECH 144 (off Vinha da Areia, Vila Franca do Campo, SMG, AZO, N37°42’11” W25°25’04”, 2006.09.05, 66 m; 2 bts, D=4–7 mm); DBUA-ECH 146 (off Ribeira das Tainhas, SMG, AZO, N37°41’57” W25°25’08”, 2006.07.24, 144–198 m; 2 bt, D=4–5 mm); DBUA-ECH 147 (off Vinha da Areia, Vila Franca do Campo, SMG, AZO, N37°42’09” W25°25’04”, 2006.09.05, 81 m; 1 bt, D=4 mm); DBUA-ECH 149 (off Ribeira das Tainhas, SMG, Azores, N37°42’01” W25°25’01”, 2006.07.24, 117–145 m; 1 bt, D=6 mm); DBUA-ECH 151 (São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1997.07.14, 30 m; 1 spm, D=7 mm); DBUA-ECH 153 (São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1997.07.14, 30 m; 1 spm, D=7 mm); DBUA-ECH 154 (Água d’Alto, SMG, AZO, *c.* N37°42’55” W25°28’27”, 1991.07.30; 1 spm, D=7 mm); DBUA-ECH 155 (Poços de São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.08, intertidal; 1 spm, D=7 mm); DBUA-ECH 159 (Vila Franca do Campo, SMG, AZO, N37°41’39” W25°27’11”, 2006.07.21, 95–121 m; 3 bts, D=5–6 mm); DBUA-ECH 160 (São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1997.07.14, 1991.07.11; 1 specimen, D=7 mm); DBUA-ECH 186 (Vila Franca do Campo, SMG, AZO, N37°41’34” W25°27’15”, 2006.07.19, 126–171 m; 1 bts, D=5 mm); DBUA-ECH 204 (Baixa do João Lopes, SMA, AZO, *c.* N37°01’13” W25°10’05”, 2014.06.26, 30–35 m; 1 spm, D=6 mm); DBUA-ECH 221 (São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1997.07.14, 1997.07.11, 20 m; 1 spm, D=5 mm); DBUA-ECH 327 (Sabrina Bank, SMG, N37°52’55” W25°54’25”, 2011.07.08, 200 m; 1 spm, D=8 mm); L09D9B20S01 (Gorringe Bank, N36°42’49” W11°09’54”, 2009.09.13, 130 m; 2 bt, TD=6 mm); DOP 3015 (Channel PIX–FAY, AZO, N38°34’15.60” W28°32’31.20”, 2008–06–16, 50 m; 1 spm, D=8 mm).

Description: test hemispherical, relatively high, height varying from about 48–50%D in smaller specimens (D<4 mm) to 65–70% D in larger specimens (D>6 mm). Apical disc dicyclic with oculars well separated from periproct. Periproctal membrane with one large naked round plate (with conspicuous radial striation) and few very small additional plates. Genital plates with 3 to 5 spines and oval (elongated) pores. Peristome mostly naked except for the small buccal plates with few pedicellariae. Ambulacra with one primary tubercle per plate, occasionally slightly smaller than the corresponding one in the interambulacral plates, forming a more or less regular vertical series; bases of primary tubercles indented, particularly in the ambulacral areas. Ambulacral plates trigeminate with the pores forming a regular straight vertical series; pore-zones slightly sunken. Interambulacra presenting a single primary tubercle per plate forming a regular vertical series. Spines smooth relatively small (16–24%D). Globiferous pedicellaria with double poison glands and a single, tooth on one side beneath the terminal tooth. Colour: naked test green, brown or light brown with white spots just above the ambitus; spines hyaline, with red or pink bands; exceptionally white with traces of pink bands on some of the spines (DBUA-ECH 327).

Remarks: Mortensen (1927b) described a new extant *Genocidaris* species, *G*. *splendens* based on material collected by RV 'Talisman' in the Canaries. This species differed from the typical *G*. *maculata* by its bright red colour, low test, the presence of a depression in the ambulacral (and interambulacral) midline aborally and a relative smaller suranal plate. In a later review, Mortensen (1943b) downgraded his species to a variety of *G*. *maculata* as all discussed diagnostic characters proved to be unreliable with both species presenting intermediate characters. Mortensen (1943b) concluded that *G*. *splendens* was at best just a colour variability of *G*. *maculata*. In spite of the great morphological variation revealed by the material herein examined, we found no clear evidence was to suggest that any of the specimens belong to the variety '*splendens*'. None had a particularly small suranal plate, a low test, or mid-line depressions. Regarding the colour pattern our material comprehended all possible transitions from the 'typical' olive through various shades of red. Our observations agree with Mironov (2006) who also questioned the validity of the variety 'splendens', based on animals from the Ormonde and Gorringe seamounts (NE Atlantic).

In the DBUA-ECH collection, we have found a small white echinoid collected from the Sabrina Bank, SW of São Miguel Island (DBUA-ECH 327, Figs.3.27J–L). At first it was assumed to be the small echinoid *Trigonocidaris albida*, a species that also lives in the Azores at similar depths (see above). This species generally presents a white test with the distal edge of the apical disc light orange or greenish-yellow and white spines that aborally present a light red band just above the base. However, on closer examination, we have found it to be a typical morphological characteristics of *G*. *maculata* with exception of its very unusual colour. Aside from the colour pattern, the specimen does not present many of the typical morphological characteristics of the genus *Trigonocidaris* or the species *T. albida*, such as a low test height (≤50%D), buccal membrane covered by large imbricate plates or a periproct with four large angular plates (see Mortensen 1943b). On the contrary, the specimen presented a relatively high hemispherical test (≈60%D), a naked buccal membrane with exception of the buccal plates and a peristome with a very large round and green suranal plate. Also, the test of DBUA-ECH 327 was not conspicuously ornamented as is typical observed in *T. albida*. The globiferous pedicellaria can be differentiated easily based on the poison glands, which are single in *T. albida* and double in *G. maculata* and in our white specimen from the Azores (see Mortensen 1903, pl. 8, fig. 7). Though both species present globiferous pedicellaria with a single unpaired tooth beneath the terminal tooth, the ones of our white specimen look like typical *G. maculata* pedicellariae: a widened basal part with sharp corners, a very narrow blade (see Mortensen 1903, pl. 7, fig. 30).

Historically, *G. maculata* was mistakenly reported in the Azores by Agassiz (1872, as *Tenmechinus maculatus*) based on material collected in the Josephine Seamount. Later, Agassiz (1881) identified the species *Sphaerechinus granularis* among the material collected by the RV 'H.M.S. Challenger' in the Azores (sta 75: N38°37' W28°30'), which later were re-identified by Clark (1925) as red coloured *G. maculata* (see also remarks under *S. granularis*).

G. maculata is a small echinoid typical of low subtidal waters up to 500 m. However, among the material examined we have found one specimen (DBUA-ECH 155) labelled as being collected in the intertidal waters of São Miguel Island. The possibility of mislabelling could not be overruled. However, the area where the specimen was collected is characterized by a sheltered and rather large tide-pool. Small animals of this species could survive among the crevices, algae or under the boulders in the relative protected waters of this tide-pool, in a similar fashion of the much larger echinoid *Centrostephanus longispinus*, also a typical deeper inhabitant of littoral waters but seen in waters as low as 5 m depth in some places in the Azores (see remarks under *C. longispinus*). Conversely, Agassiz (1881) reported two different depths for the 'H.M.S. Challenger' station 75 where *G. maculata* was identified (92–165 m and 823 m), suggesting perhaps a mislabelling. Studying the known depth ranges of other echinoderms species also collected at this station, we believe that shallower depth values are likely to be the correct ones (see remarks under *Astropecten hermatophilus*).

Order Echinothurioida Claus, 1880

Family Echinothuriidae Thomson, 1872b

Genus *Araeosoma* Mortensen, 1903

Araeosoma fenestratum (Thomson, 1872b)

1980. *Araeosoma fenestratum* Wyville Thomson, 1872; Marques: 104.

$^{\$}$2006. *Araeosoma fenestratum* (W. Thomson, 1869); Mironov: 103.

Type locality: off the coast of Portugal.

See: Thomson (1872b: 741–744, pl. 63, figs. 9–10, pl. 66, figs. 1–5, pl. 67, figs. 1–9, as *Calveria fenestrate*); Mortensen (1935: 233–237, pl. 29–30, pl. 78, fig. 11); Gage *et al.* (1985: 179–180); Harvey *et al.* (1988: 174); Stevenson & Rocha (2012).

Distribution: North Atlantic, from the Denmark Strait to the Caribbean and the Gulf of Mexico, eastwards from off Scotland and the Rockall Trough to Portugal, including the Azores and the Meteor Seamounts.

Depth: 148–1,270 m (AZO: ?900 m).

Habitat: soft sediments, on fine sand to mud; gut contents include bottom sediments together with a variety of sponges and plant fragments; feeds also on deep sea reef building corals such as *Lophelia pertusa* and *Madrepora oculata*.

Type of Development: lecithotrophic.

Remarks: it is likely that when Marques (1980) mentioned the presence of *Araeosoma fenestratum* in the Azores he was referring to unreported specimens collected by ‘Biacores’ expedition in the archipelago. These specimens were mentioned by Mironov (2006) who noted that in the collection of MNHN Paris there are numerous *Araeosoma* taken in the Azorean waters by RV ‘Jean Charcot’ (‘Biacores’ cruise, unreported) Cruise and mostly labelled by Vasco Marques as belonging to *A. fenestratum*. Additionally, the later author identified several specimens belonging to *A. fenestratum* in Meteor waters bordering the Azores.

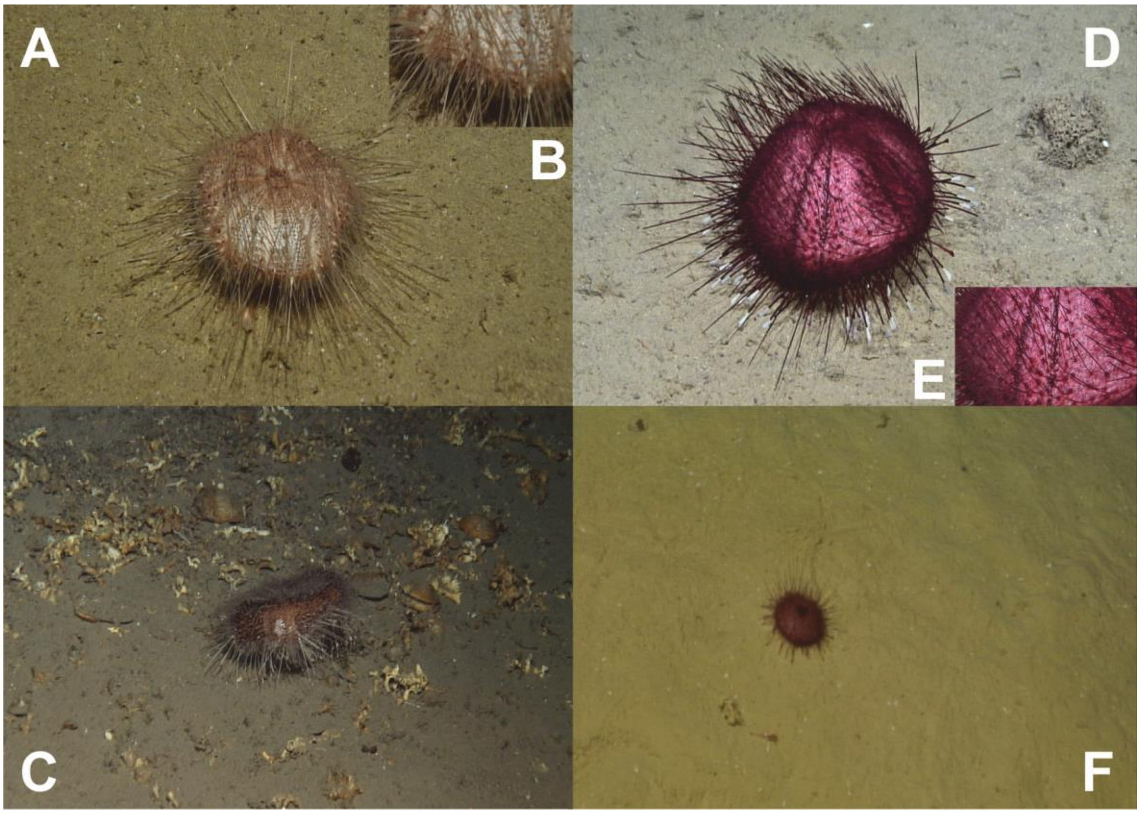


Figure 5.28. Echinothuriids in the Azorean deep waters, most probably belonging to *Araeosoma fenestratum* (Thomson, 1872b) (EMEPC-LUSO, N38°42’18” W28°01’18”, 2009.10.02, 900 m: A, B; N36°36’25” W28°06’43”, 2009.10.21, 1,102 m: C) and *Hygrosoma petersii* (Agassiz, 1880) (EMEPC-LUSO, N38°34’12” W28°03’17”, 2008.11.10, 1,250 m: D, E; N37°56’12” W26°10’31”, 2009.10.08, 3,237 m: F).

In 2009, during the expedition EMEPC-LUSO an echinothurid likely to belong to this species was captured on video on the seabed of the Azorean deep waters, north of São Jorge Island (N38°42'18" W28°01'18", 900 m; Figs. 3.28A–B) and south of Pico Island (N36°36'25" W28°06'43", 2009.10.21, 1,102 m; Fig. 5.28C).

Genus *Calveriosoma* Mortensen, 1934

Calveriosoma hystrix (Thomson, 1872b)

$^{\$}$1895a. *Asthenosomum hystrix* Agassiz; Koehler: 224.

$^{\$}$1895b. *Asthenosomum hystrix* Agassiz; Koehler: 228.

$^{\$}$1898. *Asthenosoma hystrix*, (Wyville Thomson); Koehler: 9–10.

$^{\$}$1909. *Areosoma hystrix*, (Wyville Thomson); Koehler: 216–217.

1927a. *Arœosoma hystrix* (Wyv. Thomson); Mortensen: 282–283, figs. 156.1, 158.2, 159.

1935. *Calveriosoma hystrix* Wyv. Thomson; Mortensen: 222–227, figs. 126–128, pl. 23, figs. 1–5, pl. 24, fig. 1, pl. 68, fig. 12.

1938. *Arœosoma histrix* (Wyv. Thomson); Nobre: 107–108, fig. 47.

$^{\$}$1992. *Calveriosoma hystrix*; Pérès: 252, 254.

2005. *Calveriosoma hystrix* (Wyville Thomson, 1872); García–Diez *et al.*: 50.

Type locality: between Faeroe Island and Scotland (N59°26' W8°23').

See: Mortensen (1903: 70–72, as *Calveria hystrix*; 1935); Gage *et al.* (1985: 180).

Distribution: Northeast Atlantic, from off SW Iceland southwards to Northeast African waters, including the Azores, and the Canaries, and Meteor seamounts.

Depth: 360–1,800 m (AZO: 800–1,528 m).

Habitat: on sand, mud to soft ooze.

Type of Development: lecithotrophic.

Remarks: historically, *Calveriosoma hystrix* was frequently confused and in many instances regarded as conspecific with *Araeosoma fenestratum* (Mortensen 1903, 1935), another echinoid native to the archipelago deep waters (see above). As a result, older records particular prior to the review by Mortensen (1903) should be regarded with caution considering that they could be referring to either of the two species.

Subfamily Hygrosomatinae Smith & Wright, 1990

Genus *Hygrosoma* Mortensen, 1903

Hygrosoma petersii (Agassiz 1880)

$^{\$}$1895a. *Phormosomum luculentum* Agassiz; Koehler: 224.

$^{\$}$1895b. *Phormosomum luculentum* Agassiz; Koehler: 228.

$^{\$}$1898. *Phormosoma uranus*, Wyville Thomson; Koehler: 10–15, pl. 1, fig. 1, pl. 3, figs. 5, 6, pl. 9, figs. 49, 50. [misidentified see comments under *P. uranus*]

$^{\$}$1903. *Hygrosoma Petersii*; Mortensen: 176, fig. 11, pl. 11, figs. 4, 27, pl. 12, fig. 42, pl. 13, figs. 8, 13.

$^{\$}$1909. *Hygrosoma Petersi*, (A. Agassiz); Koehler: 217–218.

1927a. *Hygrosoma Petersii* (A. Agassiz); Mortensen: 284–285, figs. 156.2, 158. 1, 161.

$^{\$}$1927b. *Hygrosoma Petersi* (A. Ag.); Mortensen: 27.

1932. *Hygrosoma petersi* A. Agassiz; Grieg: 41.

1935. *Hygrosoma Petersii* (A. Agassiz); Mortensen: 202–208, figs. 118–119, pl. 13, pl. 14, figs. 1–3, pl. 15, figs. 1–2, pls. 16 –17, pl. 18, fig. 2, pl. 19, fig. 2, pl. 78, figs. 1, 3–5, 24, 25.

1985. *Hygrosoma petersii* (A. Agassiz, 1880); Gage *et al.*: 180–181.

1985. *Hygrosoma petersi* (A. Agassiz 1880); Serafy & Fell: 20, fig. 17.

2005. *Hygrosoma petersii* (Agassiz, 1880); García-Diez *et al.*: 50.

2006. *Hygrosoma petersii* (A. Agassiz, 1880); Mironov: 103.

Type locality: Caribbean.

See: Grieg (1932); Mortensen (1935); Mironov (2014: 121).

Distribution: Atlantic, from the east coast of the USA to the Caribbean, eastwards from the British Isles to South Africa, including the Azores, Canaries and the Atlantis Seamount (Meteor); possibly in Bermuda's deep-waters as well.

Depth: 200–3,800 m [AZO: 1,165–2,870(?3,237) m].

Habitat: opportunistic scavenger, on soft ooze.

Type of Development: lecithotrophic.

Remarks: in a preliminary report, Koehler (1895a, 1895b, 1896c, 1898) identified specimens from the Azores and Bay of Biscay (RVs 'Hirondelle', 'Princesse Alice' and 'Caudan') as *Hygrosoma luculentum* (= '*Phormosomum luculentum'*) and *Tromikosoma uranus* (= *Phormosoma uranus*). Mortensen (1903) questioned Koehler's previous identifications based on the examination of a specimen belonging to *H. petersii* collected in the Azores by RV 'Talisman' (sta 126: N38°37'00" W28°20'46"; 1,258 m). Subsequently, Koehler (1909) agreed with Mortensen and re-identified the material as *H. petersii*. During the expedition EMEPC-LUSO (2009, 2008), animals likely to belong to this species were captured on video on the seabed of the Azores deep waters, between São Jorge and Pico islands (N38°34'12" W28°03'17", 1,250 m, Figs. 3.28D, E) and near the Hirondelle Seamount (between São Miguel and Terceira, N37°56'12" W26°10'31", 3,237 m, Fig. 5.28F).

Subfamily Sperosomatinae Smith & Wright, 1990
Genus *Sperosoma* Koehler, 1897b

Sperosoma grimaldii **Koehler, 1897b**

[$]1897b. *Sperosoma Grimaldii* Koehler; Koehler: 302–307.

[$]1898. *Sperosoma Grimaldii*, Kœhler; Koehler: 16–21, pl. 2, fig. 2, pl. 3, figs. 3, 4, pl. 4, fig. 8, pl. 9, fig. 48.

[$]1903. *Sperosoma Grimaldii* Koehler; Mortensen: 75–78, pl. 4, figs. 3–5, pl. 11, fig. 9. pl. 12, fig. 16, pl. 13, figs. 12, 23, pl. 14, figs. 2, 4, 4a, 6, 11, 31, 33.

[$]1909. *Sperosoma Grimaldii*, Kœhler; Koehler: 218–217.

1927a. *Sperosoma Grimaldii* Koehler; Mortensen: 287–288, figs. 156.3, 163.

[$]1927b. *Sperosoma Grimaldii* Kœhler; Mortensen: 27.

1932. *Sperosoma grimaldii* Koehler; Grieg: 40–41.

1935. *Sperosoma Grimaldii* Koehler; Mortensen: 184–187, figs. 107–108, pl. 8, figs. 1–2.

1980. *Sperosoma grimaldii* Koehler, 1897; Marques: 105.

1985. *Sperosoma grimaldii* Koehler, 1897; Gage *et al*.: 181.

2005. *Sperosoma grimaldii* Koehler, 1897; García-Diez *et al*.: 50.

2006. *Sperosoma grimaldii* Koehler, 1897; Mironov: 103–104.

$^{\$}$2008. *Sperosoma* cf. *grimaldii*; Mironov: 4, tab. 1.

2014. *Sperosoma grimaldii* Koehler, 1897; Mironov: 121.

Type locality: Azores.

See: Koehler (1897b); Mortensen (1903); Emlet (1995: 486).

Distribution: Northeast Atlantic, from south of Iceland and Faroe south to the Gulf of Guinea including the Azores, Canaries and Cabo Verde archipelagos, and the Great Meteor Seamount.

Depth: 235–2,910 m (AZO: 1,213–2,107 m).

Habitat: sand, mud to ooze.

Type of Development: lecithotrophic.

Remarks: Koehler (1897b, 1898) described a new species of echinothuroid, *Sperosoma grimaldii* based on material collected in Azorean deep waters by the RVs 'Hirondelle' and 'Princesse Alice'. Until recently, the presence of this species in the archipelago has been restricted to the type material and to the historical reports by this author. Mironov (2008) published a table mentioning this echinoid collected by RV 'G.O. Sars' ('MAR–ECO' expedition), which included stations located in the northern-most waters of the Azores.

Genus *Tromikosoma* Mortensen, 1903

Tromikosoma koehleri Mortensen, 1903

$^{\$}$2008. *Tromikosoma* cf. *koehleri*; Mironov: 4, tab. 1.

2014. *Tromikosoma koehleri* Mortensen, 1903; Mironov: 122.

Type locality: Davis Strait.

See: Mortensen (1935: 167–168, fig. 100, pl. 5).

Distribution: North Atlantic, from the Davis Strait south to the Charlie-Gibbs Fracture Zone and north of the Azores.

Depth: 2,517–3,527 m (AZO: 2,954–2,968 m).

Habitat: probably a bottom-feeder living on soft sediments.

Remarks: *Tromikosoma koehleri* was only known from its type locality. More recently, Mironov (2008) reported this species among the material collected by RV 'G.O. Sars'

(‘MAR-ECO’ expedition) in the Charles-Gibbs Fracture Zone. The same author listed material likely to belong to this rare species collected at stations located in the northern waters of the Azores (RV ‘G.O. Sars’, ‘MAR-ECO’ cruise, sta 40/367: N42°55” W30°20”; 2,954–2,968 m). Later, however, Mironov (2014) placed the ‘MAR-ECO’ station from the Azores in the geographical distribution of this species. Mironov also added that this species is very closely related to *T. uranus* also known from the Atlantic (see below). Both species are known from very little material, and may prove to be identical.

***Tromikosoma uranus*? (Thomson, 1877)**

?$^{\$}$1881. *Phormosoma uranus*; Agassiz: 103–104, pl. 18c, fig. 12.

non 1898. *Phormosoma uranus*, Wyville Thomson — Koehler: 7, 10–15, pl. 1, fig. 1, pl. 3, figs. 5–6, pl. 9, figs. 49, 50. [misidentified *H. petersii*]

? $^{\$}$1925. *Echinosoma uranus*; Clark: 57.

Type locality: Gorringe Ridge, off Portugal (N36°23’ W11°18’).

See: Mortensen (1927b: 25–26; 1935: 168–170, pl. 6, figs. 2–3, pl. 75, figs. 19–21); Mironov (2014: 121–122).

Distribution: Northeast Atlantic, from off Portugal to off the Western Sahara coast and the ?Azores.

Depth: 938–2,745 m (?AZO: 1,830 m).

Habitat: most probably a bottom-feeder on soft sediments.

Remarks: *Tromikosoma uranus* was recorded from the Azores based on specimens collected by the RVs ‘H.M.S. Challenger’ (Agassiz 1881), ‘Hirondelle’ and ‘Talisman’ (Koehler 1898). Except for RV ‘H.M.S. Challenger’ material, all other were re-examined and re-assigned to *H. petersii* (Mortensen 1903; Koehler 1909; Mortensen 1935). The specimen from RV ‘H.M.S. Challenger’ was a young specimen (7 mm) in a poor state of preservation, which rendered the identification impossible (see Mortensen 1903). The occurrence of this species in the area should be considered with caution, until new material is retrieved from the Azores (see remarks under *T. koehleri*).

Family Phormosomatidae Mortensen, 1934

Genus *Phormosoma* Thomson, 1872b

Species *Phormosoma placenta* Thomson, 1872b

Phormosoma placenta placenta Thomson, 1872b

$^{\$}$1927b. *Phormosoma placenta* W. Th.; Mortensen: 25.

1935. *Phormosoma placenta* Wyv. Thomson; Mortensen: 125–135, figs. 80–82, pl. 1, figs. 1–5, pl. 2, figs. 1–19, pl. 74, figs. 1–6, 19.

1980. *Phormosoma placenta* Wyville Thomson, 1872; Marques: 105.

2012. *Phormosoma placenta* Wyville Thomson, 1872; Benavides-Serrato *et al*.: 53.

Type locality: about 100 miles to the north of the Butt of the Lewis, in Scottish waters (N59°43' W7°40').
See: Thomson (1872b: 732–737, pl. 62, figs. 1–5, pl. 63, figs. 1–9, 9a); Mortensen (1935); Chesher (1966: 214); Serafy & Fell (1985: 20, fig. 15).

Distribution: North Atlantic, in the Davis Strait south to the Northeast coast of USA eastwards to south of Iceland to Gulf of Guinea, including the Azores, Canary and Cabo Verde archipelagos. The subspecies *P. placenta sigsbey* Agassiz, 1880 and *P. placenta africana* Mortensen, 1934 are reported from the Caribbean and South African waters, respectively.

Depth: 215–2,500 m (AZO: 1,257 m).

Habitat: gregarious bottom-feeder on soft sediments; on muddy sand to soft ooze.

Type of Development: lecithotrophic.

Remarks: the record of *Phormosoma placenta* in the Azores is based on Mortensen (1927b) who identified this species among the material collected by RV 'Talisman' (sta 127, 1883: N38°38'00" W28°20'46", 1,257 m).

Infraclass Irregularia Latreille, 1825
Superorder Atelostomata Zittel, 1879
Order Spatangoida Agassiz, 1840
Suborder Brissidina Stockley *et al.*, 2005
Family Brissidae Gray, 1855b
Genus *Brissopsis* Agassiz, 1840
Species *Brissopsis lyrifera* (Forbes, 1841)

Brissopsis lyrifera lyrifera (Forbes, 1841)

$^{\$}$1895a. *Brissopsis lyrifera* Agassiz; Koehler: 225.

$^{\$}$1898. *Brissopsis lyrifera*, Agassiz; Koehler: 7, 24, 73.

1932. *Brissopsis lyrifera* Forbes; Grieg: 43.

1938. *Brissopsis lyrifera* (Forbes); Nobre: 132–133, fig. 57.

1997. *Brissopsis lyrifera* (Forbes, 1841); Pereira: 335.

2010. *Brissopsis lyrifera* (Forbes, 1841); Micael & Costa: 323.

2012. *Brissopsis lyrifera* (Forbes, 1841); Micael *et al*.: 4.

2005. *Brissopsis lyrifera* (Forbes, 1841); García-Diez *et al*.: 51.

Type locality: Scotland, British Isles.

See: Forbes (1841: 187–189); Mortensen (1951b: 380–390, pl. 30, figs. 1–4, 7–13, pl. 32, figs. 15, 20, 22, pl. 57, fig. 15); Chesher (1968: 90–96, figs. 8, 18–19; pl. 21, figs. a–b, as *Brissopsis lyrifera capensis*); Harvey *et al.* (1988: 178–180); Mecho *et al*. (2014: 286–288, figs. 6A–B).

Distribution: Mediterranean Sea and East Atlantic, from Iceland and Scandinavia to NW Africa, including the Azores; the subspecies *B. lyrifera capensis* Mortensen, 1907 was reported from South Africa, the Gulf of Guinea and the Caribbean.

Depth: 5–2,250 m (AZO: 130 m).

Habitat: buried in sand, mud to detritic substrates.

Type of Development: planktotrophic.

Remarks: the only known material of *Brissopsis lyrifera* from the Azores is restricted to a single small specimen identified by Koehler (1895a, 1898) among the material collected by RV 'Hirondelle' (sta 226: N38°31'19" W28°34'31") in the channel between the islands of Pico and Faial islands, at a reported depth of 130 m.

Genus *Brissus* Gray, 1825

Brissus unicolor (Leske, 1778)
(Fig. 5.29)

$1888. *Brissus unicolor* Klein; Barrois: 111.

1917. *Brissus brissus*; Clark: 218-219.

1921b. *Brissus unicolor* Klein; Koehler: 133–134, fig. 92.

1927a. *Brissus brissus* (Leske); Mortensen: 326.

$1925. *Brissus brissus*; Clark: 218.

1951b. *Brissus unicolor* (Leske); Mortensen: 509–514, pl. 38, fig. 10.

1956. *Brissus brissus* (Leske); Harvey: 67.

1965. *Brissus unicolor* (Leske); Tortonese: 375–378, figs. 170, 184–185.

$1993. *Brissus unicolor* (Leske, 1778); Wirtz & Martins: 58–59.

1997. *Brissus unicolor* (Leske, 1778); Pereira: 335.

$1998. *Brissus unicolor*; Morton *et al*.: 146, fig. 7.4M1.

2002. *Brissus unicolor* (Leske, 1778); Pérez-Ruzafa *et al*.: 286–287.

$2003. *Brissus unicolor*; Wirtz & Debelius: 261.

2006. *Brissus unicolor* (Leske 1778); Schultz: 385, figs. 727–728.

2010. *Brissus unicolor* (Leske, 1778); Micael & Costa: 323.

2012. *Brissus unicolor* (Leske, 1778); Micael *et al*.: 4.

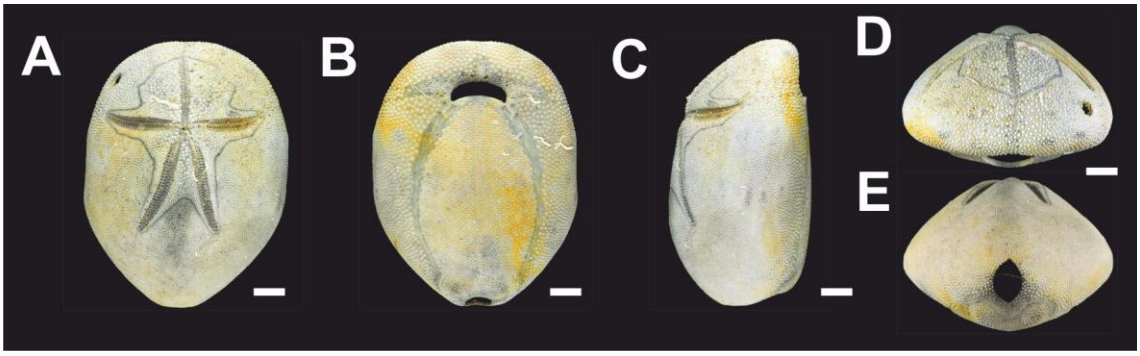


Figure 5.29. *Brissus unicolor* (Leske, 1778) (DBUA-ECH 045). Aboral view (A); oral view (B); lateral view (C); anterior view (D); posterior view (E); scale bars are 10 mm.

See: Mortensen (1951b); Pawson (1978: 24); Schultz (2006).

Distribution: Mediterranean Sea and Atlantic; in the West Atlantic from Florida and the Caribbean to Brazil, including Bermuda; in the east present in the Azores, Madeira, Selvagens, Canaries and Cabo Verde; reported as well from ?Saint Helena and Ascension islands.

Depth: 0–?240 m (AZO: ?7–45 m).

Habitat: buried on soft substrates or under stones.

Material examined: DBUA-ECH 008 (Carapacho, GRA, AZO, *c.* N39°00’44” W27°57’28”, 2010.09.05, 17 m; 1 bt, TL=85 mm)**;** DBUA-ECH 009 (Calheta do Nesquim, PIX, AZO, *c.* N38°24’08” W28°04’42”, 7–10 m; 1 bt, TL=86 mm)**;** DBUA-ECH 010 (Lajes, PIX, AZO, *c.* N38°23’22” W28°15’04”, 2010.09.25, 5–6 m; 1 bt, TL=111 mm); DBUA-ECH 012 (FRM, AZO, *c.* N37°16’14” W24°46’52”, 1990.06, 45 m; 1 spm, TL=9 mm).

Description: test outline elongated to oval (weight about 70–80%TL); no anterior notch; aboral side convex with the posterior interambulacrum raised as a keel; in lateral view posterior end low, rounded in the smallest individual (DBUA-ECH 012; TL=9 mm) to obliquely truncate in the larger specimens; oral side flattened, slightly convex; sides of test somewhat tumid. Frontal ambulacrum flush, narrow with vertically elongated, minute unipores; paired ambulacra distinctly petaloid, sunken; anterior petals forming an almost straight line, perpendicular to the major axis of the test; posterior petals longer than the anterior ones, diverging at 45°. Pore-series equally developed. Apical disc anterior, ethmolytic, with four genital pores, the posterior pair significantly larger than the anterior one. Genital pores not formed in the smallest specimen (DBUA-ECH 012; TL=9 mm). Madreporite extended posteriorly beyond the posterior oculars. Periproct on the posterior end of the test, elliptical in shape with pointed ends. Peristome near the anterior edge of the test, semilunar, about 16–20%TL. Labrum short and wide; sternum large and broad, densely covered by tubercles in more or less fan-shaped arrangement. Antero-lateral ambulacra strongly developed adorally, forming conspicuous phyllodes; postero-lateral ambulacra narrow and naked on the oral side. Subanal fasciole bilobed, distinct and complete, enclosing five pores pairs on each side in all, except for the smallest specimen (TL=9 mm), in which the fasciole as not yet fully formed and only 4 subanal tubefeet are present on each side. Peripetalous fasciole well developed, more or less bilaterally symmetrical along the anterior-posterior axis, bending inwards between the petals. In the anterior interambulacra it forms two more or less sharp angles on each side. Tuberculation dense and uniform, only in the anterior interambulacra the tubercles are somewhat larger. Spines short and fine; Plastron spines spatulate. Colour: test greyish white to creamy white. All examined dead tests showed a circular borehole, assumed to be evidence of drilling predation (possibly by gastropods).

Remarks: the specimens housed in the DBUA-ECH collection show all the features of a typical *Brissus unicolor*, with one single exception. The posterior end in this species is described as vertically truncated, an important diagnostic feature distinct from other *Brissus* species such as *B. latecarinatus* (Leske, 1778) (*e.g.,* Mortensen 1951b; Schultz 2006). However, in our adult animals the shape of the posterior end is closer to what is described for the later species. Another atypical feature presented by DBUA-ECH' specimens is the number of pores (five) enclosed within the subanal fasciole, which is typically four in *B. unicolor*, only occasionally five (Mortensen 1951b). The adult specimens observed herein, however, all have five per ambulacrum.

Brissus unicolor was reported from the archipelago by Barrois (1888) who at the time commented that this species was one of the rarest echinoderms in the archipelago. In the DBUA-ECH collection this species is represented only by five specimens, and all but one are dead tests, showing signs of having been exposed on the bottom surface for some time (erosion and encrustation by serpulids). However, the small number in the collection does not simply suggest a rare status locally. This species is a large echinoid that lives typically buried in the sand, though occasionally individuals can be found under rocks (personal observation), outside the scope of direct observation or sampling by divers. Barrois also commented that the only locality where this species appears to be common was inside of the crater of Vila Franca Islet

(São Miguel Island). With the exception of the young specimen (DBUA-ECH 012) for which we have no collection details, all the remaining specimens derived from areas with similar habitat characteristics to the one described by Barrois, *i.e.* sandy to muddy sandy bottoms in relatively protected areas (see also Morton *et al*. 1998).

Family Palaeotropidae Lambert, 1896

Genus *Palaeotropus* Lovén, 1874

***Palaeotropus josephinae* Lovén, 1871**

$^{\$}$1874. *Palæotropus Josephinæ* n.; Lovén: 17–18, pl. 12, fig. 105, pl. 13, figs. 108–113, pl. 32, fig. 200.

1881. *Palæotropus josephinæ* Lov.; Agassiz: 218.

$^{\$}$1895a. *Palaeotropus Hirondellei*, sp. nov.; Koehler: 226–227.

$^{\$}$1895b. *Palaeotropus Hirondellei* Koehler; Koehler: 230–231.

$^{\$}$1898. *Palæotropus Hirondellei*, Kœhler; Koehler: 29–30, pl. 5, figs. 12–14, pl. 6, figs. 26–27, pl. 9, fig. 47.

$^{\$}$1909. *Palæotropus Hirondellei*, Kœhler; Koehler: 244–245, pl. 30, figs. 18–23, pl. 31, figs. 4–5.

1917. *Palaeotropus josephinae*; Clark: 152–153.

$^{\$}$1921a. *Palæotropus Hirondellei* Kœhler; Koehler: 3.

1927a. *Palæotropus Josephinæ* Lovén; Mortensen: 322.

1950. *Palæotropus Josephinæ* Lovén; Mortensen: 294–298, figs. 205, 206a, 207b, pl. 25, figs. 14, 19, 21–22, 30–33.

2005. *Palaeotropus josephinae* Lovén, 1898; García-Diez *et al*.: 51.

2006. *Palaeotropus josephinae* Loven, 1871; Mironov: 115–117, figs. 6–7.

Type locality: Azores (Vila Franca, São Miguel).

See: Lovén (1874); Mortensen (1950); Mironov (2006).

Distribution: East Atlantic, known from the Bay of Biscay, the Azores Archipelago, Hyeres and Tropic NE Atlantic seamounts; also reported from a seamount located north of St. Helena (S11°37' W5°12').

Depth: 300–1,600 m (AZO: 500–1,600 m).

Habitat: soft to hard bottoms (mud, sand, gravel and rock).

Type of Development: planktotrophic.

Remarks: Lovén (1871, 1874) described the deep-water species *Palaeotropus josephinae* based on material collected by RV 'Josephine' near Vila Franca do Campo, in the south of São Miguel Island. Throughout the historical bibliography this species is a constant presence in deep-water tows in the Azorean deep waters. For example, Koehler (1895a, 1898) described a new species *Palaeotropus hirondellei* based on material collected in the Azores by RV 'Hirondelle' (sta 102: N38°23'45" W28°31'16", 927 m). Clark (1917) argued that Koehler overlooked *Palaeotropus josephinae* described by Lovén from the same area, that both species portrayed animals of different sizes, and synonymized the two species, an opinion shared by later authors (*e.g.,* Mortensen 1950; Mironov 2006).

Superfamily Spatangoidea Gray, 1825
Family Loveniidae Lambert, 1905
Genus *Araeolampas* Serafy, 1974

Araeolampas atlantica **Serafy, 1974**

$^{\$}$1949. *Homolampas fragilis* (Agassiz); Clark: 376.
$^{\$}$1974. *Araeolampas atlantica*, new species; Serafy: 44–46, figs. 1a–c, 2a–b.
2014. *Araeolampas atlantica* Serafy, 1974; Mironov: 127.

Type locality: off Virginia (N37°50' W73°04').
See: Serafy (1974); Mironov (2008).

Distribution: North Atlantic, in the west from off Virginia to north of Haiti, in the east from north of the Azores to off Gabon.

Depth: 1,920–3,595 m (AZO: 2,585 m).

Habitat: probable endobenthic in soft substrata.

Remarks: the presence of *Araeolampas atlantica* in the archipelago is based on the material collected by RV 'Atlantis' west of São Miguel Island, firstly identified by Clark (1949) as *Homolampas fragilis* (Agassiz, 1869) and then reassigned to *Araeolampas atlantica* by Serafy (1974) upon re-examination.

Subfamily Echinocardiinae Cooke, 1942
Genus *Echinocardium* Gray, 1825

Echinocardium cordatum **(Pennant, 1777)**
(Fig. 5.30A)

?$^{\$}$1888. *Echinocardium flavescens* Agassiz; Barrois: 110. [early juveniles, identification doubtful]
$^{\$}$1983. *Echinocardium cordatum* (Pennant, 1777); Marques: 6.
1997. *Echinocardium cordatum* (Pennant, 1777); Pereira: 334.
$^{\$}$2003. *Echinocardium cordatum*; Wirtz & Debelius: 261.

2010. *Echinocardium cordatum* (Pennant, 1777); Micael & Costa: 323.

2011. *Echinocardium cordatum* (Pennant, 1777); Madeira *et al*.: 257

2012. *Echinocardium cordatum* (Pennant, 1777); Micael *et al*.: 4.

See: Mortensen (1927a: 331–334, figs. 194.1–2); Higgins (1974, 1975); de Ridder *et al.* (1987); Jesus & Abreu (1998: 64); Schultz (2006: 411, fig. 772); Schipper *et al.* (2008); Madeira *et al.* (2011).

Distribution: antitropical, present in the W Pacific, E Atlantic and Mediterranean Sea; in the east from Scandinavia and the British Isles to Morocco, including the Azores, Madeira and Canaries; also present in South Africa.

Depth: 0–230 m (AZO: 15–20 m).

Habitat: buried in mud, sand to gravel.

Type of Development: planktotrophic (31–35 days).

Fossil record: fossil remains belonging to the genus *Echinocardium* were documented in the Pliocene fossiliferous outcrops of Santa Maria.

Material examined: DBUA-ECH 083 (Baia do Rosto do Cão, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1990.07.5; 15–20 m; 1 broken spm; TL=38 mm);

Description: test very fragile (oral side missing) with a subrounded (greatest weight ≈ TL). Anterior end truncated in lateral view; frontal ambulacrum sunken. Larger tubercles mostly absent, except for the edge of the anterior ambulacrum. Apical disc posterior with four genital pores. Internal fasciole shield-shaped, longer than wide (width=42%length), almost half of the test length; 35–36 pores on each side of ambulacrum III within the fasciole, arranged in the following manner: small pores aligned proximally in a single series relatively; in the mid-section larger pores somewhat transversely elongated and more crowded forming an irregular biserial arrangement (area of largest weigh of the fasciole); at the anterior end circular pores more widely spaced, forming again a single series. Specialized penicillate tube feet present. Rows of the pair petals somewhat convergent and depressed; petal IV and V with 9(IVa)–14(IVb) and 12(Vb)–11(Va) pore pairs, respectively. Periproct round and truncated. Anal fasciole expanding along the sides of the periproct onto the aboral side. Spines relatively uniform through the aboral region with the exception of elongated spines of the frontal ambulacrum forming an apical tuft. No pedicellaria were found, except for a few small tridentate (≈200 µm) with leafshaped valves with irregularly serrate edge. Colour: naked test cream, spines light brown and brown tube feet.

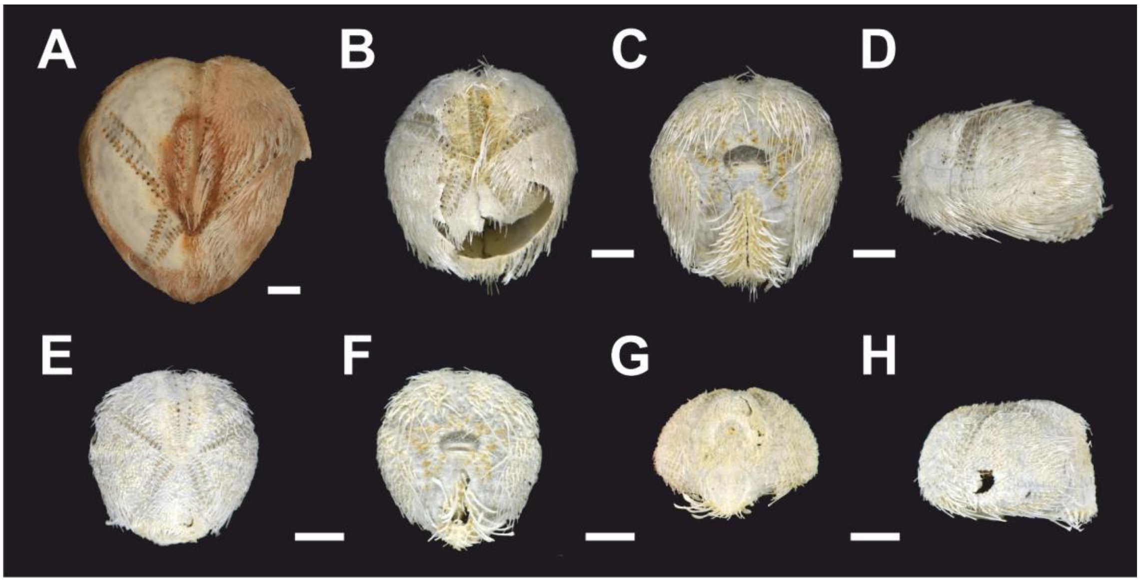


Figure 5.30. *Echinocardium cordatum* (Pennant, 1777) (DBUA-ECH 083: A) and *Echinocardium* sp. (DBUA-ECH 084: B–D; DBUA-ECH 278: E–H). Apical view (A, B, E); oral view (C, F); posterior view (G); lateral view (D, H); scale bars are 5 mm.

Remarks: Marques (1983) was the first to report *Echinocardium cordatum* from the archipelago. We have not found the specimen(s) in the Vasco Marques collection at the Bocage Museum. Nevertheless, later Wirtz & Debelius (2003) published a photograph portraying an *E. cordatum in situ* in Faial Island. Unfortunately, none of the authors have specified at which depth this species seems to occur in the archipelago (see below remarks under *E. flavescens*).

The specimen housed in DBUA-ECH collection was rather damaged, lacking the entire oral area. Regardless, this specimen presents the typical double arrangement of the pores of ambulacrum III of *E. cordatum*. In contrast, the specimen lacks many features expected in a typical *E. cordatum*, having a weakly sunken ambulacrum III aborally. On the other hand, *E. cordatum* is characterised by a high degree of morphological variation and the observed departure from the norm is well inside the documented variability of this species (see Higgins 1974, 1975). Unfortunately, only one type of pedicellariae was found. The small tridentate pedicellariae are similar to what (Mortensen 1907) described for *E. cordatum*. However, this type of pedicellariae is not diagnostic, and similar morphologies can be found in other species known from the NE Atlantic such *E. flavescens* (Mortensen 1907).

***Echinocardium* sp.**

(Figs. 3.30C–H)

Material examined: DBUA-ECH 084 (SMG, AZO; 1 damaged spm, TL=24 mm); DBUA-ECH 086 (off Vinha da Areia, SMG, AZO, N37°42'11" W25°25'04", 2006.09.05, 66 m; 3 spms, TL=11–14 mm); DBUA-ECH 091 (Vila Franca do Campo, SMG, AZO, N37°42'33" W25°24'35", 2006.07.25, 36 m; 2 spms, TL=7–9 mm); DBUA-ECH 093 (Vila Franca do Campo, SMG, AZO, N37°42'37" W25°24'34", 2006.07.25, 23 m; 1 spm, TL=9 mm); DBUA-ECH 094 (Azores, 20 m; 2 broken spms, TL=18 mm); DBUA-ECH 097 (off Ribeira das Tainhas, Vila Franca do Campo, SMG, AZO, N37°42'04" W25°25'02", 2006.07.24, 48–117 m; 1 spm, TL=7 mm); DBUA-ECH 278 (off Vinha da Areia, Vila Franca do Campo, SMG, AZO, N37°42'12" W25°25'15", 2006.09.05, 63 m; 1 spm, TL=13 mm); DBUA-ECH 419 (off Vinha da Areia, Vila Franca do Campo, SMG, AZO, N37°42'00" W25°25'15", 2006.09.05, 81 m; 1 spm, TL=14 mm); DBUA-ECH 420 (off Vila Franca do Campo, SMG, AZO, N37°42'12" W25°25'08", 2006.10.03, 58 m; 1 spm, TL=14 mm).

Description: test very fragile, round to oval, moderately high (61–67%TL); anterior contour high and truncated in lateral view. Frontal ambulacrum somewhat sunken, being more obvious in larger specimens. Larger tubercles mostly absent, except for a few at the edge of ambulacrum III. Apical disc posterior of centre; genital pores not visible in specimens of 14 mm or smaller. Paired petals slightly depressed with pore-series somewhat convergent; petals IV and V with 5–9(IVa), 8–14(IVb) and 7–11(Vb), 7–11(Va) pore pairs, respectively. Oral side flattened with relative large peristome (21–23%TL) slightly anterior; labrum rounded, slightly projecting, reaching the second adjoining ambulacra plate; plastron keeled toward a sharp posterior point; presence of phyllodal tube feet. Periproct round and truncate; Internal fasciole shield-shaped, wider in the smaller specimens (width ≥70% length; TL ≤9 mm) becoming narrower in larger specimens (width=50% length; TL=24 mm; DBUA-ECH 084); the overall size of the internal fasciole larger in the larger specimens (48%TL; DBUA-ECH 084) than in the smaller individuals (33%TL, TL ≤9 mm); pores of frontal ambulacrum within the fasciole in regular single series with specialized penicillate tube feet; pore size increasing towards the anterior end (size difference more apparent in smaller individuals). Number of pores on each side of the anterior ambulacrum within the fasciole increases from the smallest size class (TL=7 mm) to the largest specimen (TL=24 mm, DBUA-ECH 084), from 9 to 22, respectively. Subanal fasciole diamond shaped, acute at its lower end and with up to two pore pairs per ambulacrum in the larger individuals. Anal fasciole expanding along the sides of the periproct onto the aboral side, adjoining but separate from subanal fasciole. Spines relatively uniform through the aboral region with the exception of the conspicuous presence of elongated spines forming an apical tuft in the frontal ambulacrum adapically. No pedicellaria were found. Colour (in ethanol): white test and spine and brown tube-feet.

Remarks: in the Atlantic the genus *Echinocardium* is represented by 12 extant species (Mironov 2006), five of which are known to occur in the NE Atlantic: *E. cordatum*, *E. flavescens*, *E. pennatifidum*, *E. mediterraneum* and *E. meteorense* (Mortensen 1951b; Mironov 2006). Jesus & Fonseca (1999) reported two additional species previously thought to be endemic to the Mediterranean Sea from the south of Portugal: *E. fenauxi* and *E. mortenseni*. *Echinocardium* species typically live in shallow-waters, though most could be characterized almost as 'eurybathic' by having a bathymetric range that extends to waters below the 200 m (Tortonese 1965). *E. meteorense* is an exception as it occurs at waters between 300–450 m (Mironov 2006).

In general, the genus *Echinocardium* is characterised by rather difficult systematics with many morphological diagnostic characters overlapping interspecifically and showing great intraspecific variability (individual or ontological variation; David & Laurin 1996). The first record of *Echinocardium* in the Azores was made by Barrois (1888) based on very small specimens dredged in São Miguel Island. Later Koehler (1909) re-examined Barrois' material and commented that it contained only very small and fragile specimens, lacking many diagnostic structures such as the pedicellaria. Curiously, both authors' remarks could be used to characterise the material presently housed in the DBUA-ECH collection. Most of these specimens were collected during the 'Third International Workshop of Malacology and Marine Biology' (2006). *Echinocardium* was a frequent presence in the tows but few individuals survived the sediment weight while handling the dredge. The material stored at the DBUA-ECH collection is composed by heavily damaged tests, not exceeding 23 mm in size. Nevertheless, these specimens can be easily distinguished from *E. mediterraneum* and *E. pennatifidum* as both species lack specialized tube feet in the anterior ambulacrum. This feature is reflected by the shape and arrangement of the pores inside the internal fasciole, which in both species is characterised by widely spaced small sized pores (Mortensen 1907). Our specimens from the Azores can also be distinguished from *E. flavescens* by the presence of a depressed frontal ambulacrum and almost complete absence of larger tubercles on the aboral side. Moreover, the number of pore pairs in the pair petals appears to be significantly higher in our individuals than what was published in the bibliography for *E. flavescens* of similar size classes (*e.g.,* Mortensen 1907). A closely resembling species of *E. flavescens*, *E. mortenseni*, is also distinct from the examined material by having a relatively longer test contour, slightly lower test height, with no obvious frontal depression, a relative shorter inner fasciole (≤33%TL) and shorter anterior petals (≤10 pores) at comparable size classes (Mortensen 1907; Koehler 1909, as *E. intermedium*). The deep-water *E. meteorense* can be ruled out by being characterized by relative small and inconspicuous internal fasciole (<25–27%TL) and by a parallel arrangement in the pore columns of the paired petal (Mironov 2006). Also *E. meteorense* known depth range is significantly deeper than the reported depth for DBUA-ECH specimens. In contrast, the diagnostic features mentioned above place the examined material close to *E. cordatum*. However, none of the examined specimens presented the pores in the frontal ambulacrum in an irregular double series arrangement, a feature unique in *E. cordatum* (Mortensen 1951b). On the other end, *E. fenauxi* has the pores in the frontal ambulacrum disposed in a similar fashion as our specimens, *i.e.* in a single series. At first instance the examined specimens appear to belong to this species. However, *E. fenauxi* is also characterised by having a large depressed test and a periproct wider than long, which is not consistent with the observations on the specimens from the Azores.

The validity of *E. fenauxi* has been contested (Egea *et al*. 2016), since its original description by Péquignat (1963). In a preliminary genetic study, *E. cordatum* and *E. fenauxi* were ordered on the molecular trees according to their geographic origin, failing to separate the morphospecies (Laurin *et al*. 1994). Féral *et al*. (1998) also failed to genetically differentiate *E. fenauxi* from *E. cordatum*. Furthermore, the diagnostic characteristics listed above for *E. fenauxi* appear to fall well in the known variability the polymorphic *E. cordatum* as was demonstrated the studies by Higgins (1974, 1975). In contrast, available genetic data on *E. cordatum* indicates that it is a cryptic species complex (Egea *et al*. 2016).

Mortensen (1936) tentatively identified a damaged specimen of about 20 mm from Cabo Verde (7–11 m of depth) as *E. connectens*. This species is still known only by the fragmentary type material from Saint Helena (Mortensen 1933c). Nevertheless, Mortensen's description and figures of the specimen from Cabo Verde are in every aspect consistent with the material examined here, particularly when comparing specimens of similar size (DBUA-ECH 94, TL=18–19 mm). Unfortunately, no further material of *Echinocardium* from Cabo Verde has been recorded to date. In the future it would be interesting to compare specimens from these archipelagos as new and better-preserved material becomes available.

Echinocardium flavescens **(Müller, 1776)**

?$1888. *Echinocardium flavescens* A. Agassiz; Barrois: 110. [early juveniles, identification doubtful]

1914b. *Echinocardium flavescens*; Koehler: 279.

1921b. *Echinocardium flavescens* O.F. Müller; Koehler: 136–137, fig. 95.

1927a. *Echinocardium flavescens* (O. Fr. Müller); Mortensen: 334–335, figs. 194.3, 195.4, 196.2, 197.1.

1938. *Echinocardium flavescens* O.F. Müller; Nobre: 128–129, fig. 55.

1951b. *Echinocardium flavescens* (O.Fr. Müller); Mortensen: 158–160.

$1965. *Echinocardium flavescens* (O.F. Müll.); Tortonese: 366–367, fig. 180.

1997. *Echinocardium flavescens* (O.F. Müller, 1776); Pereira: 334.

2010. *Echinocardium flavescens* (O.F. Müller, 1776); Micael & Costa: 323.

2011. *Echinocardium flavescens* (Müller, 1776); Madeira *et al*.: 257.

2012. *Echinocardium flavescens* (O.F. Müller, 1776); Micael *et al*.: 4.

See: Tortonese (1965); Jesus & Abreu (1998: 64); Schultz (2006: 413, fig. 413).

Distribution: Mediterranean and Northeast Atlantic, from Iceland and Scandinavia south to Portugal, Madeira and the Azores.

Depth: 5–360 metres (?AZO: 15–30 m).

Habitat: buried in gravel, sand, muddy, detritic and coralligenous bottoms.

Type of Development: planktotrophic.

Remarks: *Echinocardium flavescens* was first reported by Barrois (1888), who noted that all his specimens though quite abundant in all the dredges between 15 and 30 meters, appeared unusually small to what he had seen in French coasts. On re-examination of Barrois' material, Koehler (1909) disagreed with the previous author's identification, observing that all specimens appear to be young *E*. *cordatum* and not *E*. *flavescens* (see above). However, the author also added that the animals were far too small for an accurate determination and lacked important diagnostic characters such as the pedicellaria. Nonetheless, Tortonese (1965) later examined animals coming from Faial Island and confirmed the presence of this species in the archipelago.

Additionally, Barrois failed to collect *Echinocyamus pusillus* (=*Echinocyamus angulosus*) from the Azores. This author used the absence of this species from his dredges together with the minute sized that supposedly characterize the insular *E. flavescens* to explain that in his opinion Drouët (1861) mistook *E. flavescens* for *Echinocyamus pusillus*. During the International Workshop of Malacology and Marine Biology (2006) abundant material of both *Echinocardium* and *Echinocyamus* was retrieved from several dredges in the south coast of São Miguel Island. On that account, we are inclined to disagree with Barrois since both *Echinocardium* and *Echinocyamus* appear to be quite common in the Azores. Notwithstanding, *E. pusillus* tends to occur in coarser sediments than *Echinocardium* species (Nichols 1959; Higgins 1974), and this apparent biotope partitioning could explain why Barrois reported one species and failed to do so for the other (see as well remarks under *E. pusillus*).

Suborder Paleopneustina Markov & Solovjev, 2001
Family Paleopneustidae Agassiz, 1904
Genus *Peripatagus* Koehler, 1895b

Peripatagus cinctus Koehler, 1895b

$1895b. *Peripatagus cinctus*, nov. gen., nov. sp.; Koehler: 231–233.
$1909. *Peripatagus cinctus*, Kœhler; Koehler: 248–251, pl. 31, figs. 6–18.
1927a. *Peripatagus cinctus* Koehler; Mortensen: 322.
1950. *Peripatagus cinctus* Koehler; Mortensen: 306.
2005. *Peripatagus cinctus* Koehler, 1895; García-Diez *et al*.: 51.
2006. *Peripatagus cinctus* Koehler, 1895; Mironov & Krylova: 32.
2006. *Peripatagus cinctus* Koehler, 1895; Mironov: 119.

Type locality: Azores (N38°47’40” W28°17’05”).
See: Koehler (1895b, 1909); Mironov (2006).

Distribution: cosmopolitan, scattered records from both East Atlantic and Pacific water; in the Atlantic reported from the Azores and the seamounts of Atlantis (Meteor), Tropic (off NW Africa), Zubov and Valdivia (Walvis Ridge, off the coast of

Namibia); also reported from a seamount located north of St. Helena (S11°37' W05°12').

Depth: 290–1,494 m (AZO: 880–1,494 m).

Habitat: sand and rock.

Remarks: the geographical distribution of this *Peripatagus cinctus* in the Atlantic is presently restricted to oceanic systems. Firstly described for the Azores by Koehler (1895b; RV 'Princesse Alice', sta 616: N38°47'40" W28°17'05", 1,022 m) this species was then later reported from several oceanic seamounts.

Family Schizasteridae Lambert, 1905

Genus *Aceste* Thomson, 1877

Aceste bellidifera Thomson, 1877

$^{\$}$1909. *Aceste bellidifera*, Wyville Thomson; Koehler: 246–247.

1927a. *Aceste bellidifera* Wyv. Thomson; Mortensen: 321.

2005. *Aceste bellidifera* Wyville Thomson, 1877; García-Diez *et al*.: 51.

2006. *Aceste bellidifera* Wyv. Thomson, 1877; Mironov: 115.

2014. *Aceste bellidifera* Thomson, 1877; Mironov: 127.

Type locality: off Gomera Island, Canaries.

See: Thomson (1877: 349–351, figs. 95–96); Mortensen (1950: 332–333, figs. 224, 225); Serafy & Fell (1985: 23); Mironov (2006, 2014).

Distribution: Atlantic, in the west recorded from the USA (*c.* N37°) and the Caribbean to southern America, and Tristan da Cunha; in the east recorded from the Iberian Basin, Morocco, Josephine Seamount, the Azores and Canaries.

Depth: 550–5,400 m (AZO: 1,360 m).

Habitat: buried on soft substrates, mud to sandy mud and shells.

Remarks: the record of *Aceste bellidifera* in the Azores is based on a single small specimen (≈14 mm TL) identified by Koehler (1909) among the material collected by RV 'Princesse Alice' (sta 703: N39°21'20" W31°05'45", 1,360 m).

Superorder Neognathostomata Smith, 1981

Order Clypeasteroida Agassiz, 1872

Suborder Scutellina Haeckel, 1896

Infraorder Laganiformes Desor, 1847

Family Echinocyamidae Lambert & Thiéry, 1914

Genus *Echinocyamus* van Phelsum, 1774

Echinocyamus grandiporus **Mortensen, 1907**

(Fig. 5.31)

p.p.$^{\$}$1898. *Echinocyamus pusillus*, Gray; Koehler: 24.

$^{\$}$1907. *Echinocyamus grandiporus* n. sp.; Mortensen: 33–36, fig. 2a, pl. 12, figs. 1, 3, 5, 8, 10–16, 21, 25, 28.

$^{\$}$1909. *Echinocyamus grandiporus*, Mortensen; Koehler: 234, pl. 4, fig. 8.

1927a. *Echinocyamus grandiporus* Mrtsn; Mortensen: 315.

1948. *Echinocyamus grandiporus* Mrtsn; Mortensen: 183.

$^{\$}$1984. *Echinocyamus grandiporis* Mortensen, 1907; Mironov & Sagaidachny: 183–184, fig. 2(1).

2005. *Echinocyamus grandiporus* Mortensen, 1907; García-Diez *et al*.: 51.

2006. *Echinocyamus grandiporus* Mortensen, 1907; Mironov: 113–114.

2011. *Echinocyamus grandiporus* Mortensen, 1907; Madeira *et al.*: 255.

2012. *Echinocyamus grandiporus* Mortensen, 1907; Benavides-Serrato *et al*.: 99.

See: Mortensen (1907); Mironov (2006).

Distribution: North Atlantic; from Florida to Brazil, eastwards to off Mauritania, and the Azores and Canaries archipelagos; also reported from the Antialtair, Josephine, Gorringe and Meteor seamounts.

Depth: 110–2,310 m (AZO: 320–1,385 m).

Habitat: typically from soft substrates (sand to gravel).

Material examined: EMEPC-LUSO L09D17B68R (E of TER, AZO, N38°40’07” W26°51’27”, 2009.09.30, 460 m; 1 bt, TL=7 mm); EMEPC-LUSO L09D22S1 (D. João de Castro Bank, AZO, *c.* N38°14’02” W26°33’37”, 2009.10.09, 718–825 m; 4 bts, D=4–5 mm); EMEPC-LUSO L09D22S2 (D. João de Castro Bank, AZO, *c.* N38°13’52” W26°33’58”, 2009.10.09, 476–718 m; 2 bts, TL=4–5 mm); EMEPC-LUSO L09D22S3 (D. João de Castro Bank, AZO, *c.* N38°13’52” W26°33’58”, 2009.10.09, 476–718 m; 1 bt, TL=4 mm); EMEPC-LUSO L09D25B14 (Channel SJG–PIX, AZO, N38°36’19.09” W28°06’46.64”, 2009.10.21, 1,180 m; 1 bt, TL=9 mm); EMEPC-LUSO L09D25B43 (Channel SJG–PIX, AZO, N38°36’19.09” W28°06’46.64”, 2009.10.21, 1,180 m; 1 spm, TL=4 mm); EMEPC-LUSO L09D26RB17a (Channel SJG–PIX, AZO, N38°37’32” W28°08’23”, 2006.10.23; 2 bts, TL=3–4 mm).

Description: test oval (width=85–90%TL) and relatively low (height=36–45%TL). Five ocular pores forming a circle with four genital pores; ocular pores as large as the genital pores, though distinctly narrowing inwards; madreporic plate a little elevated with a central pore skew to the anterior part. Petals short, not reaching the edge of the test; pore-series parallel, with two or three (TL ≤4 mm) in small up to six pore pairs (TL=9 mm, EMEPC–L09D25B14) in large specimens per row of the posterior ambulacra.

Oral area flat. Peristome round to subpentagonal about 20–24%TL. Periproct small (9–11%TL), fully oral and round to transverse oval. Primary spines slender up to 15%TL. Colour: white naked test, also spines (tinge with green after preservation in ethanol).

Remarks: Koehler (1898) examined the rich clyperasteroid material collected by RV 'Hirondelle' in the Azores, which he reported as all belonging to *Echinocyamus pusillus*. On erecting a new deep-water species of *Echinocyamus*, Mortensen (1907) re-examined material from RVs 'Hirondelle' and 'Princesse Alice' and referred part of the specimens to *E*. *grandiporus*. Later, Koehler (1909) agreeing with the previous author reported further Azorean material from RV 'Princesse Alice' under Mortensen's new species. In a review of this genus, Mironov & Sagaidachny (1984) also examined material *E*. *grandiporus* from the Azores. The material examined here further re-enforces the presence of this deep-water species in the Azores.

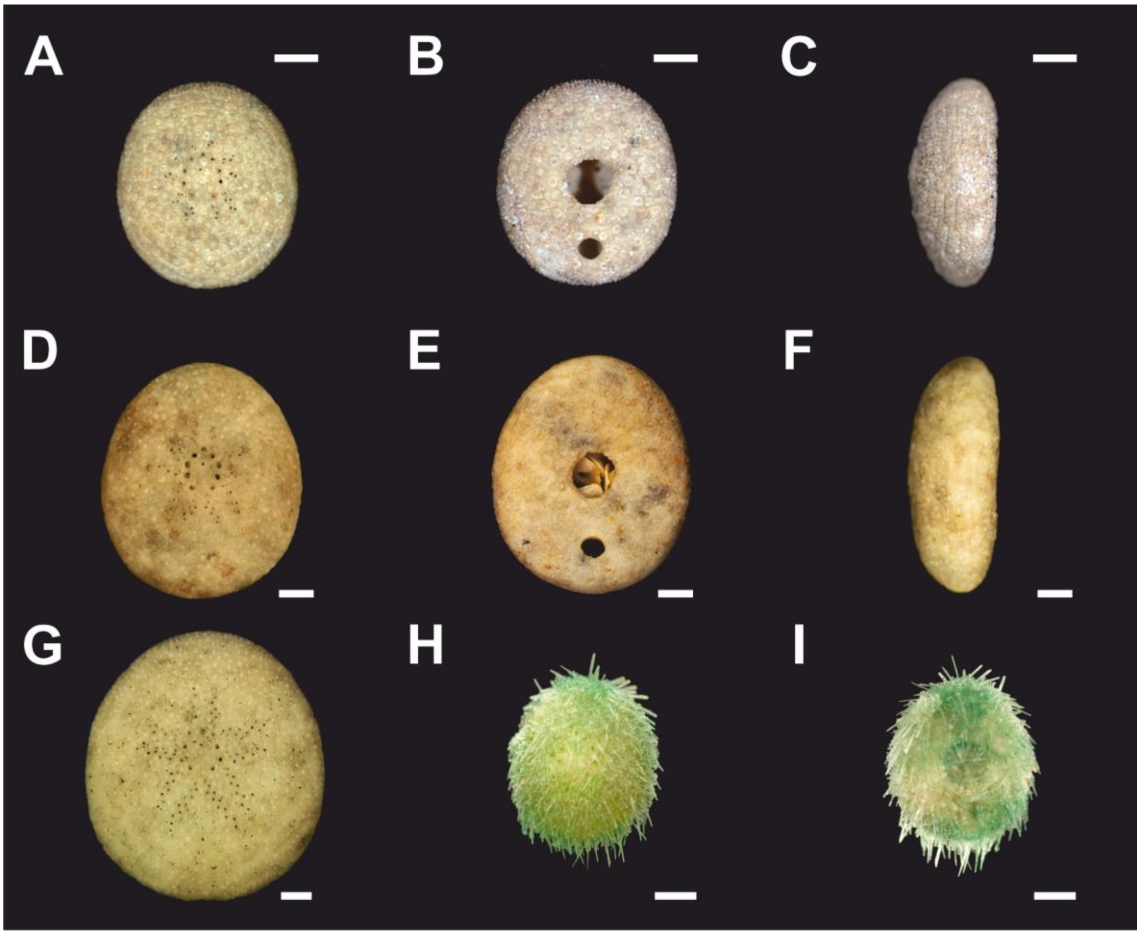


Figure 5.31. *Echinocyamus grandiporus* Mortensen, 1907 (EMEPC-LUSO L09D22S2: A–C; EMEPC-LUSO L09D17B68R: D–F; EMEPC-LUSO L09D25B14: G; EMEPC-LUSO L09D25ARB43: H–I). Apical view (A, D, G, H); oral view (B, E, I); lateral view (C, F); scale bars are 1 mm.

Generally, this species differs from other *Echinocyamus* species known in the archipelago by its large ocular pores that together with the gonopores form a conspicuous circle. *E*. *grandiporus* is further distinct from *E*. *pusillus* by the less developed petals (Mortensen 1907). Mironov (2006) remarked that the close related species *E. scaber macrostomus* occasionally also features large ocular pores. Nonetheless, this later species can also be separated by having relative larger peristome and periproct and by the rudimentary petals (Mortensen 1948). See also remarks under *E*. *pusillus*.

Echinocyamus pusillus **(Müller, 1776)**

(Fig. 5.32)

p.p.$^{\$}$1861. *Echinocyamus angulosus* Leske; Drouët: 211.

1872. *Echinocyamus pusillus* Gray; Agassiz: 111–112, pl. 11, fig. 3, pl. 13, figs. 1–8.

1881. *Echinocyamus pusillus* Gray; Agassiz: 226.

$^{\$}$1888. *Echinocyamus pusillus* (Müll.); Simroth: 231.

1892. *Echinocyamus pusillus* O.F. Müll.; Bell: 160–161, pl. 16, figs. 8–9.

p.p.$^{\$}$1898. *Echinocyamus pusillus*, Gray; Koehler: 24.

$^{\$}$1907. *Echinocyamus pusillus* (O.F. Müller); Mortensen: 31–33, fig. 2, pl. 12, figs. 4, 6, 9, 18–20, 22, 23, 26, 27, 29–31.

$^{\$}$1909. *Echinocyamus pusillus*, (O.-F. Müller); Koehler: 235–236, pl. 4, fig. 10.

1914b. *Echinocyamus pusillus*; Koehler: 278.

$^{\$}$1924. *Echinocyamus pusillus* (Müller); Nobre: 89.

1927a. *Echinocyamus pusillus* (O.Fr. Müller); Mortensen: 316–317, figs. 182–183.

$^{\$}$1930. *Echinocyamus pusillus* (Müller); Nobre: 69.

1932. *Echinocyamus pusillus* O. F. Müller; Grieg: 42.

$^{\$}$1938. *Echinocyamus pusillus* (O.F. Müller); Nobre: 122–123, fig. 2.

1948. *Echinocyamus pusillus* (O.Fr. Müller); Mortensen: 178–183.

1956. *Echinocyamus minutus* (Pallas); Harvey: 66.

$^{\$}$1965. *Echinocyamus pusillus* (O.F. Müll.); Tortonese: 346–348, fig. 164.

$^{\$}$1983. *Echinocyamus pusillus* (O. F. Muller, 1776); Marques: 6.

$^{\$}$1984. *Echinocyamus pusillus* (Müller, 1776); Mironov & Sagaidachny: 126–183.

1997. *Echinocyamus pusillus* (O.F. Müller, 1776); Pereira: 334.

$^{\$}$1998. *Echinocyamus pusillus*; Morton *et al*.: 143, fig. 7.4L1.

2005. *Echinocyamus pusillus* (Müller, 1776); García-Diez *et al*.: 51.

2006. *Echinocyamus pusillus* (Müller, 1776); Mironov: 114.

2006. *Echinocyamus pusillus* (O.F. Müller 1776); Schultz: 317–318, figs. 597–598.

$2009. *Echinocyamus pusillus* (O.F. Müller, 1776); Wirtz: 48, fig. 1f.

2010. *Echinocyamus pusillus* (O.F. Müller, 1776); Micael & Costa: 323.

2011. *Echinocyamus pusillus* (O.F. Müller, 1776); Madeira *et al.*: 255, fig. 11.

2012. *Echinocyamus pusillus* (O.F. Müller, 1776); Micael *et al.*: 3.

See: Mortensen (1907); Cadenat (1938: 369–370); Picton (1993: 58); Mironov (2006); Madeira *et al.* (2011, 2017a).

Distribution: Mediterranean Sea and Northeast Atlantic, from Iceland and Scandinavia, along the European coasts to Sierra Leone, including the archipelagos of the Azores, Madeira, Canaries and Cabo Verde, and the Ampère, Gorringe and Meteor seamounts.

Depth: AZO: 0–207(?1,250) m.

Habitat: lives buried in soft substrates, in sand, detritic and gravelly bottoms where it feeds on detritus and foraminifera.

Type of Development: planktotrophic.

Fossil record: also reported from the Pliocene and Pleistocene outcrops of Santa Maria Island.

Material examined: DBUA-ECH 011 (Água d'Alto, SMG, AZO, N37°42'55.48" W25°28'27.39", 2006.08, intertidal; 1 bt, TL=7 mm); DBUA-ECH 036 (Água d'Alto, SMG, AZO, *c.* N37°42'55" W25°28'27", 2009.04.25, intertidal; 47 bts, TL=4–8 mm); DBUA-ECH 037 (off Marina of Vila Franca do Campo, SMG, AZO, N37°41'42" W25°25'22", 2006.07.17, 135 m; 1 spm, 15 bts, TL=3–5 mm); DBUA-ECH 038 (Vila Franca do Campo, SMG, AZO, N37°41'34" W25°27'34", 2006.07.19, 167–189 m; 16 bts, TL=3–5 mm); DBUA-ECH 039 (Vila Franca do Campo, SMG, AZO, N37°41'39" W25°27'11", 2006.07.21, 95–121 m; 70 bts, TL=3–6 mm); DBUA-ECH 040 (Vila Franca do Campo, SMG, AZO, N37°41'52" W25°27'13", 2006.07.24, 45–47 m; 11 bts, TL=4–6 mm); DBUA-ECH 041 (off Praia da Vinha da Areia, SMG, AZO, N37°42'45" W25°25'24", 2006.07.21, 14 m; 14 bts, TL=4–6 mm); DBUA-ECH 042 (off Ribeira das Tainhas, SMG, AZO, N37°42'01" W25°25'14", 2006.07.24, 98–108 m; 13 bts, TL=3–5 mm); DBUA-ECH 043 (off Ribeira das Tainhas, SMG, AZO, N37°42'01" W25°25'01", 2006.07.24, 117–145 m; 8 bts, TL=3–5 mm); DBUA-ECH 044 (off Ribeira das Tainhas, SMG, AZO, N37°41'57" W25°25'08", 2006.07.24, 144–198 m; 24 bts, TL=4–7 mm); DBUA-ECH 045 (off Ribeira das Tainhas, SMG, AZO, N37°42'17" W25°25'09", 2006.07.24, 34–63 m; 14 bts, TL=3–5 mm); DBUA-ECH 046 (off Cais do Tagarete, Vila Franca do Campo, SMG, AZO, N37°42'07" W25°25'14", 2006.07.25, 52 m; 1 spm, 32 bts, TL=2–5 mm); DBUA-ECH 047 (off Cais do Tagarete, Vila Franca do Campo, SMG, AZO, N37°41'53" W25°25'15", 2006.07.25, 180 m; 11 bts, TL=3–6 mm); DBUA-ECH 048 (Vila Franca do Campo SMG, AZO, N37°41'17" W25°25'10", 2006.07.25, 129–207 m; 4 bts, TL=3–4 mm); DBUA-ECH 049 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42'43" W25°21'33", 2006.07.26, 38 m; 2 bts, TL=4 mm); DBUA-ECH 050 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°41'57" W25°22'08", 2006.07.26, 156–360 m; 2 bts, TL=4 mm); DBUA-ECH 051 (off Praia de Água d'Alto, SMG, AZO, N37°42'24" W25°28'59", 2006.07.26, 66 m; 62 bts, TL=2–7 mm); DBUA-ECH 052 (off Vinha da Areia, Vila Franca do Campo, SMG, AZO, N37°42’37” W25°25’18”, 2006.07.26, 56 m; 58 bts, TL=2–7 mm); DBUA-ECH 124 (São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 2012.11.16, intertidal; 1 spm, TL=2 mm); DBUA-ECH 129 (Rosto do Cão, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1990.07.4, 9.5 m; 3 spms, TL=5 mm); DBUA-ECH 183 (Baixa do Porto, Lajes, FLS, AZO, *c.* N39°22’50” W31°10’00”, 1990.10.27; 1 bts, TL=3 mm); DBUA-ECH 293 (Baia de Belém, São Roque, SMG, AZO, *c.* N37°44’37” W25°38’19”, 1990.07.4, 8,6 m; 1 spm; TL=5 mm); DBUA-ECH 311 (off Ribeira das Tainhas, SMG, AZO, N37°42’33” W25°25’53”, 23 m; 2 spms, TL=3 mm); DBUA-ECH 324 (Sabrina Bank, SMG, AZO, N37°52’23”, W25°54’00”, 2011.07.07, 140 m; 1 spm, 7 bts, TL=3–4 mm); DBUA-ECH 367 (Vila Franca, SMG, AZO, N37°42’39” W25°27’26”, 2006.07.21, 18–20 m; 2 spms, TL=5 mm); DBUA-ECH 370 (Vila Franca, SMG, AZO, N37°42’42” W25°24’38”, 2006.07.25, 17 m; 1 spm, TL=4 mm); DBUA-ECH 373 (Islet of Via do Porto, SMA, AZO, *c.* N36°56’23” W25°10’16”, 7 m; 2 spms, TL=3–4 mm); DBUA-ECH 383 (Horta, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2010.03.02; 1 spm, TL=4 mm); DBUA-ECH 435 (Vila Franca do Campo, SMG, AZO, N37°41’41” W25°25’26” – N37°41’17” W25°25’10”, 2006.07.25; 129–207 m; 1 spm, TL=3 mm); EMEPC-LUSO L9D9B20(S1) (Gorringe Bank, NE Atlantic, N36°42’49” W11°09’54”, 2009.09.13, 130 m; 20 bts, TL=2–5 mm).

Description: test small, flattened, variable in form; outline generally elongated oval, though among the smallest specimens frequently ellipsoid (width ≈66–74%TL; TL<3 mm) becoming more circular or subpentagonal in larger individuals (width ≈100%TL; TL ≥7 mm). Apical disc central to slightly posterior, with large genital pores and five small ocular pores. The lower half of the apical side locally depressed in larger individuals (TL=7–8 mm). Oral area mostly flat; depression between the peristome and periproct particularly evident in the larger specimens (TL>5 mm). Peristome circular to subpentangular, relatively concave; diameter of the peristome about 30–33% TL in smaller individuals (TL <3 mm) decreasing to 13–19%TL in larger specimens (TL ≥7 mm). Periproct ellipsoid to round, small (6–12%TL) lies halfway between the peristome and the posterior margin. Petals well developed, but not reaching the edge of the test; pore-series almost parallel, open distally, reaching ten pore pairs per column in the posterior ambulacra in the largest specimens (TL=7–8 mm). Spines short, relatively uniform. Colour (in ethanol): test and spines white or cream, occasionally green.

Remarks: in general, the genus *Echinocyamus* shows a great deal of intraspecific morphological variation, often depending on the age and size of the animal. Mironov & Sagaidachny (1984) attempted to clarify the limits between intra and interspecific

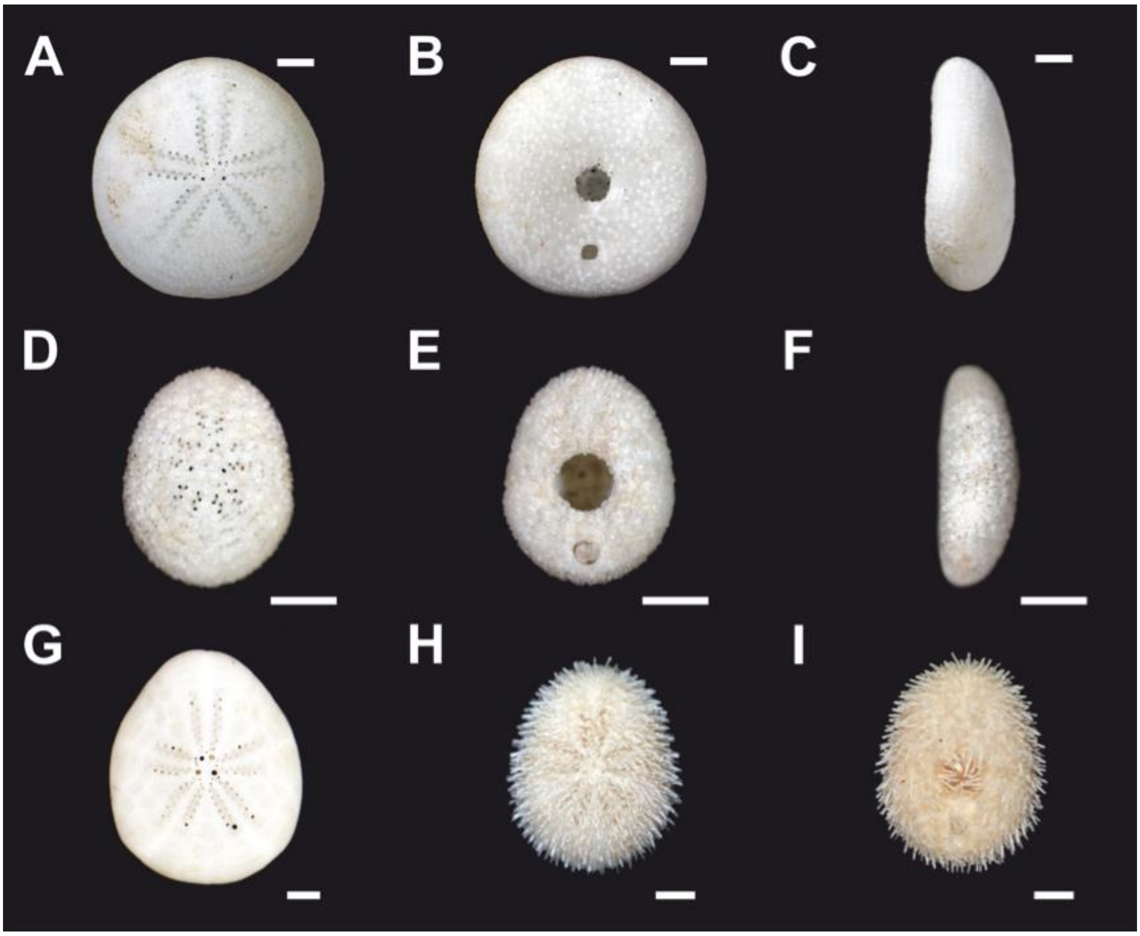


Figure 5.32. *Echinocyamus pusillus* (Müller, 1776) (DBUA-ECH 036: A–C, G; L09D17S5: D–F; DBUA-ECH 129: H–I); Apical view (A, D, G, H); oral view (B, E, I); lateral view (C, F); scale bars are 1 mm.

variability in several *Echinocyamus* species, constructing a diagnostic set made of several morphometric and meristic characters. The Azorean specimens herein examined showed as expected, high intraspecific variation, explained for the most part by differences in size of the specimens and thus dismissed as allometric variation (see remarks under *E*. *grandiporus*).

The first report of this species in the archipelago comes from Drouët (1861) who noted they are quite common on the coasts of São Miguel. Barrois (1888) believed that Drouët confused *E*. *pusillus* with *Echinocardium flavescens*. The material reported by Drouët (1861) could not be located, thus making impossible to verify Barrois' statement. However, we are inclined to believe Drouët's original identification. In São Miguel, dead tests of *E*. *pusillus* are relatively easy to find in the intertidal, particularly on sandy beaches, among the debris left by the low tide (Nobre 1930, *personal observation*). They are also a common presence among the material dredged in the Azores at depths up to 200 m. Also, the maximum recorded depth of this species was reported by Koehler (1909) based on dead tests collected by ‘Princesse Alice’ in Azorean waters between 650 and 914 m (sta 2214: N39°26’10” W31°21’30”) and 1,250 m (sta 1349: N38°35’30” W28°05’45”). The recorded depths may not represent a real bathymetric limit but rather be biased by transportation, as Koehler remarked. The light but robust *Echinocyamus* tests make it possible to keep their overall integrity even long after the animal is dead. Unfortunately, many of the documented reports for this species do not provide any description of the specimens, thus making impossible to understand the real depth range of this species. Storage in the DBUA-ECH collection we have found living specimens to a maximum reported depth of 140 m. Even though it is more than likely that *E*. *pusillus* lives at higher depths, we have accepted this value as the maximum depth in the archipelago for this species at present. Additionally, Mironov (2006) referred to station 166 (RV ‘Princesse Alice’) where Koehler (1909) had reported *E*. *pusillus* as being located in the Mid-Atlantic Ridge to the north of the Azores. This station is not in Azores waters but in the western shores of France (N47°26’30” W3°12’05”). Apparently Mironov had confused the symbol representing the degree of latitude with a zero.

Species *Echinocyamus scaber* de Meijere, 1903

Echinocyamus scaber macrostomus **Mortensen, 1907**

$^{\$}$1907. *Echinocyamus macrostomus* n. sp.; Mortensen: 36–37, pl. 12, figs. 2, 7, 17, 24.

$^{\$}$1909. *Echinocyamus macrostomus,* Mortensen; Koehler: 235, pl. 4, figs. 9–10.

1927a. *Echinocyamus macrostomus* Mrtsn.; Mortensen: 315.

1948. *Echinocyamus macrostomus* Mrtsn.; Mortensen: 183–184.

$^{\$}$1984. *Echinocyamus scaber macrostomus* Mortensen, 1907; Mironov & Sagaidachny: 186–187, fig. 2.2.

2005. *Echinocyamus macrostomus* Mortensen, 1907; García-Diez *et al.*: 51.

2006. *Echinocyamus scaber macrostomus* Mortensen, 1907; Mironov: 113–114.

2011. *Echinocyamus macrostomus* Mortensen, 1907; Madeira *et al.*: 255.

2014. *Echinocyamus scaber macrostomus*, Mortensen 1907; Mironov: 124.

See: Mortensen (1907; 1927b: 30–31); Mironov & Sagaidachny (1984); Mironov (2006; 2014).

Distribution: North Atlantic, in the west from the Blake Plateau to Cuba, in the east from Portugal to Cabo Verde, including the archipelagos of the Azores and Madeira and the Josephine, Tropic and Meteor seamounts. The subspecies *E. scaber scaber* de Meijere, 1903 is reported from the Indo-Pacific.

Depth: 1,010–2,820 m, though bare tests have been reported as deep as 3,140 m (AZO: 1,560–2,178 m).

Habitat: mud to sand.

Remarks: Mortensen (1907) described two species of *Echinocyamus*, *E. macrostomus* and *E. grandiporus* using material, which included animals collected in Azorean deep waters. Mortensen (1907) considered his two new deep-water species closely related though *E. macrostomus* tended to live in deeper waters. In contrast, Mironov & Sagaidachny (1984) considered *E. macrostomus* closely related with *E. scaber* and downgraded Mortensen species to a variety of the later. Additionally, Mironov (2006) observed that some of the specimens from Meteor and Antialtair seamounts presented intermediate characteristics between this subspecies and *E. grandiporus*, suggesting that they could represent hybrids.

Class Holothuroidea de Blainville, 1834

Order Apodida Brandt, 1835

Family Chiridotidae Östergren, 1898

Genus *Chiridota* Eschscholtz, 1829

Chiridota abyssicola Marenzeller, 1892

$^{\$}$1892. *Chiridota abyssicola*, n. sp.; Marenzeller: 65.

$^{\$}$1893. *Chiridota abyssicola*, nov. sp.; Marenzeller: 19, pl. 1, fig. 5, pl. 2, fig. 7.

1902. *Chiridota abyssicola*, Marenzeller; Perrier: 276.

p.p.1907. *Chiridota lævis* (Fabricius); Clark: 28–29.

1927a. *Chiridota abyssicola* v. Marenzeller; Mortensen: 437.

2005. *Chiridota abyssicola* Marenzeller, 1893; García-Diez *et al*.: 52.

Type locality: North of the Azores (N41°40’41” W26°44’09”).

See: Marenzeller (1893); Clark (1907: 119–120, as *Chiridota lævis*).

Distribution: known only from the Azores.

Depth: AZO: 2,870 m.

Habitat: soft substrates (clay mud).

Remarks: Marenzeller (1892, 1893) described *Chiridota abyssicola* based on a single specimen collected by RV ‘Hirondelle’ within the archipelago waters (sta 248:

N41°40’41” W26°44’9”, 2,870 m). This species is known only from the type specimen. In a review of apodous holothurians, Clark (1907) united under the name *C. laevis* several species described from both the Atlantic and Pacific, turning a species previously known only to the Antarctic shallow waters to one of the most widely distributed species of the genus *Chiridota*, both in terms of geographic and bathymetric range. Notwithstanding, the same author believed that among the shallow and deep-water forms there was more than one species. However, the variability of the diagnostic characters was such (often depending on the age and size of the animal) that Clark was unable to clearly define each of the species. The decision of making *C. abyssicola* conspecific with *C. laevis* did not reunite consensus as the latter was viewed as a cold shallow-water species (*e.g.,* Mortensen 1927a; Deichmann 1930; Heding 1935). Regardless, whether *C. abyssicola* should be merged with the highly variable *C. laevis* will depend on future work. For now, we have chosen to retain the historical species, restricted to the Azorean deep waters.

Family Synaptidae Burmeister, 1837

Genus *Leptosynapta* Verrill, 1867

***Leptosynapta inhaerens* (Müller, 1776)**

$^{\$}$2009. *Leptosynapta inhaerens* (O.F. Müller, 1776); Wirtz: 48, fig. 1e.

Type locality: Norway.

See: Tortonese (1965: 104–105, fig. 45); Pérez-Ruzafa *et al.* (1992a: 178); Picton (1993: 82–83).

Distribution: Mediterranean Sea and Northeast Atlantic; from Scandinavian arctic waters south to Portugal, including the Azores and Canaries.

Depth: 0–173 m, mostly between the first few meters and 50 m deep; also found in tide-pools (AZO).

Habitat: soft sediments buried in muddy sand or gravel, and amongst *Zostera* and *Caulerpa* and in sandy tide pools.

Type of Development: Planktotrophic, hermaphroditic.

Remarks: recently, Wirtz (2009) discovered small specimens belonging to *Leptosynapta inhaerens* in tide-pools in Faial Island, turning the archipelago to the westernmost limit for this species.

Order Dendrochirotida Grube, 1840

Family Cucumariidae Ludwig, 1894

Genus *Abyssocucumis* Heding, 1942

Abyssocucumis abyssorum (Théel, 1886a)

$^{\$}$1892. *Cucumaria abyssorum* Théel; Marenzeller: 64.

$^{\$}$1893. *Cucumaria abyssorum*, Théel; Marenzeller: 14.

1894. *Cucumaria abyssorum* Théel; Ludwig: 122-127, pl. 9, figs. 28, 29, pl. 13, figs. 1–5.

1902. *Cucumaria abyssorum*, Théel; Perrier: 275.

1927a. *Cucumaria abyssorum* Théel; Mortensen: 396.

1930. *Cucumaria abyssorum* Théel; Deichmann: 139.

1932. *Cucumaria abyssorum* Théel; Grieg: 11, fig. 9.

$^{\$}$1941. *Cucumaria abyssorum* Théel; Cherbonnier: 93–103, figs. 1, 3.

2005. *Abyssocucumis abyssorum* (Théel, 1886); García-Diez *et al*.: 51.

Type locality: off Crozet Island (S46°16’ E48°27’).

See: Théel (1886a: 66–67 pl. 4, fig. 6, pl. 16, fig. 6); Heding (1942: 33–35, figs. 34–36); Gage *et al.* (1985: 191); Massin & Hendrickx (2011: 418).

Distribution: cosmopolitan, known from all oceans except in the Arctic; in the Atlantic from the Davis Strait eastwards from south of Iceland and the Rockall Trough to the Azores.

Depth: 869–4,810 m (AZO: 2,870 m).

Habitat: soft substrates (muddy sand to ooze).

Remarks: the presence of this species in Azores is based on a single dredge by ‘Hirondelle’ (sta 248: N41°40’41” W26°44’9”) (Marenzeller 1892, 1893). Though this abyssal holothurian was never re-collected again in the archipelago, more recently *A. abyssorum* was repeatedly retrieved from the Mid-Atlantic Ridge just north of the Azorean waters (Gebruk 2008; Rogacheva *et al*. 2013).

Genus *Pawsonia* Rowe, 1970

Pawsonia saxicola? (Brady & Robertson, 1871)

$^{\$}$1892. *Cucumaria Montagui* Flem.; Marenzeller: 65.

$^{\$}$1893. *Cucumaria Montagui*, Fleming; Marenzeller: 15–17.

1902. *Cucumaria Montagui*, Flemming; Perrier: 275.

1921b. *Cucumaria montagui* Fleming; Koehler: 150–152, fig. 101.

1927a. *Cucumaria saxicola* Brady and Robertson; Mortensen: 401–402, fig. 240.

1965. *Cucumaria saxicola* Br. Rob.; Tortonese: 75–76.

1992a. *Pawsonia saxicola* (Brady et Robertson, 1871); Pérez-Ruzafa *et al*.: 167.

1997. *Pawsonia saxicola* (Brady & Robertson, 1871); Pereira: 333.

2005. *Pawsonia saxicola* (Brady & Robertson, 1871); García-Diez *et al*.: 51.

2010. *Pawsonia saxicola* (Brady & Robertson, 1871); Micael & Costa: 323.

2012. *Pawsonia saxicola* (Brady & Robertson, 1871); Micael *et al*.: 4.

Type locality: Ireland.

See: Brady & Robertson (1871: 690-691, pl. 71, figs. 1–4, as *Cucumaria saxicola*); McKenzie (1991: 156–157, figs. 8e–i).

Distribution: Mediterranean Sea and Northeast Atlantic, from the British Islands to the Iberian coast, including the ?Azores.

Depth: 0–50 m (?AZO: ?130 m).

Habitat: muddy sand to rocky bottoms, in rock crevices, under stones or among algae.

Type of Development: lecithotrophic.

Remarks: during the late 19 and early 20th centuries, a serious debate took place to decide if *Cucumaria montagui* was a valid species or a junior synonym of *Pawsonia saxicola* or *Aslia lefevrei* (*e.g.,* Marenzeller 1893; Norman 1905; Orton 1914). *Cucumaria montagui* was reported from the Azores by Marenzeller (1892, 1893) based on the material collected by RV 'Hirondelle' on a station located in the channel between Pico and Faial islands, at a depth of 130 m. Marenzeller proved later to be incorrect on the use of the name 'montagui' for this cucumarid, and the report from the Azores was accepted under the synonymy of *P. saxicola* in later works. In his review, McKenzie (1991) considered that the depth of the Azorean record was far too deep for this shallow-water species and suggested that it could be a result of a misidentification. However, it is hard to believe that Marenzeller, who was very familiar with the forms we now know as *P. saxicola,* could have misidentified the species. Among the fauna collected by RV 'Hirondelle' at this station, we find a collection of animals belonging to the shallow-water realm are also listed, such as *Thyone inermis* (see below), a species with a depth range very similar to *P. saxicola*. This suggests that the depth at which these holothurians were collected could have been much shallower than the reported 130 m. Regardless, this species was never recollected in the archipelago and thus the inclusion of *P. saxicola* in the Azorean fauna should be considered with caution.

Family Phyllophoridae Östergren, 1907

Genus *Thyone* Jaeger, 1833

***Thyone inermis*? Heller, 1868**

$^{\$}$1892. *Thyone inermis* Heller; Marenzeller: 66.

$^{\$}$1893. *Thyone inermis*, Heller; Marenzeller: 17.

?$^{\$}$1902. *Thyone inermis*, Heller; Hérouard: 45.

1902. *Thyone inermis*, Heller; Perrier: 276.

1927a. *Thyone inermis* Heller; Mortensen: 408, fig. 246.

1938. *Thyone inermis* Heller; Nobre: 142.

1954. *Thyone inermis* Heller; Deichmann: 397.

1965. *Havelockia inermis* (Heller); Tortonese: 90–91, fig. 37B.

1984. *Thyone inermis* Heller, 1868; Miller & Pawson: 40–41, figs. 32, 33.

1997. *Thyone inermis* Heller, 1868; Pereira: 333.

2004. *Thyone inermis* Heller, 1868; Bohn: 518.

2005. *Thyone inermis* Heller, 1868; García-Diez *et al*.: 51.

2010. *Havelockia inermis* (Heller, 1868); Micael & Costa: 323.

2012. *Havelockia inermis* (Heller, 1868); Micael *et al*.: 4.

Type locality: Adriatic Sea, Mediterranean Sea.

See: Koehler (1921b: 167, fig. 167); McKenzie (1991: 141–146); Bohn (2004); Pawson *et al.* (2010: 28).

Distribution: Northeast Atlantic and Mediterranean Sea, reported from the English Channel south to Portugal and the ?Azores.

Depth: mostly above 30 m (?AZO: ?130–?1,385 m).

Habitat: lives buried in muddy to sandy habitats (infaunal).

Remarks: the shallow-water cucumarid *Thyone inermis* was recorded in the archipelago by Marenzeller (1892, 1893) and Hérouard (1902) at unusual depths, both well below the maximum depth accepted for this species. The first author identified this species among the material collected by RV 'Hirondelle' (sta 226) between Pico and Faial islands, at a depth of 130 m. However, it is possible that material was collected at shallower depths than what was reported (see remarks under *Pawsonia saxicola*). In the second report, Hérouard recorded *T. inermis* at two stations sampled by RV 'Princesse Alice' in the Azorean waters (sta 553: N37°42'40" W25°05'15"; sta 575: N38°27'00" W26°30'15") between 1,165–1,385 m. The depth values alone seem to suggest that the material was neither *T. inermis* nor a species of *Thyone*, a shallow-water genus (Pawson & Miller 1981).

The taxonomy of the *Thyone* as in other dendrochirote holothurians is rather intricate (with a resulting problematic synonymy) particularly in the case of the European species, which are still awaiting an extensive revision (McKenzie 1991). Most of the characters used to separate species show a great degree of overlap, frequently forcing the identifications to be based on a sum of characteristics rather than on a single character. Moreover, dendrochirote holothurians are also characterized by species showing a large degree of morphological plasticity resulting from ontogenetic, environmental and genetic variability, coupled with the occasional drastic effects of fixation (*e.g.,* partial to total dissolution of ossicles) (Pawson & Miller 1981; McKenzie 1991) making the identification rather difficult and in some cases impossible. The inclusion of this species in the Azorean extant fauna should be considered under caution, until new material belonging to *T. inermis* is taken in the area that could corroborate the historical records.

Order Elasipodida Théel, 1882
Family Elpidiidae Théel, 1882
Genus *Amperima* Pawson, 1965

Amperima furcata (Hérouard, 1899)

$1899. *Kolga furcata*, n. sp.; Hérouard: 171, fig. 2.
$1902. *Kolga furcata* Hérouard; Hérouard: 40–41, pl. 3, fig. 7, pl. 6, figs. 4–10, pl. 8, fig. 17.
1902. *Periamma* [*Kolga*] *furcatum*, Hérouard; Perrier: 276.
1923. *Periamma furcata*, Herouard; Hérouard: 91.
1927a. *Periamma furcata* (Hér.); Mortensen: 368.
1930. *Periamma furcatum (Kolga)* Herouard, 1899; Deichmann: 134.
$1975. *Amperima furcata* (Hérouard, 1899); Hansen: 159, fig. 75.
2005. *Amperima furcata* (Hérouard, 1899); García-Diez *et al*.: 51.
$2008. *Amperima furcata* (Hérouard, 1899); Gebruk: 50, 51.
2013. *Amperima furcata* (Hérouard, 1899); Rogacheva *et al*.: 600–601, figs. 7A, E, 17K, 18M, N, 19C.

Type locality: Mid-Atlantic Ridge, Azores (N39°11’00” W30°44’40”).

See: Hérouard (1902); Rogacheva *et al.* (2012: 217; 2013: 600–601, figs. 7A E, 17K, 18M, N, 19C).

Distribution: Atlantic and Pacific deep-waters; in the Mid-Atlantic Ridge, from the Charles-Gibbs Fracture Zone south to the Azores and east to the Bay of Biscay.

Depth: 1,846–4,700 m (AZO: 1,846–2,968 m).

Habitat: frequent swimmer (benthopelagic); on muddy sand.

Remarks: *Amperima furcata* was initially described by Hérouard (1899, 1902, as *Kolga furcata*) based on specimens collected by RV 'Princesse Alice' in the Azores. The type material was later reviewed by Hansen (1975) who transferred this species to the genus *Amperima* Pawson 1965. More recently, Gebruk *et al*. (2008) identified new material collected by RV 'G.O. Sars' ('MAR–ECO' Cruise) in northern-most Azorean waters (sta 40/367: N42°55' W30°20', 2,954–2,968 m), thus confirming the historical record.

Rogacheva *et al*. (2012) observed this deposit feeder swimming above the sea floor for the first time. According to these authors, though spending most of its time feeding on sedimentary plains this species is a frequent swimmer, a possible adaptation to the patchy nature of its habitat. The ability to swim together with its known abyssal depth range may explain the rarity of records in the archipelago throughout its range.

Genus *Ellipinion* Hérouard, 1923

Ellipinion delagei (Hérouard, 1896)

$^{\$}$1896. *Scotoplanes Delagei*, n. sp.; Hérouard: 167–168, fig. 3.

$^{\$}$1902. *Scotoplanes Delagei* (Hérouard); Hérouard: 39–40, pl. 6, figs. 1–3, pl. 8, figs. 8–9.

1902. *Scotoplanes Delagei* Hérouard; Perrier: 276.

$^{\$}$1923. *Ellipinion* (*Scotoplanes*) *Delagei*, Herouard; Hérouard: 90–91.

1927a. *Ellipinion Delagei* (Hérouard); Mortensen: 368, figs. 218.4–5.

1930. *Ellipinion delagei* Hérouard; Deichmann: 133.

$^{\$}$1975. *Ellipinion delagei* (Hérouard, 1896); Hansen: 163.

1988. *Ellipinion delagei* (Hérouard, 1896); Harvey *et al*.: 185–186.

2005. *Ellipinion delagei* (Hérouard, 1896); García-Diez *et al*.: 51.

Type locality: Azores (N37°42'40" W25°05'15").

See: Hérouard (1902); Pawson (1982: 136, fig. 2c); Rogacheva *et al.* (2012: 217; 2013: 601, figs. 7F–N, 19K).

Distribution: North Atlantic, from the Mid-Atlantic Ridge (Charlie-Gibbs Fracture Zone) to the Azores, east to the Rockall Trough, south to Cabo Verde and west to the Bahamas.

Depth: 1,165–2,750 m (AZO: 1,165–1,494 m).

Habitat: frequent swimmer (benthopelagic); on soft substrates.

Remarks: *Ellipinion delagei* was first described by Hérouard (1896, 1902; as *Scotoplanes delagei*) based on material collected by RV 'Princesse Alice' in the Azores. Later, Hérouard (1923) identified further material belonging to *E. delagei* collected by RV 'Hirondelle' in Azorean waters (sta 3293: N38°47' W30°16', 1,331 m). Hansen (1975) re-analysed the type material in a review of the deep-water holothurians. Aside from the specimens collected by the historical cruises, no further individuals are known from the Azores Archipelago. Rogacheva *et al*. (2012), the first to observe this deposit feeder swimming above the sea floor, classified this species as a frequent swimmer, spending most of its time feeding on the sea floor (see above remarks under *Amperima furcata*).

Genus *Peniagone* Théel, 1882

Peniagone azorica Marenzeller, 1892

$^{\$}$1892. *Peniagone azorica*, nov. sp.; Marenzeller: 64.

$^{\$}$1893. *Peniagone azorica*, nov. sp.; Marenzeller: 12–13, pl. 1, fig. 4, pl. 2, fig. 5.

$^{\$}$1902. *Peniagone azorica*, Marenzeller; Hérouard: 42–43, pl. 6, figs. 21–26.

1902. *Peniagone azorica*, Marenzeller; Perrier: 275.

1923. *Peniagone azorica*, Marenzeller; Hérouard: 87–88.

1927a. *Peniagone azorica* v. Marenzeller; Mortensen: 369.

1930. *Peniagone azorica* v. Marenzeller, 1893; Deichmann: 137.

1932. *Peniagone azorica* v. Marenzeller; Grieg: 8, fig. 4.

$^{\$}$1956. *Peniagone azorica* V. Mar.; Hansen: 44.

$^{\$}$1975. *Peniagone azorica* von Marenzeller, 1893; Hansen: 138–142, fig. 63, pl. 10, figs. 1–3.

?$^{\$}$1992. *Peniagone azorica*?; Pérès: 254.

2005. *Peniagone azorica* Marenzeller, 1893; García-Diez *et al*.: 51.

Type locality: Azores (N41°40'41" W26°44'09").

See: Marenzeller (1893); Hansen (1975); Tyler *et al.* (1985b); Rogacheva *et al.* (2012: 218; 2013: 603–605, figs. 9, 12H,I, 17J, 19D).

Distribution: North Atlantic, from Iceland south to the Bay of Biscay and along the Mid-Atlantic Ridge to the Azores.

Depth: 1,385–4,020 m (AZO).

Habitat: frequent swimmer (benthopelagic); on soft sediments, sand, mud, clay to ooze.

Type of Development: lecithotrophic.

Remarks: *Peniagone azorica* was first described by Marenzeller (1892, 1893) based on material collected in Azores by RV 'Hirondelle'. Hérouard (1902) also identified this species based on material collected in the Azores by RV 'Princesse Alice' (sta 527: N38°09' W23°15'45", 4,020 m). In a review of the deep-water holothurioids, Hansen (1956, 1975) re-examined the material collected by RV 'Princesse Alice' and discover further unreported specimens collected by the same cruise in the Azores. In spite of the Azores being the type locality, no other material belonging to *P*. *azorica* is known from the Azorean deep waters. Rogacheva *et al*. (2012) classified *P. azorica* as a frequent swimmer, thought spending most of its time feeding on the sea floor.

Peniagone diaphana (Théel, 1882)

$^{\$}$1899. *Scotoanassa translucida*, n. sp.; Hérouard: 171–172, fig. 3.

$^{\$}$1902. *Scotoanassa translucida*, Hérouard; Hérouard: 43–45, pl. 3, figs. 4–6, pl. 6, figs. 17–20.

1902. *Scotoanassa translucida*, Hérouard; Perrier: 276.

1927a. *Scotoanassa translucida* Hérouard; Mortensen: 368, figs. 217.2, 218.2–3.

Type locality: Great Australian Bight, Pacific (S42°42' E134°10').

See: Théel (1882: 55–56, pl. 9, figs. 3–5, pl. 35, fig. 18, pl. 44, fig. 9, as *Scotoanassa diaphana*); Hansen (1975: 153–155, fig. 71, pl. 10, figs. 7–8); Gage *et al.* (1985: 200); Tyler *et al.* (1985a); Gebruk *et al.* (1997: 155–156, figs. 1A–D); Bohn (2006: 23).

Distribution: cosmopolitan, in the Atlantic, Pacific and Antarctic Oceans; recorded from several isolated localities throughout the Atlantic, including the Charlie-Gibbs Fracture Zone (Mid-Atlantic Ridge), Rockall Trough, Porcupine Abyssal Plain, Bay of Biscay, Gulf of Guinea, Angola Basin and the Azores.

Depth: 1,520–5,600 m (AZO: 5,005 m).

Habitat: benthopelagic (preferential swimmer); on soft sediments (mud).

Type of Development: lecithotrophic.

Remarks: Hérouard (1899, 1902) described a new species, *Scotoanassa translucida*, based on specimens collected by RV 'Princesse Alice' between the Azores and the European continent, at a station located in the easternmost waters of the archipelago (sta 749: N39°54'00" W21°06'45", 5,005 m). Later, Hansen (1975) established the synonymy of Hérouard's species with the Pacific *P*. *diaphana* (Théel, 1882). This species is a benthopelagic animal that spends a considerable amount of time in the water column (Miller & Pawson 1990). Gebruk *et al*. (1997) described juveniles taken about 10 to 200 m above the seabed, at a depth from 4,031 to 4,565 m. The great difficulty of sampling benthopelagic holothurians at great depths could be the reason for its somewhat sparse distribution in the Atlantic, particularly in the Azores, where only a single tow from about 5,000 m depth delivered specimens of *P. diaphana*.

Peniagone longipapillata **Gebruk, 2008**

$^{\$}$2008. *Peniagone longipapillata* sp. nov.; Gebruk: 56–58, figs. 1B, 9–10.

2014. *Peniagone longipapillata* Gebruk, 2008; Gebruk *et al.*: 162.

Type locality: Mid-Atlantic Ridge, north of the Azores waters (N43°01’ W28°33’).

See: Gebruk (2008); Rogacheva *et al.* (2012: 218; 2013: 606–608, figs. 12K–M, 17O, 18F, G, P).

Distribution: Northeast Atlantic, on the Mid-Atlantic Ridge from the Charlie-Gibbs Fracture Zone to the north of the Azores and eastwards to the Whittard Canyon and Porcupine Seabight.

Depth: 2,272–3,500 m (AZO: 2,954–3,050 m).

Habitat: frequent swimmer (benthopelagic).

Remarks: Gebruk (2008) recently reported specimens belonging to *Peniagone longipapillata* among the material taken in northern Azorean waters (RV ‘G.O. Sars’, ‘MAR–ECO’, sta 40/367: N42°55’ W30°20’; 2,954–2,968 m; sta 46/372: N42°46’ W29°16’, 3,005–3,050 m). This holothurian was observed swimming for the first time by Rogacheva *et al*. (2012) and classified by these authors as a frequent swimmer, though spending most of its time feeding on the sea floor.

Peniagone marecoi **Gebruk, 2008**

$^{\$}$2008. *Peniagone marecoi* sp. nov.; Gebruk: 54–56, figs. 7–8.

2014. *Peniagone marecoi* Gebruk, 2008; Gebruk *et al.*: 162.

Type locality: Mid-Atlantic Ridge, Azores (N42°46’ W29°16’).

See: Gebruk (2008).

Distribution: known only from the Mid-Atlantic Ridge, from the Charlie-Gibbs Fracture Zone to the north of the Azores.

Depth: 1,702–3,505 m (AZO: 2,063–3,050 m).

Habitat: a probable benthopelagic species.

Remarks: Gebruk (2008) described a new species, *Peniagone marecoi*, based on material collected in the Mid-Atlantic Ridge, in the northern waters of the Azores EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 46/372: N42°46' W29°16', 3,005–3,050 m).

Genus *Penilpidia* Gebruk, 1988

Penilpidia midatlantica Gebruk, 2008

$^{\$}$2008. *Penilpidia midatlantica* sp. nov.; Gebruk: 52–54, figs. 4–6.

2013. *Penilpidia midatlantica* Gebruk, 2008; Rogacheva *et al.*: 610–611.

Type locality: Mid-Atlantic Ridge, Azores (N42°48' W29°38').

See: Gebruk (2008); Rogacheva *et al.* (2012: 219).

Distribution: known only from the Mid-Atlantic Ridge, from SE of the Charlie-Gibbs Fracture Zone south to the Azores.

Depth: 2,063–2,750 m (AZO: 2,063–2,107 m).

Habitat: a probable benthopelagic species.

Remarks: Gebruk (2008) described a new species *Penilpidia midatlantica* based on material collected in the Mid-Atlantic Ridge, in the northern waters of the Azores EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 42/368: N42°48' W29°38', 2,063–2,107 m). Additionally, on reviewing the genus *Penilpidia* with a redescription of its type species *P. ludwigi* (Marenzeller, 1893), Gebruk *et al.* (2013) recently concluded that due to differences in ossicles composition and morphology, *P. midatlantica* should be assigned to a new genus.

Family Laetmogonidae Ekman, 1926

Genus *Benthogone* Koehler, 1895c

Benthogone rosea Koehler, 1896c

$^{\$}$1923. *Benthogone rosea*, Kœhler; Hérouard: 38–39.

1927a. *Benthogone rosea* Koehler; Mortensen: 363–364, figs. 215–216.

1932. *Benthogone rosea* Koehler; Grieg: 5–6.

1938*. Benthogone rosea* Kœhler; Nobre: 162–163.

2005. *Benthogone rosea* Koehler, 1896; García-Diez *et al.*: 51.

Type locality: Bay of Biscay.

See: Koehler (1896c: 114–117, figs. 2, 3, 36, 37); Cherbonnier (1970); Hansen (1975: 48–49, fig. 15); Bisoll *et al.* (1984); Gage *et al.* (1985: 198); Tyler *et al.* (1985c).

Distribution: cosmopolitan; in the Atlantic from Ireland south to Cabo Verde, including the Azores, Madeira and Canaries; recorded elsewhere off Kenya and north of New Zealand.

Depth: 450–2,480 m, common at about 2,000 m (AZO: 1,900 m).

Habitat: epibenthic deposit-feeder on muddy sand to *Globigerina* ooze substrates.

Type of Development: direct development.

Remarks: Hérouard (1923) identified the only known specimen from the Azores, collected by RV 'Princesse Alice' (sta 1334: N39°30' W29°02'15", 1,900 m).

Genus *Laetmogone* Théel, 1879

Laetmogone violacea Théel, 1879

?$^{\$}$1902. *Lætmogone Wyville-Thomsoni*, (Théel); Hérouard: 31–32, pl. 4, figs. 10–16.
$^{\$}$1902. *Lætmogone violacea,* Théel; Perrier: 390–398, pl. 19, figs. 1–7.
1927a. *Lætmogone violacea* Théel; Mortensen: 361–363, figs. 213, 214.
1930. *Laetmogone violacea* Théel; Deichmann: 120–121.
1932. *Laetmogone violacea*Théel; Grieg: 5.
$^{\$}$1975. *Laetmogone violacea* Théel, 1879; Hansen: 58–61, figs. 21–22, pl. 8, fig. 8, pl. 9, figs. 9–10.
1992a. *Laetmogone violacea* Théel, 1879; Pérez-Ruzafa *et al.*: 171.
2005. *Laetmogone violacea* Théel, 1879; García-Diez *et al.*: 52.

Type locality: South Pacific Ocean.

See: Perrier (1902); Hansen (1975); Tyler *et al.* (1985a,c).

Distribution: cosmopolitan, present in the Atlantic, Pacific and Indian Oceans; from Greenland and Iceland south to Cabo Verde, including the archipelagos of the Azores.

Depth: 225–1,804 m (AZO: 1,442–?1,550 m).

Habitat: epibenthic deposit-feeder on soft sediments, muddy sand to mud.

Type of Development: lecithotrophic.

Remarks: Perrier (1902) identified *L. violacea* among the material collected by RV 'Talisman' in the NE Atlantic, including specimens from the Azores (sta 121, 1883: N37°35' W29°25'46", 1,442 m). During the same year, Hérouard (1902) described another species of the same genus from Azorean waters, the Antarctic *Laetmogone wyvillethomsoni* (RV 'Princesse Alice', sta 683: N38°20' W28°04'45", 1,550 m). Historically, *L. violacea* has been confused with *L. wyvillethomsoni*. Hansen (1975) considered that *L. wyvillethomsoni* was restricted to the Southern Ocean and

Antarctica waters and all historical reports from the Atlantic (*e.g.,* Koehler 1896c; Grieg 1932) would prove to be misidentifications with closely similar species such as *L. violacea*. However, when Hansen re-examined the material assigned to *L. wyvillethomsoni* dredged by RV 'Princesse Alice' in the Azores, the author believed that it belonged to a new species. Unfortunately, the poor preservation and the small number of specimens that constituted RV 'Princesse Alice's material did not allow Hansen to further provide a clear identification. No other specimens sharing the characteristics of RV 'Princesse Alice' material were reported again and the matter is still unresolved. Nevertheless, some authors like García-Diez *et al*. (2005) have placed the record of *L. wyvillethomsoni* by Hérouard in the synonymy of *L. violacea*.

Family Psychropotidae Théel, 1882

Genus *Benthodytes* Théel, 1882

Benthodytes gosarsi **Gebruk, 2008**

$2008. *Benthodytes gosarsi* sp. nov.; Gebruk: 49–52, figs. 1A, 2–3.

2013. *Benthodytes gosarsi* Gebruk, 2008; Rogacheva *et al*.: 598–599, fig. 17E.

2014. *Benthodytes gosarsi* Gebruk, 2008; Gebruk *et al*.: 160.

Type locality: Mid Atlantic Ridge, Azores (N42°55' W30°20').

See: Gebruk (2008); Rogacheva *et al.* (2012: 217, figs. J–L; 2013: 598–599, fig. 17E).

Distribution: North Atlantic, Mid-Atlantic Ridge from Iceland south to the Azores.

Depth: 2,238–3,680 m (AZO: 2,954–2,968 m).

Habitat: occasional swimmers (benthopelagic); on soft substrates.

Remarks: Gebruk (2008) described *Benthodytes gosarsi*, based on specimens collected by 'G.O. Sars' ('MAR–ECO' expedition) in the northern-most waters of the Azorean EEZ. More recently, Rogacheva *et al*. (2012) observed *in vivo* animals belonging to this species swimming above the sea-floor in the area of the Charles-Gibbs Fracture Zone, north of the Azores. These authors inferred that *B*. *gosardi* is deposit-feeder that rarely swims and does so usually as a response to local disturbances or to travel to a different location on the sea floor.

Benthodytes janthina **Marenzeller, 1892**

$1892. *Benthodytes janthina* n. sp.; Marenzeller: 66.

$1893. *Benthodytes janthina*, nov. sp.; Marenzeller: 10–11, pl. 1, fig. 3, pl. 2, fig. 4.

1902. *Benthodytes janthina*, Marenzeller; Perrier: 275.

1927a. *Benthodytes janthina* v. Marenz.; Mortensen: 373.

2005. *Benthodytes janthina* Marenzeller, 1893; García-Diez *et al*.: 52.

Type locality: North of the Azores (N41°40'41" W26°44'09").

See: Marenzeller (1893).

Distribution: known only from the type specimen collected in the northern waters of the Azores.

Depth: 2,870 m (AZO).

Habitat: soft bottoms (clayish sand).

Remarks: Marenzeller (1892, 1893) erected a new species, *Benthodytes janthina*, based on a single specimen collected by RV 'Hirondelle', roughly 160 miles north of Terceira Island. The specimen lacked complete information on important diagnostic characters, such as the ossicles that were broken and partially dissolved. Nevertheless, *B. janthina* was later recorded from several localities in the NE Atlantic, from Greenland (Heding 1942) to Cabo Verde (Hérouard 1923). Hérouard (1902) attempted to complete Marenzeller's initial description based on individuals collected by RV 'Princesse Alice', which included material dredge within Azorean waters (sta 673: N37°51'00" W26°53'45", 2,252 m). Hansen (1975) reviewed these reports and concluded that they resulted from confusion with other *Benthodytes* species, such as *B. typica*. As a result, *B*. *janthina* was again reduced to the type specimen. Furthermore, Hansen (1975) commented that due to the poor preservation state of the holotype it was not possible to review the species' status and its affinities. On studying deep sea material from the Porcupine Abyssal Plain (SW Ireland), Billett (1988) believed that both *B*. *janthina* and *B*. *lingua* Perrier, 1896b were junior synonyms of the Indo-Pacific *B*. *sordida* Théel, 1882, dismissing many of the diagnostic characters as individual variation or a result of the preservation process (*e.g.,* shrinkage and retraction, loss of colour, absence of ossicles). Recently, Rogacheva *et al*. (2009) considered *B*. *sordida* to be conspecific with Indo-Pacific *B. abyssicola* Théel, 1882, and dismissed the Atlantic records as misidentifications. The matter whether Azorean *B. janthina* is conspecific with other Atlantic *Benthodytes* species (*B. lingua*?) or indeed *B. abyssicola*, is still pending on future revisions of the genus.

Benthodytes lingua **Perrier, 1896b**

$^{\$}$1902. *Pannychia glutinosa*, nov. sp.; Hérouard: 32, pl. 4, fig. 17.

1902. *Pannychia glutinosa*, Hérouard; Perrier: 286, 373.

1927a. *Pannychia glutinosa* Hérouard; Mortensen: 360.

1930. *Benthodytes lingua* Perrier; Deichmann: 124–125.

1975. *Benthodytes lingua* R. Perrier, 1896; Hansen: 80–82, fig. 29, pl. 9, figs. 3–5, pl. 12, figs. 2–3.

1992a. *Benthodytes lingua* Perrier, 1896; Pérez-Ruzafa *et al*.: 172, fig. 1H.

2005. *Pannychia glutinosa* Hérouard, 1902; García-Diez *et al*.: 52.

$^{\$}$2008. *Benthodytes lingua* R. Perrier, 1896; Gebruk: 51.

Type locality: off Morocco (N30°08'00" W11°40'46").

See: Perrier (1896b: 302; 1902: 456–461, pl. 12, figs. 1–2, pl. 21, figs. 1–9); Deichmann (1930); Hansen (1975); Rogacheva *et al.* (2012: 217; 2013: 599, fig. 18B).

Distribution: Atlantic; in the west from off the coast of New England to the Gulf of Mexico, eastwards from Greenland and along the Mid-Atlantic Ridge in the Charlie-Gibbs Fracture Zone, and from the Rockall Trough to South Africa, including the Azores and Canaries.

Depth: 860–4,700 m (AZO: 2,102–3,050 m).

Habitat: benthopelagic; soft sediments, fine sand, clay, mud to ooze.

Remarks: Hérouard (1902) described a new species, *Pannychia glutinosa*, based on a specimen of about 60 mm, collected by RV 'Princesse Alice' in the Azores (sta 624: N38°59'00" W28°18'05", 2,102 m). Later, Deichmann (1930) assumed that Hérouard' specimen was a juvenile of *B*. *lingua* and synonymised the two species, an opinion shared by later authors.

Recently, Gebruk *et al*. (2008) identified animals belonging to *B*. *lingua* in waters north of the islands (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m; sta 46/372: N42°46' W29°16', 3,005–3,050 m) substantiating the presence of this species in the archipelago.

Benthodytes sanguinolenta **Théel, 1882**

$^{\$}$2008. *Benthodytes sanguinolenta* Théel, 1882; Gebruk: 51.

Type locality: off the coast of Chile, Pacific.

See: Hansen (1975: 94–96, pl. 3, figs. 1–4, pl. 4, figs. 1–4, pl. 5, figs. 1–4, pl. 6, figs. 1–4, pl. 9, figs. 6–7, pl. 12, figs. 4–5); Miller & Pawson (1990: 4, 15); Rogacheva *et al.* (2013: 599).

Distribution: cosmopolitan, Atlantic and Indo-Pacific; reported in the Puerto Rico Trench, off the Bahamas and in the Charlie-Gibbs Fracture Zone to north of the Azores.

Depth: 768–7,250 m, mostly below 2,000 m (AZO: 2,954–2,968 m).

Habitat: facultative swimmer; on sandy clay to *Globigerina* ooze.

Remarks: Gebruk (2008) recently identified *Benthodytes sanguinolenta* among the material collected at the northern border of the Azorean EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m). During the EMEPC (2009), ROV Luso has captured footage of a *Benthodytes* holothurian, likely to belong to *B. sanguinolenta* near the Hirondelle Seamount (sta L09D21: N37°56'11" W26°10'32", 3,236 m; Fig. 5.33).

Figure 5.33. An elasipodid in the Azorean deep waters, most probably belonging *Benthodytes sanguinolenta* Théel, 1882 (EMEPC-LUSO N37°56'11" W26°10'32", 2009.10.08, 3,236 m).

Benthodytes typica Théel, 1882

?$^{\$}$1892. *Benthodytes typica* Théel; Marenzeller: 66.

?$^{\$}$1893. *Benthodytes*? *typica*, Théel; Marenzeller: 12.

1900. *Benthodytes glutinosa*; Perrier: 119.

$^{\$}$1902. *Benthodytes janthina*, Marenzeller; Hérouard: 30.

1902. *Benthodytes typica*, Théel; Perrier: 274, 456.

1927a. *Benthodytes glutinosa* Perrier; Mortensen: 374.

1927a. *Benthodytes typica* Théel; Mortensen: 273, fig. 221.

1930. *Benthodytes typica* Theel; Deichmann: 123–124.

1932. *Benthodytes typica* Théel; Grieg: 10, fig. 8, pl. 3, figs. 6–7.

1932. *Benthodytes glutinosa* R. Perrier; Grieg: 10–11, pl. 3, figs. 1–2.

1938. *Benthodytes typica* Théel; Nobre: 170.

$^{\$}$1972. *Benthodytes typica* Theel, 1882; Sibuet: 123.

$^{\$}$1975. *Benthodytes typica* Théel, 1882; Hansen: 89–93, fig. 36, pl. 1, figs. 1–4, pl. 2, figs. 1–4.

1992a. *Benthodytes typica* Théel, 1882; Pérez-Ruzafa *et al*.: 172–173.

2005. *Benthodytes typica* Théel, 1882; García-Diez *et al*.: 52.

$^{\$}$2008. *Benthodytes typica* Théel, 1882; Gebruk: 51.

Type locality: Gulf of Cadiz (N35°47' W8°23').

See: Théel (1882: 103–104, pl. 27, fig. 7, pl. 35, fig. 4, pl. 38, fig. 5, pl. 44, fig. 8); Hansen (1975); Bisoll *et al.* (1984); Miller & Pawson (1990: 4).

Distribution: cosmopolitan, present in the Pacific, Indian and Atlantic Oceans; from Nantucket to the Gulf of Mexico and the Caribbean; in the east from the Porcupine Abyssal Plain south to the Azores, Canaries and ?Cabo Verde .

Depth: 1,873–4,700 m, though reported at depths as shallow as 315 m (AZO: 2,063–3,300 m).

Habitat: benthopelagic (juveniles only); deposit feeder on muddy sediments.

Type of Development: produces large eggs (up to 3 mm), possibly indicative of a direct development.

Remarks: *Benthodytes typica* is a highly variable species (Hansen 1975) rarely recovered in good conditions, mostly just 'broad muscle bands and some shreds of skin' (Deichmann 1954). Marenzeller (1893) reported this species to the Azores for the first time, based on two specimens collected by RV 'Hirondelle' (sta 248: N41°40'41", W26°44'9", 2,870 m). However, the author left his identification as uncertain due to the incomplete and deteriorated state of the animals. Perrier (1900) mentioned the Azores as the type locality for *B. glutinosa* (= *B. typica*), though the material came from two RV 'Talisman' stations located in the Mid-Atlantic Ridge area, about 400 to 600 miles south of the Azores (see Perrier 1902). Hérouard (1902, 1923) reported *B. janthina* among the material dredged by RV 'Princesse Alice', which included specimens collected within Azorean waters (sta 673: N37°51'00" W26°53'45", 2,252 m). Hansen (1975) re-examined RV 'Princesse Alice' material and concluded that the specimens were quite different from *B. janthina* type material but strikingly similar to *B. typica*. Sibuet (1972) identified four animals collected by the bathyscaphe 'Archimède' at stations west and east of Santa Maria Island, between 2,500–3,300 m depths. More recently, Gebruk *et al*. (2008) identified specimens belonging to *B. typica* at several stations located in waters north of the islands substantiating the presence of this species in the archipelago.

Benthodytes valdiviae **Hansen, 1975**

$^{\$}$2008. *Benthodythes* aff. *valdiviae* Hansen, 1975; Gebruk: 50.

2014. *Benthodytes valdiviae* Hansen, 1975; Gebruk *et al.*: 159–160.

Type locality: off Western Sahara (N24°35' W17°05').

See: Hansen (1975: 82–84, figs. 30–31); Thandar (1999: 384–386, fig. 7).

Distribution: Atlantic, known from off the coast of the Western Sahara, off south-western Cape (South Africa) and north of the Azores.

Depth: 2,480–3,050 m (AZO: 3,005–3,050 m).

Remarks: the poorly known holothurian *Benthodytes valdiviae* was identified by Gebruk (2008) among the material collected in the northernmost waters of the Azorean EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 46/372: N42°46' W29°16', 3,005–3,050 m).

Genus *Psychropotes* Théel, 1882

Psychropotes depressa **(Théel, 1882)**

$^{\$}$1902. *Euphronides Talismani*, nov. sp.; Perrier: 441–444, pl. 20, fig. 15.

$^{\$}$1902. *Euphronides Talismani*, R. Perrier; Hérouard: 30–31, pl. 2, figs. 19–22.

1927a. *Euphronides Talismani* Perrier; Mortensen: 375.

1930. *Euphronides talismani* Perrier; Deichmann: 129.

$^{\$}$1975. *Psychropotes depressa* (Théel, 1882); Hansen: 106–111, figs. 43–44, pl. 7, figs. 1–3, pl. 12, fig. 8, pl. 14, figs. 1–2.

2005. *Psychropotes depressa* (Théel, 1882); García-Diez *et al*.: 52.

$^{\$}$2008. *Psychropotes depressa* (Theél, 1882); Gebruk: 50, 51.

Type locality: Gulf of Cadiz (N35°47' W8°23').

See: Hansen (1975); Tyler & Billett (1987); Rogacheva *et al.* (2012: 217; 2013: 599, figs. 17F–G).

Distribution: cosmopolitan, in the Pacific and Atlantic; from off the coast of the United States (*c.* N40°) south to the Gulf of Mexico and the Caribbean, eastwards off Iceland

and the Charlie-Gibbs Fracture Zone south along the Mid-Atlantic Ridge to the Azores and from the Rockall Trough south to the Gulf of Guinea, including the Canaries.

Depth: 957–4,060 m (AZO: 2,063–3,050 m).

Habitat: benthopelagic; soft sediments.

Type of Development: direct.

Remarks: Perrier (1896b, 1902) described a new species, *Euphronides talismani*, based on a poorly preserved specimen collected by RV 'Talisman' in Azorean waters (sta 129, 1883: N38°00'00" W27°02'46", 2,220–2,155 m). Hansen (1975) re-examined the holotype and established the synonymy with *P. depressa*. Recently, Gebruk (2008) identified specimens at several stations on the north border of the Azorean waters, further substantiating the presence of this cosmopolitan species in the archipelago. Additionally, both juveniles and adults of *P. depressa* are known to occasionally swim when disturbed or to change locations on the sea floor (Gebruk *et al.* 1997; Rogacheva *et al.* 2012).

Psychropotes longicauda Théel, 1882

$1896. *Psychropotes Grimaldii* n. sp.; Hérouard: 164, fig. 2.

1900. *Psychropates fucata* n. sp.; Perrier: 119.

$1902. *Psychropotes Grimaldii*, Hérouard; Hérouard: 25–27, pl. 3, figs. 1–2.

1902. *Psychropotes Grimaldii*, Hérouard; Perrier: 276.

1927a. *Psychropotes Grimaldii* Hérouard; Mortensen: 376.

1930. *Psychropotes grimaldi* Herouard; Deichmann: 130.

$1975. *Psychropotes longicauda* Théel, 1882; Hansen: 115–126, figs. 49–54, 118, pl. 7, figs. 4–6, pl. 12, fig. 7.

2005. *Psychropotes grimaldii* Hérouard, 1896; García-Diez *et al*.: 52.

$2008. *Psychropotes longicauda* Théel, 1882; Gebruk: 50, 51.

Type locality: Pacific (S53°55' E108°35').

See: Hansen (1975); Tyler & Billett (1987); Miller & Pawson (1990: 4).

Distribution: cosmopolitan, present in the Atlantic, Pacific, Indian and Southern Oceans; from the Rockall Trough and SE of the Charlie-Gibbs Fracture Zone south to southern Africa and Antarctic waters, including the Azores.

Depth: 2,210–5,173 m (AZO: 2,954–4,020 m).

Habitat: benthopelagic (juveniles only); on muddy sediments.

Type of Development: direct.

Remarks: *Psychropotes longicauda* is a highly variable species, a fact reflected by its high number of synonyms (Hansen 1975). Historically, two of the junior synonyms were associated with Azorean waters: *P. grimaldii* by Hérouard (1896) and *P. fucata* by Perrier (1896b). The first species was known only from the type material collected by RV 'Princesse Alice', east of São Miguel waters (sta 527: N38°09' W23°15'45", 4,020 m). Initially, Perrier (1900) listed the Azores as the type area for the second species, but in reality the material of *P. fucata* was dredged by RV 'Talisman' between the archipelago and the European continental shores (sta 135, N43°15' W21°40') (Perrier 1902). Regardless, on the re-examination of *P. grimaldii* and *P. fucata* Hansen (1975) remarked that the diagnostic characters found by both Hérouard and Perrier were mere individual differences and thus proposed their synonymy with *P. longicauda*. Recently, Gebruk (2008) identified *P. longicauda* from the northern border of the Azorean EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m), further substantiating the presence of this species in the archipelago.

Psychropotes semperiana Théel, 1882

$^{\$}$1902. *Psychropotes Kerhervei*, nov. sp.; Hérouard: 27–30, pl. 4, figs. 1–9.
1902. *Psychropotes Kerhervei*, Hérouard; Perrier: 287.
1927a. *Euphronides Kerhervei* (Hér.); Mortensen: 375.
1938. *Psychropotes Kerhervei* Hérouard; Nobre: 172.
$^{\$}$1975. *Psychropotes semperiana* Théel, 1882; Hansen: 102–105, figs. 41–42.
1992a. *Psychropotes semperiana* Théel, 1882; Pérez-Ruzafa *et al.*: 173.

Type locality: ?South Atlantic.

See: Théel (1882: 100–101, pl. 34, figs. 10–11); Hansen (1975); Tyler & Billett (1987); Gebruk *et al.* (1997: 157, figs. 2B–D); Bohn (2006: 4, 10–12, figs. 2B–E, 5).

Distribution: cosmopolitan, in Atlantic and Indian Oceans; in the Caribbean south to the Mid-Atlantic Ridge, east of Tristan da Cunha (S35°41' W20°55') and eastwards from the Porcupine Abyssal Plain south to Angola Basin (S22°27'36", E03°27'54"), including the Azores and Canaries archipelagos.

Depth: 2,695–5,610 m (AZO: 5,005 m).

Habitat: benthopelagic (juveniles); soft sediments, from sandy mud to *Globigerina* ooze.

Type of Development: direct.

Remarks: Hérouard (1902) described *Psychropotes kerhervei* based on two individuals collected by RV 'Princesse Alice' in the easternmost waters of the archipelago (sta 749: N39°54' W21°06'45", 5,005 m). Later Hérouard (1923) identified specimens belonging to this species among the material collected by RV 'Princesse Alice' at two further stations, one located near Tenerife (Canaries, sta 1757) and the other between the Azores and Portugal (sta 1306). Hansen (1975) re-examined animals belonging to *Psychropotes kerhervei*, including the material identified by Hérouard (1902, 1923), and established the synonymy with *P. semperiana*.

Order Holothuriida Miller *et al.*, 2017
Family Holothuriidae Burmeister, 1837
Genus *Holothuria* Linnaeus, 1767
Subgenus *Halodeima* Pearson, 1914

***Holothuria* (*Halodeima*) *mexicana*? Ludwig, 1875**

?$^{\$}$1902. *Holothuria mexicana*, Ludwig; Hérouard: 7–8, pl. 1, fig. 16.
1957. *Holothuria mexicana* Ludwig; Deichmann: 9–11, figs. 21–38.
1997. *Holothuria mexicana* Ludwig, 1875; Pereira: 333.
2005. *Holothuria mexicana* Ludwig, 1875; García-Diez *et al.*: 51.
2010. *Holothuria mexicana* Ludwig, 1875; Micael & Costa: 323.
2012. *Holothuria* (*Halodeima*) *mexicana* Ludwig, 1875; Micael *et al.*: 4.

Type locality: Gulf of Mexico.

See: Deichmann (1930: 74–76, pl. 5, figs. 15–20; 1954: 391–292, figs. 66.20–22; 1957); Cutress (1996: 55, 63, figs. 4E–J, 7–9); Laguarda-Figueras *et al.* (2001: 18–20, figs. 5A–D); Purcell *et al.* (2012: 68–69); Benavides-Serrato *et al.* (2012: 186–187).

Distribution: Western Atlantic, in the Gulf of Mexico and the Caribbean; possibly extending its distribution to the ?Azores.

Depth: 0–20 m (?AZO: 98 m).

Habitat: sand, coralligenous to rocky substrates, coral reefs, seagrass beds, sandy or rubble bottoms and mangrove habitats.

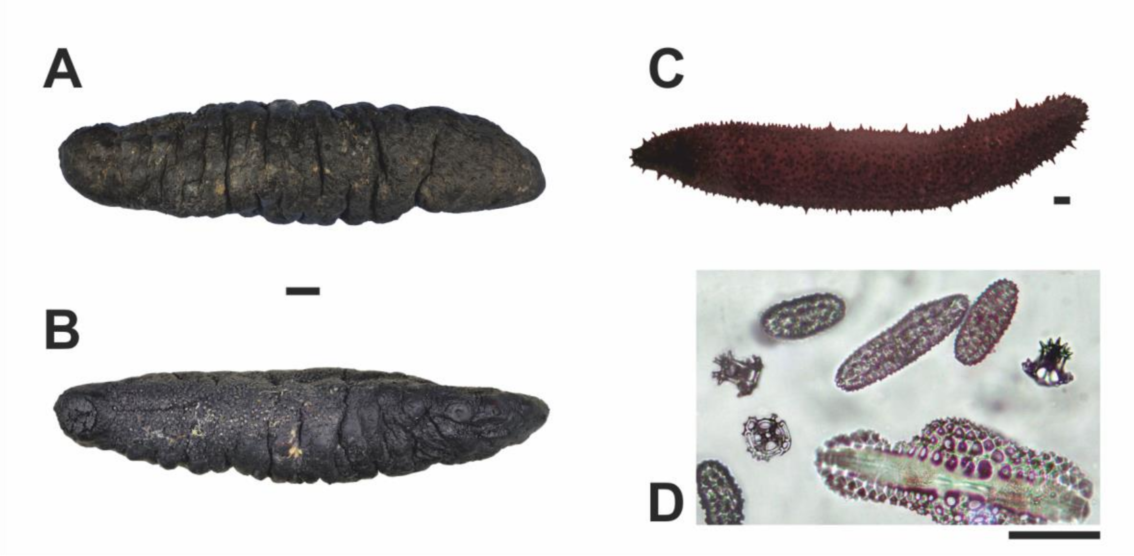


Figure 5.34. *Holothuria* (*Holothuria*) *mammata* Grube, 1840 (DBUA-ECH 397: A, B, D; DBUA-ECH 406: C). Dorsal view (A); ventral view (B); alive specimen (C); ossicles (D); scale bars are 10 mm (A–C) and 100 µm (D).

Type of Development: planktotrophic.

Commercial value: edible.

Remarks: Hérouard (1902) believed that the two specimens collected by RV 'Princesse Alice' in the Azores (sta 882: N38°3'40" W28°34'45", 98 m) belonged to the tropical shallow-water species *H. mexicana*. Deichmann (1954), however, considered that the presence of *H. mexicana* in the East Atlantic was either due to mislabelling or to a recent introduction, but 'without being really established'. We are more incline to believe that it was a result of a misidentification. Hérouard (1902) described the Azorean individuals as small and poorly preserved, with the calcareous ring partially dissolved, a particularity that could explain the absence of ossicles in the specimens, *i.e.* most probably dissolved by the used preservation medium. In the absence of diagnostic characters, the identification by Hérouard rested entirely on the colour pattern. He remarked on the small brown spots covering the dorsal side, which can be found in a number of holothurians species present in the NE Atlantic, including the Azores. In contrast, adults of *H. mexicana* typically have a black or dark brown upper side and light coloured under side, occasionally totally black or with brown spots ventrally and pale dorsally (Deichmann 1930, 1954, 1957). Cutress (1996) described a colour pattern in small juveniles belonging to this species similar to what was observed by Hérouard. However, Cutress also noted that by the time juveniles reach 20 mm, the brown flecks already started to coalesce forming irregular dark patches. Hérouard did not mention the precise size of the second specimen, but the illustration given (pl. 1, fig. 1) was of a specimen of about 70 mm TL when alive (30 mm TL after preservation). Thus, the colour pattern as presented in this specimen does not support Hérouard identification as an animal at this size should have had a more solid colour pattern closer to what is observed in a typical *H. mexicana* adult. Furthermore, *H. mexicana* is a strictly shallow-water species, with a typical reported depth of 20 m, which places the Azorean specimens outside its maximum depth range. Though, the small size of the RV 'Princesse Alice' specimens and the destruction of main diagnostic characters make the identification of the specimens virtually impossible, the colour pattern and depth may offer some clues. For example, comparing the description and illustration presented by Hérouard with the one presented by Marenzeller (1893) for *H. lentiginosa* the two seem strikingly similar. The later was described based on a single specimen dredged by RV 'Hirondelle' near Pico and Faial islands.

Subgenus *Holothuria* Linnaeus, 1767

***Holothuria* (*Holothuria*) *mammata* Grube, 1840**
(Fig. 5.34)

$^{\$}$1924. *Holothuria tubulosa* (Gmelin); Nobre: 89.

$^{\$}$1930. *Holothuria tubulosa* (Gmelin); Nobre: 23, 70.

1938. *Holothuria tubulosa* Gmelin; Nobre: 143–144, figs. 58.1, 69.1.

1969. *Holothuria dakarensis* Panning, 1939; Rowe: 153, 154.

1977. *Holothuria* (*Holothuria*) *tubulosa* Gmelin; Pawson & Shirley: 915.

$^{\$}$1977. *Holothuria* (*Holothuria) mammata*? Grube; Pawson & Shirley: 915, 919.

$^{\$}$1983. *Holothuria tubulosa* Gmelin, 1790; Marques: 4, fig. 8.

1992b*.* *Holothuria* (*Holothuria*) *dakarensis* Panning, 1939; Pérez-Ruzafa *et al.*: 154–155.

1997. *Holothuria tubulosa* Gmelin, 1788; Pereira: 333.

$^{\$}$1998. *Holothuria tubulosa;* Morton *et al.*: 98, 169, figs. 5.2T, 8.8R.

1999. *Holothuria* (*Holothuria*) *dakarensis* Panning, 1939; Pérez-Ruzafa *et al.*: 57.

2002. *Holothuria* (*Holothuria*) *dakarensis* (Panning, 1939); Pérez-Ruzafa *et al.*: 287–288

$^{\$}$2009. *Holothuria mammata* Grube, 1840; Borrero-Pérez *et al.*: 51–69, figs. 1–7.

$^{\$}$2009. *Holothuria tubulosa*; Wirtz: 46.

$^{\$}$2010. *Holothuria* (*Holothuria*) *mammata*; Borrero-Pérez *et al.*: 900.

2010. *Holothuria tubulosa* Gmelin, 1790; Micael & Costa: 323.

$^{\$}$2010. *Holothuria tubulosa* Gmelin, 1790; Micael *et al.*: 329.

$^{\$}$2011. *Holothuria* (*Holothuria*) *mammata* Grube, 1840; Borrero-Pérez *et al*.: 1–12, figs. 1–4.

2012. *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1790; Micael *et al*.: 4.

Type locality: Mediterranean Sea.

See: Tortonese (1965: 57, fig. 18); Borrero-Pérez *et al.* (2009, 2011).

Distribution: Northeast Atlantic and the Mediterranean Sea, from south of Portugal to the Azores, Madeira, Selvagens and Canaries.

Depth: 0–77 m; a common presence in the low intertidal and infralitoral of the Azorean shores.

Habitat: sand, mud, gravel to hard substrata; on sea-grass prairies and in large tide-pools.

Type of Development: planktotrophic.

Commercial value: edible.

Material examined: DBUA-ECH 394 (Poços, São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.17, 13 m; 1 spm, TL=*c.* 200 mm); DBUA-ECH 397 (Lajes, PIX, AZO, N38°23’22” W28°15’04”, 2010.09.24, 1–2 m; 10 spms, TL=109–230 mm); DBUA-ECH 406 (Santa Cruz, FLS, AZO, N39°27’17.79” W31°07’30.48”, 2011.04.23, intertidal; 14 spms, TL=80–330 mm).

Description: body cylindrical, flattened ventrally. Tegument smooth, not thick. Mouth subventral and anus terminal. Dorsal surface with large mammillate papillae organized in six irregular longitudinal rows. Presence of a collar of small oral papillae. Ventral surface with tube-feet organized more or less in three longitudinal series (middle one somewhat subdivided in two). Most animals eviscerated. Cuvierian tubules inconspicuous. Table discs spinose, arched and somewhat reduced; tables with tetrabasal spires, of moderate height, crowded by acicular spines. Buttons, thick with a rugose appearance, covered by numerous small pointed knobs and with three or more pairs of small holes. Colour: uniform dark brown.

Remarks: in general, *H. mammata* can be easily distinguished from other shallow-water *Holothuria* species known to occur in the Azores by their inability to eject Cuvierian tubules (see remarks under *H. sanctori*). Among the sea cucumbers inhabiting the Azorean shallow waters, *H. mammata* differs also by its well developed spinose ossicles. Though closely resembling Mediterranean *H. tubulosa*, this species is distinct by the presence of a Cuvierian organ, relatively larger dorsal papillae and relatively larger tables (Rowe 1969).

Holothuria mammata is one of the most common elements of the Azorean shallow-water biota, particularly in relatively protected bays both natural (*e.g.,* natural lagoon in Lajes, Pico Island; Ávila *et al*. 2011) and manmade (*e.g.,* port of Ponta Delgada, São Miguel Island; personal observation). However, it was only in 2009 that this species was identified with certainty in the archipelago by Borrero-Pérez and co-workers. Historically, *H. mammata* was frequently confused with a closely similar species from the Mediterranean Sea, *H. tubulosa* (Gmelin 1791). Both species present a high degree of morphological variability, and in some cases the individuals may present intermediate diagnostic characters. Borrero-Pérez *et al*. (2009) showed that Atlantic records of *H. tubulosa* were a result of misidentifications with *H. mammata*, given that the former is restricted to the Mediterranean Sea. Thus, historical reports of *H. tubulosa* from the Azores should be considered as *H. mammata*. Another similar species, *H. dakarensis* Panning, 1939, was at one time included in the Azores echinoderm fauna by Rowe (1969). Pawson & Shirley (1977) believed that Rowe based his statement on specimens from Faial Island, deposited in the collection of the British Natural History Museum. On re-examination of this material, the authors concluded the animals belonged either to *H. mammata* or *H. tubulosa*. As the latter is restricted to the Mediterranean Sea these specimens are more likely to belong to *H. mammata*. Furthermore, Borrero-Pérez *et al*. (2009) also showed that in the Eastern Atlantic *H. dakarensis* is restricted to southern latitudes along the African coasts, from Senegal and Cabo Verde to Angola.

Subgenus *Panningothuria* Rowe, 1969

***Holothuria* (*Panningothuria*) *forskali* Delle Chiaje, 1823**
(Fig. 5.35)

$^{\$}$1983. *Holothuria forskali* Delle Chiaje, 1823; Marques: 4, fig. 6.

1997. *Holothuria forskali* Delle Chiaje, 1823; Pereira: 333.

$^{\$}$1998. *Holothuria forskali*; Morton *et al.*: 98, 169, figs. 5.2T, 8.8R.

2010. *Holothuria forskali* Delle Chiaje, 1823; Micael & Costa: 323.

2012. *Holothuria* (*Panningothuria*) *forskali* Delle Chiaje, 1823; Micael *et al*.: 4.

See: Koehler (1921b: 179–180, fig. 135); Pérez-Ruzafa *et al.* (1992b: 150); Bianchi *et al*. (1998: 66); O'Loughlin *et al.* (2007); Mecho *et al.* (2014: 290, figs. 9A–B).

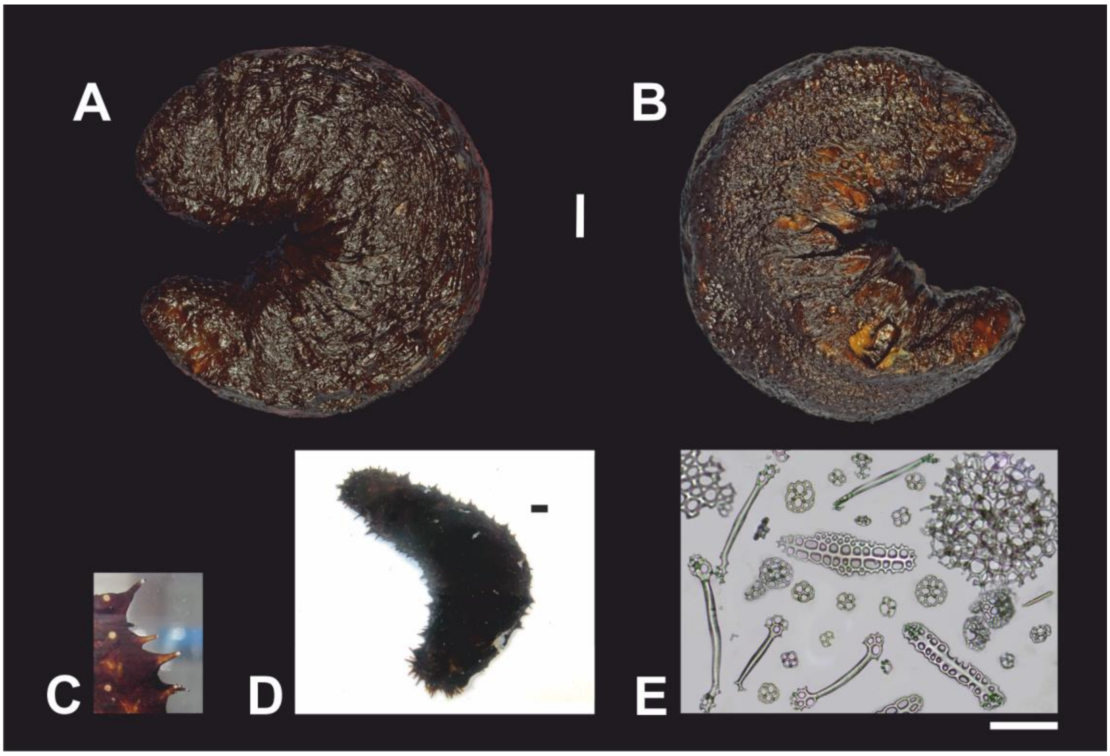


Figure 5.35. *Holothuria* (*Panningothuria*) *forskali* Delle Chiaje, 1823 (DBUA-ECH 398: A, B, E; DBUA-ECH 434: C, D). Dorsal view (A); ventral view (B); detail of the papillae (C); alive specimen (D); ossicles (E); scale bars are 10 mm (A, B, D) and 100 µm (D).

Distribution: Mediterranean Sea and Northeast Atlantic, from Scandinavia south to the coast of Morocco, including the Azores, Madeira and Canaries.

Depth: 0–850 m (AZO: 0–12 m).

Habitat: soft to hard substrata, among algae and seagrass beds, and on coralligenous bottoms.

Type of Development: probably planktotrophic (inferred from the genus).

Material examined: DBUA-ECH 392 (in front of the Marina, Ponta Delgada, SMG, AZO, *c.* N39°00’44” W27°57’28”, 1997.04.18, 12 m; 1 spm, TL=82 mm); DBUA-ECH 393 (Cerco, Caloura, SMG, AZO, N37°42’26” W25°30’37”, 1996.07.13, intertidal; 1 specimen, TL=92 mm); DBUA-ECH 398 [Capelas (Morro), SMG, AZO, *c.* N37°50’37” W25°41’18”, 1996.05.26, 9 m; 1 spm, TL=165 mm]; DBUA-ECH 434 (Horta harbour, FAY, AZO, *c.* N38°31’51” W28°37’23”, 2011.03.11, 6 m; 1 spm, TL=65 mm).

Description: body almost cylindrical, flattened ventrally. Body wall relatively thick. Epidermis smooth and very delicate. Mouth subventral surrounded by a crown of 20 peltate tentacles (cauliflower-like). Well-developed conical papillae irregularly arranged dorsally and laterally; presence of a collar of small oral papillae. Ventral surface with numerous tube feet in four rows. Well developed Cuvierian tubules. Calcareous deposits scarce, mostly composed of much reduce tables (<50 µm) with four holes; buttons absent; tube-feet and papillae also with elongate, irregularly branched rods; the tentacles with curved rods. Colour (in ethanol): solid deep brown to black bivium (papillae the same colour as the body) and trivium slightly lighter. Colour (when alive; DBUA-ECH 434): body deep brown with or without white papillae tips.

Remarks: *Holothuria forskali* can be distinguished *in situ* based on gross morphology characters, such as the very dark brown to black body colour with white papillae (although not always visible) and the presence of well developed Cuvierian tubules (Koehler 1921b). In the Azores, neither the dark colour nor the presence of Cuvierian tubules are exclusive to this sea cucumber. *Holothuria sanctori*, which is known as well to eject Cuvierian tubules if disturbed, shows an extraordinary degree of variability in its colour pattern: from dark brown or black body to a blackish ventral surface with an almost bright yellow dorsum on which the yellow rings can become so numerous that it is hard to perceive the dark background (Fig. 5.36). Intermediate colour forms in *H. sanctori* can present less conspicuous yellow (almost white) rings that could be confused with the white papillae described for *H. forskali*.

In the characterization of the marine coastal biota of the Azores, Morton *et al*. (1998) illustrated just two species of sea cucumbers, *H. mammata* (under the name *Holothuria tubulosa*) and *H. forskali*. They noted that the later species was a conspicuous presence in certain areas, such as tide-pools and marine lagoons. They also added that this species has the particularity of readily ejecting Cuvierian tubules when disturbed. We believe that Morton *et al*. (1998) may have overlooked the presence of *H. sanctori* in the studied areas. In the Azores, *H. sanctori* can be quite abundant in areas of relatively low hydrodynamism, reaching at times spectacular densities like these observed by Pérez-Ruzafa *et al*. (1992b) for the Canaries.

Subgenus *Platyperona* Rowe, 1969

***Holothuria* (*Platyperona*) *sanctori* Delle Chiaje, 1823**

(Fig. 5.36)

$^{\$}$1867. *Holothuria farcimen* sp. nov.; Selenka: 330, pl. 18, fig. 65.

1886a. Holothuria farcimen, Selenka, 1867; Théel: 220.

$^{\$}$1888. *Holothuria Sanctori* Delle Chiaje; Barrois: 112.

$^{\$}$1899. *Holothuria farcimen* Selenka; Perrier: 299.

$^{\$}$1902. *Holothuria farcimen*, Selenka; Perrier: 477–481, pl. 15, figs. 15–27.

$^{\$}$1921b. *Holothuria sanctori* Della Chiaje; Koehler: 171–174, figs. 127–128.

$^{\$}$1955. *Holothuria sanctori* Della Chiaje; Chapman: 398.

1965. *Holothuria sanctori* Delle Chiaje; Tortonese: 61–62, figs. 21A, 22.

1978. *Holothuria* (*Platyperona*) *sanctori* Delle Chiaje; Pawson: 27, figs. 11j, l.

$^{\$}$1983. *Holothuria sanctori* Delle Chiaje, 1823; Marques: 4, fig. 7.

1992b. *Holothuria* (*Platyperona*) *sanctori* Delle Chiaje, 1823; Pérez-Ruzafa *et al*.: 150–151.

1997. *Holothuria sanctori* Delle Chiaje, 1823; Pereira: 333.

1999. *Holothuria* (*Platyperona*) *sanctori* Delle Chiaje, 1823; Pérez-Ruzafa *et al*.: 55–56.

2002. *Holothuria* (*Platyperona*) *sanctori* (Delle Chiaje, 1823); Pérez-Ruzafa *et al*.: 287.

2010. *Holothuria sanctori* Delle Chiaje, 1823; Micael & Costa: 323.

$^{\$}$2010. *Holothuria sanctori* Delle Chiaje 1823*;* Micael *et al.:* 329.

2012. *Holothuria* (*Platyperona*) *sanctori* Delle Chiaje, 1823; Micael *et al*.: 4.

Type locality: Naples, Mediterranean Sea.

See: Koehler (1921b); Pérez-Ruzafa *et al.* (1992b); Borrero-Pérez *et al.* (2009, 2010).

Distribution: Mediterranean Sea and Northeast Atlantic, from the Bay of Biscay to Saint Helena and Ascension islands, including the Azores, Madeira, Selvagens, Canaries and Cabo Verde.

Depth: 0–30 m, in the Azores it is a common species in the first few meters.

Figure 5.36. *Holothuria* (*Platyperona*) *sanctori* Delle Chiaje, 1823 (DBUA-ECH 320: A, B, E; DBUA-ECH 402: C; DBUA-ECH 405: D; DBUA-ECH 398: E). Dorsal view (A, C); ventral view (B); alive specimen (D); ossicles (E); scale bars are 10 mm (A–D) and 100 µm (D).

Habitat: hard to soft substrates, under rocks and crevices, in sea-grass prairies and tide pools.

Type of Development: probably planktotrophic (inferred from the genus).

Commercial value: edible.

Material examined: DBUA-ECH 189 (Poços, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.16, 14–20 m; 1 spm, TL=120 mm); DBUA-ECH 320 (in front of the Marina, Ponta Delgada, SMG, AZO, *c.* N39°00’44” W27°57’28”, 1997.04.18, 12 m; 1 spm, TL=86 mm); DBUA-ECH 396 (Lajes, PIX, AZO, *c.* N38°23’22” W28°15’04”, 2010.09.24, 1–2 m; 15 spms, TL=77–148 mm); DBUA-ECH 400 (Poços, São Vicente, SMG, AZO, *c.* N37°50’06” W25°40’10”, 1996.07.17, 13 m; 1 spm, TL=125 mm) DBUA-ECH 401 (Banco João de Castro, AZO, *c.* N38°13’18” W26°36’12”, 1996.07.27, 30 m; 1 spm, TL=205 mm); DBUA-ECH 402 (in front of the Marina, Ponta Delgada, SMG, AZO, *c.* N39°00’44” W27°57’28”, 1997.04.18, 12 m; 1 spm, TL=115 mm); DBUA-ECH 404 (Vila do Porto, SMA, AZO, *c.* N36°56’42” W25°’08’50”, 2011.07.22; 1 spm, TL=105 mm); DBUA-ECH 405 (Santa Cruz, FLS, AZO, N39°27’17.79” W31°07’30.48”, 2011.04.23, intertidal; 20 spms, TL=70–190 mm).

Description: body arched dorsally, flattened ventrally. Body wall thick, extremely rigid when contracted. Mouth subventral and anus terminal. Dorsal surface crowded by numerous conical (somewhat rounded) papillae. Ventral surface densely cover by tube-feet organized in almost uniform manner. Cuvierian tubules well developed; many specimens eviscerated. Both buttons and disc tables with smooth round edges. Table discs slightly undulated with four central and eight distal holes; table with tetrabasal spires of moderate height, crowned by relatively short (somewhat blunt) teeth. Buttons flat with longitudinal ridge, flanked on each side by a row of holes; a second peripheral row of minute holes occasional present. Colour: dorsal surface from solid dark brown to completely covered with yellow rings (papillae tips always dark brown); ventral surface and tentacles uniformly brown.

Remarks: in general, *H. sanctori* presents a unique colour pattern among the shallow-water holothurians known from the Azores, in having large yellow rings covering its brown dorsal surface. However, *H. sanctori* can also present a uniform dark brown colour that can be easily distinguished by having a significantly thicker and rougher skin than *H. mammata* or *H. forskali*. Additionally, *H. sanctori* also differs from these shallow-water sea cucumbers by its well developed and relatively smooth ossicles.

Selenka (1867) described *Holothuria farcimen*, based on a single individual collected in the Azores deposited in the Cambridge Museum. Barrois (1888) remarked how abundant *H. sanctori* was on the coasts of São Miguel Island. Perrier (1902) criticised Barrois's identification, since the former believed *H. sanctori* to be restricted to the Mediterranean Sea and gave a full description of the material collected by RV 'Talisman' at Ponta Delgada (São Miguel Island) under the name *H. farcimen*. Later, Koehler (1921b) examined specimens from the Azores, including those of RV 'Talisman' and synonymised the Azorean species with *H. sanctori*.

Holothuria sanctori, is one of the most common elements of the Azorean shallow-water biota, particularly in relatively protected bays both natural [*e.g.,* Caloura, São Miguel Island; Lajes do Pico (Ávila *et al*. 2011)] or manmade (*e.g.,* marina of Ponta Delgada, São Miguel Island), where they can reach high densities (personal observation).

Subgenus *Vaneyothuria* Deichmann, 1958

***Holothuria* (*Vaneyothuria*) *lentiginosa lentiginosa* Marenzeller, 1892**
(Fig. 5.37)

$^{\$}$1892. *Holothuria lentiginosa*, n. sp.; Marenzeller: 66.

$^{\$}$1893. *Holothuria lentiginosa*, nov. sp.; Marenzeller: 6–7, pl. 1, fig. 1, pl. 2, fig. 1.

?$^{\$}$1902. *Holothuria mexicana*, Ludwig; Hérouard: 7–8, pl. 1, fig. 16.

1954. *Holothuria lentiginosa* v. Marenzeller; Deichmann: 391.

1958. *Holothuria lentiginosa* Marenzeller; Cherbonnier: 371.

1965. *Holothuria lentiginosa* Marenzeller; Cherbonnier: 13–14.

1969. *Holothuria lentiginosa* von Marenzeller, 1893; Rowe: 151, 152.

1979. *Holothuria lentiginosa lentiginosa* Marenzeller; Miller & Pawson: 914–915, figs. 4C–D.

1997. *Holothuria lentiginosa* Marenzeller, 1892; Pereira: 333.

1999. *Holothuria* (*Vaneyothuria*) *lentiginosa* Marenzeller, 1893; Pérez-Ruzafa *et al*.: 56–57, fig. 1C.

2005. *Holothuria lentiginosa* Marenzeller, 1892; García-Diez *et al*.: 51.

Type locality: between the islands of Faial and Pico islands, Azores (N38°31'19" W28°34'31").

See: Marenzeller (1893); Tommasi & de Oliveira (1976: 81–84, fig. 6, as *Holothuria lentiginosa brasiliensis*); Miller & Pawson (1979); Pérez-Ruzafa *et al.* (1999); Borrero-Pérez *et al.* (2010); Thandar & Mjobo (2014: 246–247, fig. 3).

Distribution: Northeast Atlantic, from Morocco to Angola waters, including the archipelagos of the Azores, Canaries, Cabo Verde and ?Gorringe seamount; reported elsewhere in the Alboran Sea (Mediterranean Sea); the subspecies *H. lentiginosa enodis* Miller & Pawson, 1979 was reported from the Gulf of Mexico and Caribbean in the West Atlantic and to ?Cabo Verde archipelago in the East Atlantic; the subspecies *H. lentiginosa brasiliensis* Tommasi & de Oliveira, 1976 is reportedly restricted to the waters between São Paulo and Rio de Janeiro, in Brazil.

Depth: (?12)100–275 (?316) m, though the tropical subspecies *H. lentiginosa enodis* was reported from depths as shallow as 8 m and as deep as 450 m [AZO: (?130)208–275(?316) m].

Habitat: sand, coralligenous, detritic to rock.

Type of Development: probably planktotrophic (inferred from the genus).

Material examined: DBUA-ECH 388 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’30” W25°20’49”, 2009.09.24, 208 m; 1 spm, TL=125 mm); DBUA-ECH 389 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’30” W25°20’49”, 2009.09.24, 208 m; 3 spm, TL=120–150 mm); DBUA-ECH 391 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’31” W25°20’14”, 2011.07.15, 275 m; 1 spm, TL=140 mm).

Description: body almost cylindrical, flattened ventrally. Body wall soft and relatively thick. Mouth subventral with 20 peltate tentacles (cauliflower-like); anal opening dorsal. On each side of the body one dorsal and one lateral longitudinal row of 7 to 10 well-developed large conical papillae. Lateral papillae slightly larger than the dorsal papillae. Ventral surface with numerous tube feet in three longitudinal rows, the central one divided at the mid-line. Table discs not smooth (with small external projections); table with tetrabasal spires of moderate width and height, crowned by numerous teeth. Buttons smooth, frequently contorted and with obliterated or incomplete perforations; buttons frequently with small knobs. Colour: lateral surface of the body cream white with numerous small dark brown spots (tube feet); towards the dorsal mid-line dorsal surface becomes gradually light brown (DBUA 388) or brown (DBUA 391); brown somewhat irregular and inconspicuous spots at the base of the dorsal papillae (with cream coloured tips); lateral papillae cream coloured as the body; ventrally, outer longitudinal row white with dark brown spots around the tube feet, inner row light brown with dark brown spots also around the tube feet; tentacles cream coloured.

Remarks: Marenzeller (1892, 1893) described a new species of sea cucumbers based on a partially damaged and eviscerated animal (160 mm TL) taken in Azorean waters, between Pico and Faial islands, at about 130 m deep (RV ‘Hirondelle’, sta 226).

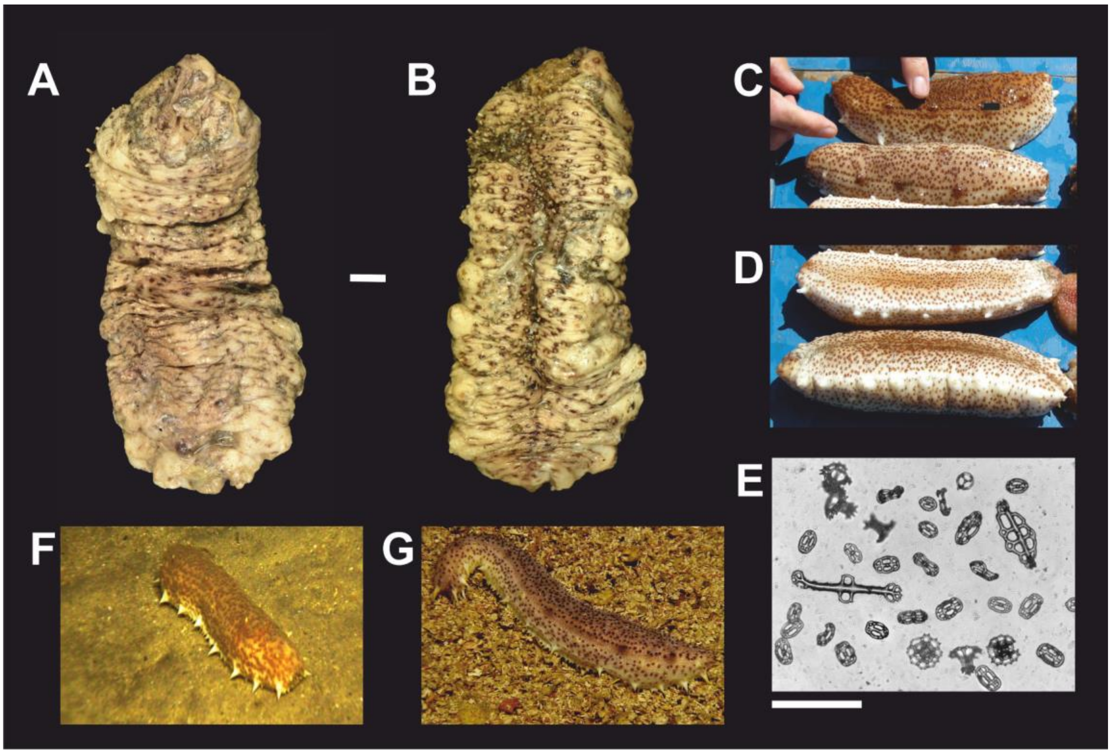


Figure 5.37. *Holothuria* (*Vaneyothuria*) *lentiginosa lentiginosa* Marenzeller, 1892 (DBUA-ECH 388: A–B; DBUA-ECH 389: E). Dorsal view (A, C); ventral view (B, D); alive specimens (C, D); ossicles (E); holothurians most likely belonging to *H. lentiginosa in situ* in Azores (EMEPC-LUSO, N37°43'15" W25°48'24", 2009.10.08, 316 m; F) and Gorringe Bank (EMEPC-LUSO, N36°42'46" W11°10'02", 2009.09.13, 145 m); scale bars are 10 mm (A–D) and 200 µm (E).

However, the accompanying echinoderms found in the same dredge indicate that the station's depth likely was much shallower than the reported 130 m (see remarks under *Pawsonia saxicola* and *Thyone inermis*). Regardless, *H. lentiginosa* was not seen in the Azores for more than 100 years. The 'Third International Workshop of Malacology and Marine Biology' offered a rare opportunity to survey the least known waters of the archipelago, by dredging depths between the maximum scuba diving (≈30–60 m) and the typical depths explored by the oceanographic cruises (≈150–250 m). Two of the least known littoral holothurians were captured: *H. lentiginosa* and *Parastichopus regalis* (Cuvier, 1817) (see remarks under this species) from depths between 208 and 275 m.

The new material agrees in most aspects with the original description and illustrations by Marenzeller (1892, 1893), except for the presence of a double row of well-developed dark brown dorsal papillae in our individuals. However, the poor preservation of the type specimen could account for this small difference. In the examined material both colour and size of the dorsal papillae became quite imperceptible (retracted) during preservation (96% ethanol) (Figs. 3.37A, B). Furthermore, Miller & Pawson (1979) commented that colour could be lost in preserved specimens. No greenish-yellow hue was observed in the lateral surface of the specimens, a feature observed by Cherbonnier (1958) in animals from Sierra Leone. Nevertheless, the dorsal dark spots presented by material from the Azores (Figs. 3.37C, D) were rather small and inconspicuous when compared with the figures presented by Miller & Pawson (1979) for *H. lentiginosa enodis*. The Azorean animals also presented a well-developed dorsolateral longitudinal row of papillae (though becoming greatly retracted during preservation), which is apparently absent in the Caribbean subspecies. This species can be easily distinguished from other sea cucumbers belonging to this genus recorded in the archipelago by its colour pattern. For example, *H. sanctori* can present (Fig. 5.36D) the same colour range as this species but arranged in a quite different pattern, *i.e.* dark brown with yellowish rings in opposition to cream with small dark brown spots, respectively.

In the West Atlantic *H. lentiginosa* was divided in two subspecies: *H. lentiginosa brasiliensis* described by Tommasi & de Oliveira (1976) from south Brazilian waters and *H. lentiginosa enodis* described by Miller & Pawson (1979) to the Caribbean waters. The Brazilian subspecies was described based on colour differences, as the animals presented a darker colour with large dark dorsal blotches. The ossicles in the Brazilian subspecies agreed with Marenzeller's original description. On the other hand, the Caribbean variety was raised fundamentally on ossicle morphology differences, as Miller & Pawson (1979) considered colour differences or papillae distribution as minor variations. Surprisingly, Pérez-Ruzafa *et al*. (1999) recorded both *H. lentiginosa lentiginosa* and *H. lentiginosa enodis* from Cabo Verde shallow-waters (12–22 m and 8–20 m depth, respectively) without offering any description of the examined material. The new material from the Azores (type area) herein examined reinforces Miller & Pawson (1979)'s opinion that colour variation should not be used as a diagnostic character as it is subject to local variation and may not survive the preservation process. Thus, the status of the *H. lentiginosa* subspecies should be re-addressed, comparing material throughout its geographical distribution on both sides of the Atlantic. Additionally, in 2009 during the expedition by EMEPC, ROV Luso captured footage portraying two holothurians likely to belong to this species, one south of São Miguel Island in the Azores (L09D20R, N37°43'15" W25°48'24", 316 m; see Fig. 5.37F) and another in Gorringe Seabank (sta L09D09L1, N36°42'46" W11°10'2.30", 145 m; see Fig. 5.37G).

Family Mesothuriidae Smirnov, 2012

Genus *Mesothuria* Ludwig, 1894

Mesothuria maroccana **Perrier, 1898**

?$1902. *Mesothuria murrayi*, Théel; Hérouard: 23–24.

$1923. *Mesothuria Murrayi*, Théel var. *grandipes* n. var.; Hérouard: 15–17, pl. 4, figs. 7–9.

1932. *Mesothuria maroccana* R. Perrier; Grieg: 4, pl. 1, fig. 1.

2005. *Mesothuria murrayi* Théel, 1886; García-Diez *et al*.: 51.

$2008. *Mesothuria maroccana* Perrier, 1902; Gebruk: 50, 51.

2012. *Mesothuria maroccana* Perrier, 1898; Gebruk *et al*.: 301–303, figs. 9A,B, 10.

2013. *Mesothuria maroccana* R. Perrier, 1898; Rogacheva *et al*.: 592, fig. 17D.

Type locality: Morocco (N32°04’00” W10°42’46”).

See: Perrier (1902: 312–317, pl. 16, figs. 32–35); Deichmann (1930: 97–98, pl. 7, figs. 2–7); Gebruk *et al.* (2012); Rogacheva *et al.* (2013).

Distribution: North Atlantic, from off Virginia, south to the Gulf of Mexico and the Caribbean, eastwards from the area between Greenland and Iceland to the Gulf of Gibraltar, including the Mid-Atlantic Ridge from the Charlie-Gibbs Fracture Zone to the Azores.

Depth: 700–3,465 m [AZO: 1,740(?1,600)–2,954 m].

Habitat: muddy sand, mud to hard substrates.

Remarks: Hérouard (1923) assigned material collected in Azorean waters (Princesse-Alice: sta 536: N37°54’00” W24°43’15”, 2178 m; RV ‘Hirondelle II’: sta 3150: N38°01’ W25°21’, 1740 m) to ‘*Mesothuria murrayi* Théel var. *grandipes*’. On revising Hérouard’s variety, Deichmann (1930) dismissed many of the diagnostic characters selected by the previous author as intraspecific or ontogenic variation. Deichmann believed that the Atlantic variety ‘grandipes’ was identical with Perrier’s *M. maroccana*. Later authors such as Hansen (1956) and Gebruk *et al*. (2012) agreed with Deichmann. Nevertheless, these authors stated that a future revision was essential given the limited present knowledge of these species’ natural variability. Additionally, Gebruk (2008) identified the *M. maroccana* among the material taken in northern Azorean waters, further substantiating the presence of this species in the Azorean deep waters.

Mesothuria milleri **Gebruk & Solís-Marín,** ***in*** **Gebruk** ***et al.*****, 2012**

$1893. *Holothuria Verrilli*, Théel; Marenzeller: 7–9, pl. 1, fig. 2, pl. 2, fig. 2.

$1902. *Allantis* (nov. gen.*) intestinalis*, (Asc. et Rathke) var. *Verrilli*, Théel; Hérouard: 18–21, pl. 1, figs. 3–6.

$1902. *Mesothuria Verrillii*, Théel, Östergren; Perrier: 307–312, figs. 3–4, pl. 16, figs. 22–31.

$1923. *Mesothuria Verrilli*, Théel; Hérouard: 10–13.

1927a. *Mesothuria Verrilli* (Théel); Mortensen: 381–382, figs. 224.4–5.

1930. *Mesothuria verrilli* (Théel); Deichmann: 93–94, pl. 6, figs. 1–8.

1938. *Mesothuria verrilli* (Théel); Nobre: 152.

1988. *Mesothuria verrilli* (Théel, 1886); Harvey *et al*.: 184.

1992b. *Mesothuria verrilli* (Théel, 1886); Pérez-Ruzafa *et al*.: 144.

2005. *Mesothuria verrilli* (Théel, 1886); García-Diez *et al*.: 51.

$2012. *Mesothuria milleri* Gebruk and Solis-Marin sp. nov.; Gebruk *et al.*: 274–283, fig. 4.

2014. *Mesothuria milleri* Gebruk et Solís-Marín, 2012 *in* Gebruk *et al*., 2012; Gebruk *et al*.: 170.

Type locality: Porcupine Seabight, NE Atlantic (N51°31’06” W12°59’00”).

See: Gebruk (2012); Gebruk *et al.* (2014).

Distribution: Northeast Atlantic, from Iceland and the Rockall Trough south to West Africa, including the archipelagos of the Azores and Canaries.

Depth: 455–4,400 m, most common between 1,430 and 1,530 m [AZO: 1,258–2,155(?3,018) m].

Habitat: soft substrates (mud).

Type of Development: lecithotrophic.

Remarks: Gebruk *et al*. (2012: 281) reviewed the historical material identified as *M. verrilli* (Théel, 1886b) from the East Atlantic, and concluded that, due to the incomplete initial description by Théel, this Caribbean species was historically confused with other similar species, particularly with *M. intestinalis* (Ascanius, 1805). Moreover, Gebruk and co-authors found a third new species among the historical material, which they described as *M. milleri*. The re-identified specimens by Gebruk and co-workers included specimens from RV ‘Talisman’ taken within Azorean waters and previously identified by Perrier (1902) as *M. verrilli*. Additionally, by examining animals of different sizes, Gebruk *et al*. (2012) characterized different ontological trends in each species ossicles, and recognized *M. milleri* in the descriptions by Marenzeller (1893) and Hérouard (1902, 1923). Both authors recorded *M. verrilli* from the Azores (see also remarks under *M. intestinalis*).

Mesothuria murrayi Théel, 1886a

p.p.?$1902. *Mesothuria murrayi*, Théel; Hérouard: 23–24.

2005. *Mesothuria murrayi* Théel, 1886; García-Diez *et al*.: 51.

$2012. *Mesothuria murrayi* (Théel, 1886); Gebruk: 303–307, fig. 11.

Type locality: Juan Fernandez (S33°42’ W78°18’), Pacific.

See: Théel (1886a: 185, pl.10, figs. 16–18, as *Holothuria murrayi*); Gebruk (2012).

Distribution: cosmopolitan, in the Atlantic and Pacific; in the Atlantic reliable records from off Florida and the Azores.

Depth: 245–6,650 m (AZO: ?1,660–1,940 m).

Habitat: soft substrate, clay to ooze.

Remarks: Hérouard (1902) reported two individuals of *M*. *murrayi* from the archipelago, collected by RV ‘Princesse Alice’ (sta 719: N39°11’ W30°24’15”, 1,600 m). Later, Deichmann (1930) re-examined one of the specimens and assigned it to a different species, *M*. *rugosa* (see below). Deichmann believed that *M*. *murrayi* was restricted to the Pacific waters and all Atlantic material assigned to this species would prove to be either *M*. *maroccana* or *M*. *rugosa*. However, Gebruk (2012) has recently identified *M*. *rugosa* in the Atlantic, including a specimen collected by RV ‘Princesse Alice’ in the Azores (sta 863: N39°22’00” W26°55’45”), not listed in Hérouard’s (1902) report. Nevertheless, the complex taxonomy of *M*. *murrayi* and other closely related species such as *M*. *maroccana* and *M*. *rugosa* shows that this group of species is in need of a thorough revision.

Mesothuria rugosa Hérouard, 1912

p.p.$1902. *Mesothuria murrayi* Théel; Hérouard: 23–24.

$1930. *Mesothuria rugosa* Herouard; Deichmann: 98–99, pl. 8, figs. 1–6.

Type locality: off Cabo Verde (N16°12’30” W24°43’45”).

See: Hérouard (1912: 1–3, fig. 1; 1923: 19–21, pl. 1, figs. 11–21, pl. 2, figs. 1, 2); Deichmann (1930); Benavides-Serrato *et al.* (2012: 206); Gebruk (2012: 308–309, figs. 9, 12).

Distribution: North Atlantic, from Caribbean waters eastwards to the Azores and Cabo Verde.

Depth: 460–3,890 m (AZO: 1,600 m).

Habitat: soft substrates.

Remarks: Deichmann (1930) re-examined one of the two specimens collected by RV ‘Princesse Alice’ southeast of Flores Island (sta 719: N39°11’00” W30°24’15”, 1,600 m) and identified by Hérouard (1902) as *Mesothuria murrayi*. She compared with her specimens of *M. rugosa* from the Caribbean waters and found them to be identical. Considering the intricate taxonomy of this species together with other closely related species such as *M. maroccana* and *M. murrayi*, some authors have expressed doubts about the validity of this species (*e.g.,* Gebruk 2012). However, present knowledge on the intraspecific variation in these species is still scarce and thus an extensive revision on these species is pending.

Genus *Zygothuria* Perrier, 1898

Zygothuria lactea (Théel, 1886a)

$1886a. *Holothuria lactea*, n. sp.; Théel: 183–184, pl. 10, figs. 9, 15.

$1902. *Mesothuria lactea*, Théel; Hérouard: 21–23, pl. 1, figs. 17–19.

1902. *Zygothuria* [*Holothuria*] *lactea* Théel; Perrier: 322–327, pl. 17, figs. 1–10.

$1923. *Mesothuria lactea*, Théel; Hérouard: 13–15, pl. 4, figs. 1–3.

1927a. *Mesothuria lactea* (Théel); Mortensen: 382–383, figs. 226–227.

1938. *Mesothuria lactea* (Théel); Nobre: 152–153.

2005. *Mesothuria lactea* (Théel, 1886); García-Diez *et al*.: 51.

2012. *Mesothuria* (*Zygothuria*) *lactea* (Théel, 1886); Benavides-Serrato *et al*.: 208–209.

$2012. *Zygothuria lactea* (Théel, 1886); Gebruk: 310–321, figs. 13, 14.

Type locality: off New Zealand, Pacific (S37°34’ W179°22’).

See: Théel (1886a); Benavides-Serrato *et al.* (2012); Gebruk *et al.* (2012).

Distribution: cosmopolitan, in the Atlantic, Pacific, Indian and Southern Oceans; in the west Atlantic reported from New England to the Gulf of Mexico and the Caribbean, in the east reported from Iceland eastwards from the Rockall Trough south to NW Africa, including the Azores, Madeira, Canaries and Cabo Verde; reported elsewhere in the South Atlantic (S25°27’ W6°10’).

Depth: 484–5,100 m (AZO: 1,165–2,102 m).

Habitat: soft sediments, muddy sand, mud to clay.

Type of Development: lecithotrophic.

Remarks: the true geographical distribution and depth range of *Zygothuria lactea* is unknown, particularly in the Western Atlantic, given that historically this species was confused with other closely related species [*e.g., Z. oxysclera* (Perrier, 1899); see Gebruk *et al*. 2012]. In the Azores, *Z. lactea* is extremely abundant between 1,200 and 2,000 m (Hérouard 1902).

Order Persiculida Miller *et al*., 2017

Genus *Benthothuria* Perrier, 1898

Benthothuria funebris **Perrier, 1898**

$2008. *Benthothuria funebris* Perrier, 1899; Gebruk: 50, 51.

Type locality: off Cape Blanc, NW Africa.

See: Perrier (1902: 365–371); Gage *et al.* (1985: 175, 194–195); Rogacheva *et al.* (2013: 591, figs. 17B, 19B); Jones *et al.* (2014: 132, fig. 6T).

Distribution: East Atlantic, from Greenland eastwards from the Rockall Trough south to Angola, including the Azores.

Depth: 782–3,757 m (AZO: 2,954–2,968 m).

Habitat: soft sediment, from mud to sand (with shells and corals); may be able to swim.

Remarks: Recently, Gebruk (2008) identified the species *B*. *funebris* among material collected at the north border of the Azorean EEZ (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m).

Family Pseudostichopodidae Miller *et al*., 2017

Genus *Pseudostichopus* Théel, 1882

Pseudostichopus peripatus **(Sluiter, 1901)**

$1902. *Pseudostichopus occultatus*, Marenzeller; Hérouard: 14–15, pl. 2, figs. 4–14.

$1923. *Pseudostichopus Marenzelleri*, n. sp.; Hérouard: 25.

$1923. *Pseudostichopus lapidus*, n. sp.; Hérouard: 26–28, pl. 4, fig. 5.

1927a. *Pseudostichopus lapidus* Hér.; Mortensen: 387.

1927a. *Pseudostichopus Marenzelleri* Hér.; Mortensen: 387.

1938. *Pseudostichopus occultatus* Marenzeller; Nobre: 156–157.

$2002. *Meseres peripatus* Sluiter; O'Loughlin: 307–309, fig. 2f.

2005. *Pseudostichopus occultatus* Marenzeller, 1893; García-Diez *et al*.: 51.

$2005. *Pseudostichopus peripatus* (Sluiter, 1901) comb. nov.; O'Loughlin & Ahearn: 174–175, figs. 1f, 10f–h, 11i–l, 12g–h.

2014. *Pseudostichopus peripatus* (Sluiter, 1901) *sensu* O'Loughlin et Ahearn, 2005; Gebruk *et al*.: 168–169.

Type locality: Indonesia.

See: O'Loughlin (2002); O'Loughlin & Ahearn (2005); Rogacheva *et al.* (2013: 593, fig. 18D).

Distribution: deep-water cosmopolitan, in the Atlantic, Pacific and Indian Oceans, in the West Atlantic from Caribbean north to off Massachusetts, eastwards from Greenland south to the Azores area.

Habitat: soft sediments; covers itself with Globigerine foraminifera.

Depth: 134–5,453 m [AZO: (?2,871)4,020–4,400 m].

Remarks: Hérouard (1902) firstly identified RV 'Princesse Alice' material collected in Azorean waters as *Pseudostichopus occultatus*. In a later report, Hérouard (1923) realized that the specimens belonged to two new different species, which he described as *P. lapidus* and *P. marenzelleri*. O'Loughlin (2002) placed both species in the synonymy of *P. peripatus*. However, O'Loughlin (2002) examined a specimen of *P. marenzelleri* collected within Azores waters (N36°58' W26°20', 2,871–2,917 m, ?unreported) present in the collection of the Muséum National d'Histoire Naturelle (Paris) and found significant differences to a point to consider its determination as *P. peripatus* as uncertain. Regardless, later O'Loughlin & Ahearn (2005) confirmed the synonymy of both *P. marenzelleri* and *P. lapidus* with *P. peripatus*.

Order Synallactida Miller *et al*., 2017
Family Deimatidae Théel, 1882
Genus *Deima* Théel, 1879
Species *Deima validum* Théel, 1879

Deima validum validum Théel, 1879

$2008. *Deima validum* Théel, 1879; Gebruk: 50, 51.

Type locality: Pacific (N36°10' E178°00').

See: Hansen (1975: 16–23, figs. 1, 109, pl. 9, fig. 1, pl. 13, figs. 1–2); Tyler *et al.* (1985a); Bohn (2006: 9–10, fig. 4); Rogacheva *et al.* (2013: 595, fig. 18E).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian Oceans; in the Caribbean deep waters to off Rio de Janeiro (Brazil), eastwards from south of the Charlie Gibbs

Fracture Zone (Mid-Atlantic Ridge) and the Rockall Trough to southern African deep-waters (S19°13'); the subspecies *D. validum pacificum* Ludwig, 1894 is restricted to the East Pacific.

Depth: 724–5,424 m (AZO: 2,954–2,968 m).

Habitat: epibenthic deposit-feeder on soft sediments, from clay to *Globigerina* ooze.

Type of Development: possibly direct (non-brooding) or lecithotrophic.

Remarks: historically, the cosmopolitan *Deima validum validum* was reported from waters between the Azores and the Iberian continental shores (*e.g.,* Hérouard 1902, as *Deima atlanticum*). Only recently Gebruk (2008) reported this species within the archipelago's waters, among material collected at the Azorean EEZ's northern border (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m).

Genus *Oneirophanta* Théel, 1879

Oneirophanta mutabilis mutabilis **Théel, 1879**

$2008. *Oneirophanta mutabilis* Théel, 1879; Gebruk: 50, 51.

Type locality: Between Marion and Crozet Islands (S46°46' E45°31').

See: Théel (1879: 6–7, pl. 1, figs. 4–6; 1882: 62–68, pl. 21, fig. 2, pl. 22, fig. 1–3, pl. 31, figs. 1–3, pl. 36, figs. 1–2, 8–11, pl. 37, figs. 4, 13, pl. 37, figs. 11–12, pl. 40, figs. 1–3, pl. 41, figs. 1–2, 4, pl. 42, fig. 9, pl. 43, fig. 1, 6, pl. 45, figs. 1–6, pl. 46, figs. 6–7); Hansen (1975: 24–32, figs. 2–5); Tyler *et al.* (1985a).

Distribution: cosmopolitan, in the Atlantic, Pacific, Indian and Southern Oceans; from the Rockall Trough south to the waters between the Azores and the Iberian Peninsula; reported elsewhere, off Uruguay, South Atlantic (S36°44' W46°16'); *O. mutabilis affinis* Ludwig 1893 is restricted to the East Pacific.

Depth: 1,804–5,900 m, mostly deeper than 3,200 m (AZO: 2,954–3,050 m).

Habitat: epibenthic on soft sediments, from sandy clay to ooze.

Type of Development: possibly direct or lecithotrophic.

Remarks: historically, the cosmopolitan *Oneirophanta mutabilis mutabilis* was recorded in the waters near the Azores, between the archipelago and the European continental shores (*e.g.,* Perrier 1902, as *Oneirophanta mutabilis*). Recently, Gebruk (2008) reported this species within the archipelago waters (RV 'G.O. Sars', 'MAR–ECO' cruise, sta 40/367: N42°55' W30°20', 2,954–2,968 m; sta 46/372: N42°46' W29°16', 3,005–3,050 m). The somehow discontinuous distribution of this cosmopolitan species in the Atlantic may reflect an artefact produced by insufficient sampling as a consequence of the great depths in which the species is usually found.

Family Stichopodidae Haeckel, 1896

Genus *Parastichopus* Clark, 1922

Parastichopus regalis **(Cuvier, 1817)**

(Fig. 5.38)

$^{\$}$2003. *Eostichopus regalis*; Wirtz & Debelius: 263.

$^{\$}$2009. *Stichopus regalis* (Cuvier, 1817); Wirtz: 48.

Type locality: Mediterranean Sea.

See: Clark (1922: 63, pl. 1, figs. 17–18, as *Stichopus regalis*); Deichmann (1954: 388, as *Stichopus regalis*); Cherbonnier (1958: 371, as *S. regalis*; 1965: 12–13); Tortonese (1965: 66–68, figs. 24, 25, as *S. regalis*); Augier (1985, as *S. regalis*); Ramón *et al.* (2010, as *S. regalis*).

Distribution: Mediterranean Sea and East Atlantic, from the British Islands south to Angola, including the Azores, Madeira and Canaries; reported elsewhere in the Caribbean and the Gulf of Mexico.

Depth: 5–800 m, mostly at depths above 50 m (AZO: 40–275 m).

Habitat: soft sediments (sand to mud).

Commercial value: edible.

Material examined: DBUA-ECH 386 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’30” W25°20’49”, 2009.09.24, 208 m; 1 spm, TL=136 mm)**;** DBUA-ECH 387 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’30” W25°20’49”, 2009.09.24, 208 m; 1 specimen, TL=140 mm); DBUA-ECH 390 (off Praia da Amora, Ponta Garça, SMG, AZO, N37°42’31” W25°20’14”, 2011.07.15, 275 m; 1 specimen, TL=185 mm).

Description: Body dorsally arched but ventrally flattened, forming a distinct sole with numerous tube feet arranged in three rows (the central one divided in two). Lateral margin separating the ventral and dorsal surfaces of body with large papillae, which is continued anteriorly above the ventrally situated mouth. Ventral surface covered by well-developed conical papillae more or less arranged in longitudinal rows. Body wall relatively thick. Cuvierian tubules absent. Calcareous deposits mostly composed of tables and flattened rods. No buttons. Table disc relatively large, perforated (up to more than 60 holes decreasing in size towards the periphery) and with an irregular round edge; medium high tetrabasal spire with the rods connected by 3 to 5 sets of cross bars armed with lateral teeth at its distal part. Rods irregularly perforated. Colour: bivium brown to orange, papillae white or cream; sole with the outer row brown or orange slightly lighter than the bivium, inner double row orange or red. Colour (in ethanol): similar to the live colouration, except for the red and orange colours, which have turned to brown.

Remarks: *P. regalis* is one of the recent additions to the Azores marine fauna. The absence of this species in the historical collections from the Azores could be explained by the species preferential depth range. The preferred depth spectrum of *P. regalis* was seldom studied in the archipelago, between the maximum scuba diving (<30–60 m) and the typical depths explored by the oceanographic cruises (>150–250 m). Also, *P. regalis* appears to co-occur with *Holothuria lentiginosa* in the Azores, as both species were capture together among the material dredged off Ponta Garça in São Miguel Island (208–275 m depth) during the 'Third International Workshop of Malacology and Marine Biology'. Though with similar colour patterns, these two species can be easily distinguished by the overall body shape, as *P. regalis* has a well-marked sole ventrally and numerous large white papillae forming a conspicuous lateral rim. In opposition, *H. lentiginosa* presents fewer dorsal or lateral papillae, which are either dyed dark or of same colour of body surface and is nearly cylindrical without distinct sole.

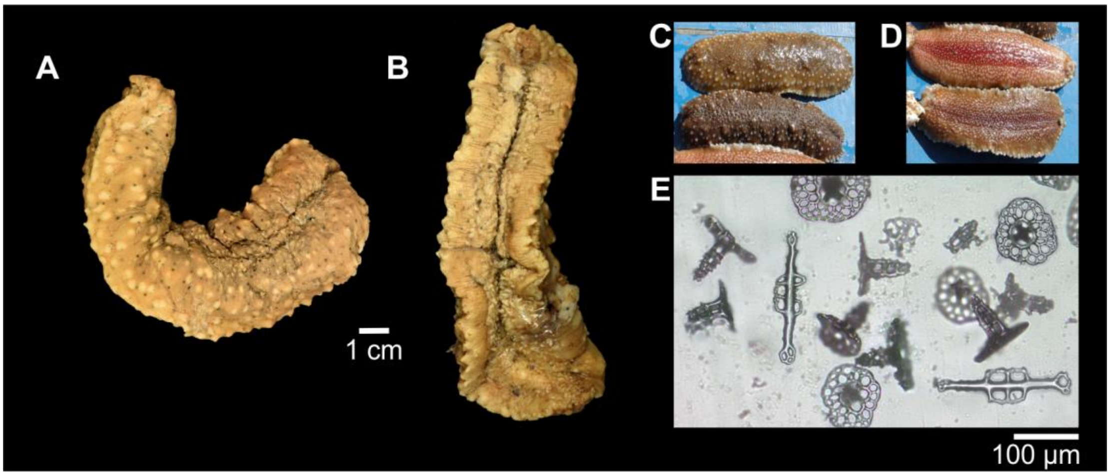


Figure 5.38. *Parastichopus regalis* (Cuvier, 1817) (DBUA-ECH 386). Dorsal view (A, C); ventral view (B, D); alive specimens (C, D); ossicles (E); scale bars are 10 mm (A–D) and 100 µm (E).

Family Synallactidae Ludwig, 1894

Genus *Paelopatides* Théel, 1886a

Paelopatides atlantica **Hérouard, 1902**

$^{\$}$1902. *Pælopatides atlantica*, nov. sp.; Hérouard: 16–17, pl. 1, fig. 15.

1927a. *Pælopatides atlantica* Hérouard; Mortensen: 388.

1930. *Pelopatides atlantica* Hérouard; Deichmann: 106.

2005. *Paelopatides atlantica* Hérouard, 1902; García–Diez *et al*.: 51.

2014. *Paelopatides atlantica* Hérouard, 1902; Gebruk *et al*.: 167.

Type locality: Azores (N38°8’00” W23°15’45”).

See: Hérouard (1902).

Distribution: endemic, only known from the Azores.

Depth: 4,020 m (AZO).

Remarks: *Paelopatides atlantica* is known only from the holotype, collected in Azorean waters by RV ‘Princesse Alice’ (sta 527: N38°08’00” W23°15’45”, 4,020 m).

5.4.2. Additional species erroneously reported from the Azores:

Phylum Echinodermata Bruguière, 1791

Class Crinoidea Miller, 1821

Order Comatulida Clark, 1908

Family Bourgueticrinidae Loriol, 1882

Genus *Democrinus* Perrier, 1883b

Erroneous – ***Democrinus rawsonii*** **(Pourtalès, 1874)**

1883b. *Rhizocrinus rawsoni*; Carpenter: 173–175.

1884. *Rhizocrinus rawsoni*, Pourtalès, 1874; Carpenter: 262–269, pl. 9, figs. 3–5, pl. 10, figs. 3–20, pl. 53, figs. 7, 8.

1909. *Rhizocrinus Rawsoni*, Pourtalès; Koehler: 255–256.

?1992. *Rhizocrinus rawsoni*?; Pérès: 256.

2005. *Democrinus rawsonii* (Pourtalès, 1874); García–Diez *et al*.: 46.

Type locality: Barbados.

See: Clark (1977: 177).

Distribution: Western Atlantic, in the Caribbean waters.

Depth: 66–652 m.

Remarks: *Democrinus rawsonii* was recorded in the Azores based on the erroneous assumption that *D. parfaiti* was conspecific with this species (for details see remarks under *D. parfaiti*). In view of this, all reports of this comatulid in the archipelago should be considered as *D. parfaiti*.

Family Bathycrinidae Bather, 1899

Genus *Monachocrinus* Clark, *in* Zittel, 1913

Erroneous – *Monachocrinus recuperatus* (Perrier, 1885a)

1980. *Monachocrinus perrieri* (Koehler & Vaney); Clark: 189.
1980. *Monachocrinus recuperatus* (Perrier); Clark: 189.
1982b. *Monachocrinus perrieri* (Koehler & Vaney); Clark: 126.
1982b. *Monachocrinus recuperatus* (Perrier); Clark: 126.

Type locality: between Azores and the Iberian Peninsula (N44°20’00” W17°10’46”).

See: Roux *et al.* (2002: 823, fig. 7e); Mironov *et al.* (2014: 115).

Distribution: rare species, known only from waters between the Azores and the Iberian Peninsula, Morocco and South Africa.

Habitat: soft sediments (mud).

Depth: 1,620–4,850 m.

Remarks: in a preliminary note on the crinoid material collected by the RVs ‘Travailleur’ and ‘Talisman’, Koehler & Vaney (1910) described a new species from Moroccan waters (N30°03’00” W11°41’46”) *Monachocrinus perrieri* (= *Bathycrinus perrieri*) and mentioned *Monachocrinus recuperatus* (= *Bathycrinus recuperatus*) from waters between the Azores and Iberian Peninsula (N44°20’00” W17°10’46”). Gislén (1951) working on the material collected by the ‘Swedish Deep-Sea Expedition’ reported material belonging to *Monachocrinus perrieri* from waters west of the Azores (N40°35’–N40°34’ W35°24’–W35°52’). Both species are now considered conspecific (Mironov *et al.* 2014). On what authority Clark (1980, 1982b) extended the geographic distribution of *M. recuperatus* to the Azores it is not clear. In spite of the close proximity of the historical records to the archipelago (both east and west) to our knowledge no specimens were actually recovered within the Azorean EEZ. Though, it is more than likely that this species does occur in the Azores deep waters, at present the inclusion of this species inside the Azorean fauna must be considered erroneous.

Order Isocrinida Sieverts-Doreck, 1952

Family Isselicrinidae Gislén, 1924

Genus *Endoxocrinus* Clark, 1908

Subgenus *Diplocrinus* Döderlein, 1912

Erroneous – Endoxocrinus (Diplocrinus) wyvillethomsoni (Thomson, 1872a)

1911a. *Endoxocrinus Wyvillethomsoni* (Wyville Thomson); Clark: 45–46.

1981. *Annacrinus wyvillethomsoni* (Jeffreys, nomen nudum; Wyville Thomson, 1872); Macurda & Roux: 169–219, pl. 7, figs. 1–10, pl. 8, figs. 1–9, pl. 9, figs. 1–12, pl. 10, figs. 1–9, pl. 11, figs. 1–8, pl. 12, figs. 1–12, pl. 13, figs. 1–10, pl. 14, figs. 1–9.

2014. *Endoxocrinus (Diplocrinus) wyvillethomsoni* (Jeffreys, 1870); Mironov *et al*.: 117.

Type locality: off Portugal (N39°42’ W9°43’).

See: Macurda & Roux (1981); David *et al.* (2006: 39–40, figs. 17, 19b, 20d).

Distribution: Northeast Atlantic, from the Bay of Biscay to Morocco, including the archipelagos of Madeira and Canaries.

Depth: 1,214(?900)–2,070 m.

Habitat: on various substrates and under a variety of hydrodynamic conditions.

Remarks: we do not know on what basis Clark (1911a) listed the Azores among the localities where *Endoxocrinus wyvillethomsoni* could be found. Surprisingly, he remarks that ?Bell may have confused Ferne Islands (British Channel) with Faial Island (Azores), since this species was not known to occur in the former area. Thus, the presence of *E. wyvillethomsoni* in the archipelago seems to be a result of Clark’s interpretation on a possible mistype by Bell. In later works by the same author (*e.g.,* Clark 1923b), the Azores was never again included in the geographical range of this species. A subsequent reference to the archipelago by Macurda & Roux (1981) was based on Clark (1911a) instead of Clark (1923b) cited by the authors. Overall, to our knowledge no specimens belonging to E. wyvillethomsoni from the Azores were ever documented and thus its historical inclusion in the fauna of the archipelago should be considered erroneous. Additionally, Jeffreys (*in* Carpenter & Jeffreys 1871) was the first author to name this deep-water crinoid. However, in a review by Macurda & Roux (1981), Jeffrey’s name was considered *nomen nudum*. For this reason, they appointed a later reference by Thomson (1872a: 767–769) in which this species is fully described, a view followed herein.

Class Ophiuroidea Gray, 1840

Order Amphilepidida O’Hara *et al*. 2017

Family Amphiuridae Ljungman, 1867

Genus *Amphiura* Forbes, 1843

***Erroneous – Amphiura chiajei* Forbes, 1843**

1927a. *Amphiura chiajei* Forbes; Mortensen: 212–213, figs. 117, 120.1–2.

1932. *Amphiura chiajei* Forbes; Grieg: 37.

1938. *Amphiura Chiajei* Forbes; Nobre: 84, fig. 41.

1965. *Amphiura chiajei* Forbes; Tortonese: 224–227, figs. 105–106.

1970. *Amphiura chiajei* Forbes; Fenaux: 262–271, figs. 1–5.

1995. *Amphiura chiajei* Forbes; Moyse & Tyler: 67, fig. 12.7.

2010. *Amphiura chiajei* Forbes, 1843; Micael & Costa: 322.

2012. *Amphiura chiajei* Forbes, 1843; Micael *et al*.: 3.

Type locality: Aegean Sea, Mediterranean Sea.

See: Forbes (1843: 150, pl. 14, figs. 8–13); Cherbonnier (1970: 1267); Fenaux (1970); Madsen (1970: 167–168, figs. 4–5a); Paterson (1985: 87–88, fig. 34); Jesus & Abreu (1998: 62); Koukouras *et al.* (2007: 72); Rodrigues *et al.* (2011: 15).

Distribution: Mediterranean Sea and Northeast Atlantic, from Scandinavia to the southern coast of Angola, including the Canaries and Madeira.

Depth: 2–1,250 m.

Habitat: soft sediments (sand, mud to silt) and among algae; lives buried in the sediment with the arms extended above the surface feeding on deposited material.

Type of Development: lecithotrophic.

Remarks: both Mortensen (1927a) and Grieg (1932) have listed the Azores under the geographical range of *Amphiura chiajei*. However, to the best of our knowledge no specimen belonging to this species was ever recorded from the archipelago. In view of this, the inclusion of *A. chiajei* in the Azorean fauna by those authors appears to be a misprint and should be dismissed as erroneous.

Family Ophiopsilinae Matsumoto, 1915

Genus *Ophiopsila* Forbes, 1843

Erroneous – *Ophiopsila aranea* Forbes 1843

1909. *Ophiopsila aranea*, Forbes — Koehler: 182.

1921b. *Ophiopsila aranea* Forbes — Koehler: 95–96, fig. 63.

1927a. *Ophiopsila aranea* Forbes — Mortensen: 180–181, fig. 101.

1965. *Ophiopsila aranea* Forbes — Tortonese: 253–255, fig. 116.

1970. *Ophiopsila aranea* Forbes — Madsen: 222, fig. 40.

2002. *Ophiopsila aranea* Forbes, 1845 — Pérez-Ruzafa *et al*.: 282–283.

2010. *Ophiopsila aranea* Forbes, 1843 — Micael & Costa: 322.

2012. *Ophiopsila aranea* Forbes, 1843 — Micael *et al*.: 3.

Type locality: Mediterranean Sea.

See: Forbes (1843: 149, pl. 14, figs. 1–7); Koehler (1921b); Mortensen (1927a); Pérez-Ruzafa *et al.* 2002).

Distribution: Mediterranean Sea and East Atlantic, in the Atlantic from the British Islands to the Gulf of Guinea, including Madeira, the Selvagens, Canaries, Cabo Verde, and the Seine Seamount.

Depth: 8–185 m.

Habitat: on coralligenous and detritic bottoms, among algae and sea-grass prairies or hidden in crevices.

Remarks: Koehler (1906b) reported material belonging to *Ophiopsila aranea* collected by RV 'Talisman' in several stations located in the Bay of Biscay, Madeira and Cabo Verde. Later, Koehler (1909) listed a specimen collected by RV 'Princesse Alice' from Seine Seamount (sta 2034: N33°47'40" W14°21', 185 m). However, in the discussion of the geographical distribution of *O. aranea*, Koehler (1909) stated that this Mediterranean species was collected in the Azores by RV 'Talisman' and taken again by RV 'Princesse Alice' in the same waters. It is clear that Koehler mistook the stations' location from both cruises, an error overlooked in subsequent literature.

Family Ophiothamnidae O'Hara *et al*., 2018

Genus *Ophiothamnus* Lyman, 1869

Erroneous – *Ophiothamnus affinis* Ljungman, 1872

1938. *Ophiothamnus affinis* Ljungman; Nobre: 75–76.

Type locality: Portugal (N38°10' W9°25').

See: Ljungman (1872: 622); Koehler (1914a: 111–112, as *Ophioleda minima*); Paterson (1985: 73, fig. 27); Bartsch (1987: 125–126, figs. 25–26).

Distribution: North Atlantic, in west recorded from Florida and in the east from the Bay of Biscay to the Western Sahara coast (NW Africa) and Madeira.

Depth: 1,425–1,935 m, though in the West Atlantic it was recorded at depths of 229–491 m.

Habitat: soft sediment (sand).

Remarks: Nobre (1938) listed a specimen of *Ophiothamnus affinis* collected by RVs 'Talisman' and 'Travailleur' between the Azores and Portugal continental shores, at N38°23' W31°10' (probably using the Paris Meridian) and at a depth of 500 m without referring to a specific station. The coordinates given by the author seem to refer to station 123 conducted by RV 'Talisman' in 1883, placing the specimen well inside the Azorean waters. However, Koehler (1906b) did not report any material of *O. affinis* or *Ophioleda minima* (as Nobre already acknowledged these species to be conspecific) from that particular station. Furthermore, Koehler (1906a,b, 1914a) described *Ophioleda minima* on the basis of specimens collected by RVs 'Travailleur' and 'Talisman' in Northern Spanish waters at a depth of 1,037–1,350 m, not between the Azores and Portugal as Nobre seemed to claim. In spite of the wide distribution of *O. affinis* in the North Atlantic, the presence of this species in the archipelago is still to be confirmed.

Family Ophiotrichidae Ljungman, 1867

Genus *Ophiothrix* Müller & Troschel, 1840a

Erroneous – *Ophiothrix cotteaui* (de Loriol, 1900)

1970. *Ophiothrix cotteaui* (de Loriol); Madsen: 215–216, figs. 36a–b.

Type locality: Liberia.

See: Koehler (1906a: 27–29; 1906b: 296–297, pl. 19, figs. 22–26, as *Ophiothrix indigna*; 1914b: 209, as *Ophiothrix gracilis*); Cadenat (1938: 357–358, as *Ophiothrix gracilis*); Marques (1980: 103).

Distribution: East Atlantic, from Portugal and the Gulf of Cadiz to Angola, including Madeira.

Depth: *c.* 0–820 m.

Habitat: soft sediments, on the branches of gorgonian corals.

Remarks: Koehler (1906a, b) described a new species, *Ophiothrix indigna*, based on material collected by RV 'Talisman' from the Gulf of Cadiz (sta 36, 1882: N35°35'00" W6°21'46", *c.* 150 m) and Madeira waters (sta 55, 1882: N32°41'20" W16°37'46", 370 m). In a review of the West African ophiuroids, Madsen (1970) concluded that *O. indigna* should be considered a junior synonymy of *O. cotteaui* as it merely represented adults of the later. However, by a lapse Madsen placed *O. indigna*'s type locality in the Azores.

Order Ophiacanthida O'Hara *et al*. 2017

Family Ophiacanthidae Ljungman, 1867

Genus *Ophiacantha* Müller & Troschel, 1842

Erroneous – *Ophiacantha anomala* Sars, 1872

1983. *Ophiacantha cuspidata* Lyman, 1878; Gage *et al.*: 291.

2005. *Ophiacantha cuspidata* Lyman, 1882; García-Diez *et al.*: 49.

2014. *Ophiacantha cuspidata* Lyman, 1878; Smirnov *et al.*: 195–196.

Type locality: Norway.

See: Sars (1872: 12–15); Lyman (1882: 191–192, pl. 15, figs. 9–10, pl. 41, figs. 12–14, as *Ophiacantha cuspidata*); Koehler (1909: 186, as *Ophiacantha cuspidata*); Paterson (1985: 24–34, fig. 14, as *Ophiacantha anomala*; 41–42, fig. 18, as *Ophiacantha cuspidata*); Stöhr (2005: 551–552, figs. 4A–H); Martynov & Litvinova (2008: 96, figs. 7B–J).

Distribution: Atlantic, from the east coast of the USA to Greenland eastwards from Iceland and Scandinavia as far south as Ascension Island.

Depth: 140–2,460 m.

Habitat: soft to hard substrates.

Type of Development: brooded within the gonads until postlarvae stage is reached; adults are also known to be hermaphrodite.

Remarks: Gage *et al*. (1983) mentioned the presence of *Ophiacantha cuspidata* in an area 'off Azores' (a species recently found to be conspecific with the North Atlantic *O. anomala*; see Martynov & Litvinova 2008). Gage and co-authors were probably referring to Koehler (1909) who reported two specimens collected by RV 'Princesse Alice' at a station located in the Mid-Atlantic Ridge, just outside the Azorean EEZ (sta 1420: N42°52'–N42°53' W28°30'45", 2,460 m). García-Diez *et al*. (2005) also erroneously placed this station within the 200 miles radius surrounding the archipelago, and thus included this species in their review of the Azorean fauna. Regardless of the widespread distribution in the North Atlantic, no material belonging to either *O. cuspidata* or *O*. *anomala* was yet documented inside the Azorean EEZ.

Erroneous – *Ophiacantha brevispina* Koehler, 1898

1987. *Ophiacantha brevispina* Koehler, 1898; Bartsch: 120–121, figs. 16, 17.

Type locality: Bay of Biscay (N46°27’00” W4°09’46”).

See: Koehler (1898: 56–57, pl. 8, figs. 43, pl. 9, fig. 44); Bartsch (1987); Jesus & Abreu (1998: 61).

Distribution: Northeast Atlantic, from the Bay of Biscay to Dakar (Senegal), including Madeira.

Depth: 90–417 m.

Habitat: soft sediment, sand to muddy sand.

Remarks: few specimens of *Ophiacantha brevispina* have been found since Koehler (1898) described this species. Cadenat (1938) identified numerous animals from an area that the author referred as Cape Blanc and Cabo Verde as *Ophiacantha* sp., though none of the specimens came from the later archipelago but from Dakar. Regardless Cadenat remarked that these brittle stars were quite close to what Koehler described as *Ophiacantha brevispina*. Later, Bartsch (1987) recorded *O. brevispina* from the same region as the previous author. Bartsch erroneously listed the Azores under geographical range of this species (citing Cadenat 1938), mistaking the Cabo Verde Islands with the Azores.

Genus *Ophiomitrella* Verrill, 1899

Erroneous – *Ophiomitrella clavigera* (Ljungman, 1865)

1927a. *Ophiomitrella clavigera* (Ljungman); Mortensen: 186–187, fig. 103.
1980. *Ophiomitrella clavigera* (Ljungman, 1864); Marques: 102.
1985. *Ophiomitrella clavigera* (Ljungman, 1864); Paterson: 71, fig. 28.
1988. *Ophiomitrella clavigera* (Ljungman, 1864); Harvey *et al.*: 170.
2005. *Ophiomitrella clavigera* (Ljungman, 1865); García-Diez *et al.*: 49.

Type locality: Norway.

See: Farran (1913: 44–45, fig. 9f, as *Ophiolebes claviger*); Mortensen (1920: 48–50; 1927a; 1933a: 39–41, fig. 23); Paterson (1985).

Distribution: North Atlantic, in the west from the Northern American coasts to Greenland and in the east from Iceland and Scandinavia to the British waters.

Depth: 166–1,952 m.

Habitat: coral epibiont and also known from muddy sand.

Type of Development: brooding, protandric hermaphrodite.

Remarks: *Ophiomitrella clavigera* was included in the Azorean fauna based on the erroneous assumption that *O. cordifera* was conspecific with this species (for details see remarks under *Ophiomitrella cordifera*).

Family Ophiobyrsidae Matsumoto, 1915

Genus *Ophiophrixus* Clark, 1911b

Erroneous – *Ophiophrixus spinosus* (Storm, 1881)

1985. *Ophiophrixus spinosus* (Storm, 1881); Paterson: 21–22, fig. 12.

1988. *Ophiophrixus spinosus* (Storm, 1881); Harvey *et al*.: 169.

Type locality: Norway.

See: Storm (1881: 88–89, as *Ophioscolex*? *spinosa*); Farran (1913: 48–49, as *Ophiobyrsa hystricis*); Mortensen (1927a: 171–172, figs. 96–97); Paterson (1985).

Distribution: Northeast Atlantic, from the Denmark Strait and off SE of Iceland to off NW African waters.

Depth: 40–1,383 m.

Habitat: soft bottoms, sand, mud to ooze.

Type of Development: viviparous.

Remarks: Koehler (1906b) reported *Ophiophrixus spinosus* (as *Ophiobyrsa hystricis*) from off the coast of Morocco (RV 'Talisman', sta 20, 1883: N33°43' W9°01'46", 1,105 m), a species previously known from Icelandic and Scandinavian waters. Mortensen (1927a) referred to this record as between Madeira and NW Africa, which later changed to 'off Madeira' (Mortensen 1933a). Paterson (1985) placed the southern limit of this species not in Morocco or Madeira, but in the Azores, which is clearly a mistake, that was repeated in subsequent literature.

Family Ophiocomidae Ljungman, 1867

Genus *Ophiocomella* Clark, 1939

Erroneous – *Ophiocomella pumila* Lütken, 1856

1970. *Ophiocoma pumila* Lütken, 1856; Devaney: 28, figs. 16, 37, 40, 44.

1985. *Ophiocoma pumila*; Mladenov: 285–295, figs. 1–3.

2011. *Ophiocoma pumila* Lutken, 1859; Benavides-Serrato *et al*.: 325–326.

Type locality: Bermuda.

See: Clark (1915: 293); Devaney (1970); Madsen (1970: 220); Hernández-Herrejon *et al.* (2008); Benavides-Serrato *et al.* (2011); Hernández *et al.* (2013: 490).

Distribution: Atlantic tropical waters, in the west from the Caribbean to Brazil and Bermuda and in the east from Senegal to the Gulf of Guinea, including the Canaries and Cabo Verde.

Depth: 0–24 m, but can reach 375 m.

Habitat: among algae or in crannies in rocks and corals.

Type of Development: planktotrophic larvae (three months at 26–27.5°C).

Remarks: we could not trace the original report in which led Devaney (1970) to include the Azores in the geographical distribution of *Ophiocoma pumila*. It seems likely that it is a product of a mistake hence we consider the inclusion of this tropical species in the archipelago as erroneous.

Family Ophiodermatidae Ljungman, 1867

Genus *Bathypectinura* Clark, 1909

Erroneous – *Bathypectinura heros* (Lyman, 1879)

1985. *Bathypectinura heros* (Lyman, 1879); Paterson: 95–96, fig. 38.

2008. *Bathypectinura heros* (Lyman, 1879); Borrero-Pérez *et al.*: 199–200, figs. 17G, H.

2011. *Bathypectinura heros* (Lyman, 1879); Benavides-Serrato *et al.*: 336–337.

2014. *Bathypectinura heros* (Lyman, 1879); Smirnov *et al.*: 208.

Type locality: Aru, Indonesia (S5°41’ E134°04’).

See: Lyman (1879: 48–49, pl. 14, figs. 389–391); Madsen (1973: 133–142); Pawson (1982: 136, 138).

Distribution: cosmopolitan, found in most oceans except the Arctic and Southern Oceans; in the Atlantic is found in the west from off North Caroline to the Caribbean and in the east from the Bay of Biscay to Angola, including Cabo Verde.

Depth: 240–3,150 m.

Habitat: soft substrates, from mud to clay; feeds on organic detritus, foraminiferans and *Sargassum*; capable of active swimming.

Remarks: Paterson (1985) listed the Azores in the geographical distribution of *Bathypectinura heros* as the southern limit in the NE Atlantic ignoring records further south reported, for example, by Madsen (1977), a work referred by the author. Paterson himself identified specimens belonging to *B. heros*, among material retrieved in NW Africa, at lower latitudes than the archipelago. Subsequent inclusions of the archipelago in this species geographical range were based on Paterson (1985). We could not find the original record for the Azores. Confirmed records of this species derive from the RV 'Michael Sars' Cruise just southwest of the Azorean waters (sta 53: N34°59' W33°01', 2,615–2,865 m) (Mortensen 1927a, as *Bathypectinura elata*; Grieg 1932, as *Pectinura elata*). Taking in account the species wide geographical range in the North Atlantic it is likely that it occurs in the Azores, however, in our opinion the presence of this species inside the archipelago waters still needs to be confirmed.

Family Ophiomyxidae Ljungman, 1867

Genus *Ophiomyxa* Müller & Troschel, 1840a

Erroneous – *Ophiomyxa pentagona* (Lamarck, 1816)

1972. *Ophiomyxa pentagona* (Lamarck); Cherbonnier & Sibuet: 396.

1980. *Ophiomyxa pentagona* (Lamarck, 1816); Marques: 103.

Type locality: Mediterranean Sea.

See: Tortonese (1965: 217–218, fig. 101).

Distribution: Northeast Atlantic and Mediterranean Sea, from Northern Spain to Senegal, including the Canaries and Cabo Verde.

Depth: 35–1,095 m in the Atlantic, but common in littoral-sublittoral Mediterranean waters.

Habitat: hard to soft substrata, including *Posidonia* and *Caulerpa* meadows.

Remarks: Cherbonnier & Sibuet (1972) and Marques (1980) listed this species for the archipelago of the Azores. Though it is not entire unlikely that this species occurs in Azorean waters considering its wide distribution throughout the Northeast Atlantic, we could not trace the original report. We believe that Cherbonnier & Sibuet (1972) inclusion of the Azores in the distribution of this species was due to a mistake.

Order Ophioscolecida O'Hara *et al*. 2017

Family Ophioscolecidae Lütken, 1869

Genus *Ophiogeron* Lyman, 1878

Erroneous – *Ophiogeron edentulus* Lyman, 1878

1882. *Ophiogeron edentulus*, Lym.; Lyman: 237, pl. 12, figs. 16–18.

Type locality: Fiji Islands (S19°02' E177°10'), Pacific Ocean.

See: Lyman (1878: 161, pl. 7, figs. 187–189; 1882).

Distribution: known only from the Fiji Islands in the Pacific.

Habitat: soft bottoms (red clay).

Depth: 2,471 m.

Remarks: see remarks under *Ophiogeron granulatus*.

Order Ophiurida Müller & Troschel, 1840a *sensu* O'Hara *et al*., 2017

Family Ophiosphalmidae O'Hara *et al*., 2018

Genus *Ophiomusium* Lyman, 1869

Erroneous – *Ophiomusium africanum* Koehler, 1909

1985. *Ophiomusium africanum* Koehler, 1901; Paterson: 147, fig. 58.

Type locality: Cabo Verde.

See: Koehler (1909: 159–160, pl. 1, fig. 10, pl. 29, figs. 5–6).

Distribution: known only from the archipelago of Cabo Verde.

Depth: 219 m.

Habitat: sand and coralline algae.

Remarks: *Ophiomusium africanum* is known only from type specimen described by Koehler (1909) and collected by RV 'Princesse Alice' in Cabo Verde. Paterson (1985) comment that this species 'was only recorded from the Azores' is clearly a mistake.

Class Asteroidea de Blainville 1830

Order Velatida Perrier 1884

Family Pterasteridae Perrier 1875

Genus *Calyptraster* Sladen 1882

Erroneous – *Calyptraster coa* Sladen, 1882

1979. *Calyptraster coa* Sladen, 1882; Walenkamp: 64–72, figs. 19, 23–25, pl. 14, figs. 1–4.

Type locality: Pernambuco, Brazil (S09°10' W34°50').

See: Sladen (1889: 489–491, pl. 78, figs. 1–2, pl. 79, figs. 1–3); Clark & Downey (1992: 308–309, figs. 49f, h, pl. 75, figs. A–B).

Distribution: Western Atlantic, from the Bahamas and Florida south to Brazil (*c.* S09°).

Depth: 260–993 m.

Habitat: soft sediment (mud).

Remarks: see remarks under *Calyptraster personatus*.

Genus *Pteraster* Müller & Troschel, 1842

Erroneous – *Pteraster alveolatus* Perrier, 1894

1894. *Pteraster alveolatus*, sp. nov.; Perrier: 183–184, pl. 13, fig. 1.

1927a. *Pteraster alveolatus* Perrier; Mortensen: 102.

1972. *Pteraster alveolatus* Perrier; Cherbonnier & Sibuet: 380.

1992. *Pteraster alveolatus* Perrier; Clark & Downey: 327, fig. 51a–e.

2014. *Pteraster alveolatus* Perrier, 1894; Dilman: 36.

Type locality: between the Azores and European continental shores (N42°19’ W21°15’46”).

See: Clark & Downey (1992).

Distribution: known only from the type locality.

Depth: 4,060 m.

Habitat: soft sediments (ooze).

Remarks: Perrier (1894) described *Pteraster alveolatus* based on a specimen collected by RV ‘Talisman’ NE of the Azores. At the time, Perrier attributed this species to the Azorean fauna, disregarding the true location of the station, a mistake repeated in subsequent literature.

Superorder Forcipulatacea Blake, 1987

Order Brisingida Fisher, 1928

Family Freyellidae Downey, 1986

Genus *Freyastera* Downey, 1986

Erroneous – *Freyastera benthophila* (Sladen, 1889)

1972. *Freyella benthophila* Sladen; Cherbonnier & Sibuet: 388.

Type locality: Pacific Ocean.

See: Sladen (1889: 641–643, pl. 111, figs. 5–8); Sibuet (1975: 99); Downey (1986: 36–38, fig. 18); Clark & Downey (1992: 480, fig. 74a–b, pl. 112, figs. C–D).

Distribution: cosmopolitan deep sea, in the Atlantic reported only to the east side, from the Bay of Biscay westwards to the Mid-Atlantic Ridge and to southern African waters.

Depth: 4,163–5,000 m.

Habitat: soft substrates (red clay).

Remarks: *Freyastera benthophila* (Sladen, 1889) was reported in the Azores by Cherbonnier & Sibuet (1972), based on the material collected by RV ‘Albatross’ during the 'Swedish Deep Sea Expedition'. However, the original record mentioned a station half way between continental Europe and the Azores, as was referred by Downey (1986) and Clark & Downey (1992). Though it is likely that this cosmopolitan deep-water species will prove to occur within the Azorean EEZ, it needs to be confirmed by actual records.

Genus *Freyella* Perrier, 1885d

Erroneous – *Freyella recta* Koehler, 1907a

1932. *Freyella recta*; Grieg: 31.
1927a. *Freyella recta* Koehler; Mortensen: 122.

Type locality: Mid-Atlantic Ridge (N31°45'30" W42°42'30").

See: Koehler (1909: 127–129, pl. 21, fig. 7, pl. 22, fig. 4, pl. 3, figs. 3–5); Downey (1986: 43–46, fig. 22); Clark & Downey (1992: 485–486, fig. 73).

Distribution: known only from the Mid-Atlantic Ridge.

Depth: 3,465 m.

Habitat: soft bottoms (*Globigerina* ooze).

Remarks: *Freyella recta* is known only with certainty from the type material (Clark & Downey 1992). This species was described by Koehler (1907a, 1909) based on a poorly preserved specimen taken by RV 'Princesse Alice' in the Mid-Atlantic Ridge, about 600 miles southwest from the Azorean waters. Later reports from the archipelago by Mortensen (1927a) and Grieg (1932) erroneously placed the record of RV 'Princesse Alice' in the archipelago.

Order Forcipulatida Perrier, 1884
Family Asteriidae Gray, 1840
Genus *Leptasterias* Verrill, 1866
Subgenus *Hexasterias* Fisher, 1930

Erroneous – *Leptasterias* (*Hexasterias*) *polaris* (Müller & Troschel, 1842)

1997. *Leptasterias (Hexasterias) polaris* (Müller & Troschel, 1842); Pereira: 336.
2010. *Leptasterias polaris* (Müller & Troschel, 1842); Micael & Costa: 321.

Type locality: Greenland.

See: Fisher (1930: 60–61, pl. 30, figs. 1, 1a–c, 2, 2a–2d, pl. 32, figs. 3, 3a, pl. 35, figs. 1–3); Clark & Downey (1992: 441–442); Rochette *et al.* (1994); Hamel & Mercier (1995).

Distribution: circumpolar Arctic; in the Atlantic, from Labrador and Greenland south to George's Bank.

Depth: 0–360 m (?AZO: intertidal).

Habitat: juveniles and small adults can be found on rocky substrates in shallow-water, below lowest water of spring tides; large adults occupy cobble to sandy and muddy areas at greater depths.

Type of Development: brooding.

Remarks: Perrier (1896a) reported *L. polaris* (as *Asterias polaris*) from the Azorean rocky intertidal, which later Koehler (1924) re-identifed to *Asterias rubens*. Later references of this species to the archipelago were based on Perrier's original report. Nonetheless, the sea surface temperatures in the Azores reach an average minimum of 14°C in the winter (Bashmachnikov *et al*. 2004) clearly providing an inhospitable environment far too warm to sustain a viable population of this Arctic species (see Hamel & Mercier 1995). The same conclusion can be reached on the possible presence of *C. crispatus* in the archipelago, *i.e.* it is unlikely that this stenothermal boreo-arctic species (see Shick *et al*. 1981) could maintain a viable population in the rocky shores of the Azores.

Family Pedicellasteridae Perrier, 1884

Genus *Hydrasterias* Sladen, 1889

Erroneous – *Hydrasterias ophidion* (Sladen, 1889)

non 1949. *Hydrasterias ophidion* Sladen; Clark: 375. [misidentified *H. sexradiata*]

Type locality: south of Halifax, Nova Scotia (N42°08' W63°39').

See: Sladen (1889: 581–582, pl. 99, figs. 3–4, pl. 103, figs. 3–4, as *Asterias* (*Hydrasterias*) *ophidion*); Clark & Downey (1992: 409, figs. 62a–b, pl. 97, figs. C–F).

Distribution: Western Atlantic, from the New England Seamounts south of Nova Scotia eastwards to the Mid-Atlantic Ridge and south to South America.

Depth: 2,286–2,330 m.

Habitat: soft bottoms (mud).

Type of Development: direct development.

Remarks: the western Atlantic *Hydrasterias ophidion* was reported from the Azores by Clark (1949) based on his identification of the material collected by RV 'Atlantis' (sta

20: N37°50’30” W26°00’00”, 2,562 m). Later, Dilman (2014) attributed Clark’s records to *H. sexradiata*, a known native to the Azorean deep waters.

Superorder Valvatacea Blake, 1987
Order Paxillosida Perrier, 1884
Family Astropectinidae Gray, 1840
Genus *Astropecten* Gray, 1840

Erroneous – *Astropecten bispinosus* (Otto, 1823)

1897. *Astropecten bispinosus* (Otto); Ludwig: 16–31, pl. 2, fig. 6, pl. 6, fig. 6.
1921b. *Astropecten bispinosus* Otto; Koehler: 46–47, fig. 33.
1927a. *Astropecten bispinosus* Otto; Mortensen: 56.
1934. *Astropecten bispinosus* (Otto); Parenzan: 211–216, fig. 7.
1938. *Astropecten bispinosus* (Otto); Nobre: 51–52, fig. 23, 24.
1950. *Astropecten bispinosus* (Otto 1823); Madsen: 181–182.
1965. *Astropecten bispinosus* (Otto); Tortonese: 140–141, fig. 62.
2010. *Astropecten bispinosus* (Otto, 1823); Micael & Costa: 322.
2012. *Astropecten bispinosus* (Otto, 1823); Micael *et al.*: 5.

Type locality: Mediterranean Sea.
See: Koehler (1921b); Tortonese (1965).

Distribution: Mediterranean Sea, reported elsewhere in the Portuguese continental shores (Northeast Atlantic).

Depth: shallow waters.

Habitat: sandy bottoms and *Zostera* prairies.

Remarks: the first report of *Astropecten bispinosus* in the Azores appears in Ludwig (1897). This author believed that *A. platyacanthus* was just a variation of *A. bispinosus*, and in his review of the Mediterranean sea stars, listed Barrois (1888)’s record in the synonymy list of later species. This caused subsequent authors, such as Koehler (1921b), to include the Azores in this species geographical range without acknowledging the synonymy or the re-examination of Barrois (1888)’s material. The debate whether *A. platyacanthus* is a variety of *A. bispinosus* seems to have ended with the publication of Zulliger & Lessios (2010) as they are now considered as two valid species (Mah 2017). Nevertheless, Clark & Downey (1992) considered both species to be endemic to the Mediterranean waters, believing that all the reports from the Atlantic were based on misidentifications or doubtful locality data. The lack of documented material from the Azorean waters appears to support these authors, and thus we consider the Azorean reports as erroneous.

Erroneous – *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827)

non 1888. *Astropecten pentacanthus* Phil.; Simroth: 231. [misidentified *A. hermatophilus*]

1914b. *Astropecten irregularis* var. *pentacanthus*; Koehler: 273.

1950. *Astropecten irregularis* f. *pentacanthus* (Delle Chiaje 1825); Madsen: 169–170.

Type locality: Mediterranean Sea.

See: Tortonese (1965: 132–137); Zulliger & Lessios (2010: 16); Pérès (1964: 19).

Distribution: Endemic to the Mediterranean Sea; possibly also present in the East Atlantic (Gorringe Seamount and Madeira); other subspecies of are also known in the Atlantic from Scandinavia to South Africa.

Depth: shallow water to 929 m, particularly abundant between 50 to 400 m.

Habitat: soft sediments, on biogenic detritus to sandy silt bottoms, and Zostera and Posidonia prairies.

Development: planktotrophic (inferred from A. *irregularis irregularis*)**.**

Remarks: Simroth (1888) was responsible for the only record of *Astropecten pentacanthus* known from the Azores. Later, Döderlein (1917) re-assigned Simroth material to *A. hermatophilus*, the only Astropecten species known to occur in the Azores with certainty (see remarks under *Astropecten hermatophilus*).

Genus *Dytaster* Sladen, 1889

Species *Dytaster grandis* (Verrill, 1884)

Erroneous – *Dytaster semispinosus* (Perrier, 1894)

1992. *Dytaster semispinosus* (Perrier); Clark & Downey: 55.

2014. *Dytaster semispinosus* (Perrier, 1894); Dilman: 26.

Type locality: off Galicia (N44°29’00” W13°31’46”).

See: Clark & Downey (1992).

Distribution: known only from abyssal waters between the Azores and the Bay of Biscay.

Depth: 4,275–5,005 m.

Habitat: soft sediments.

Remarks: Clark & Downey (1992) placed *Dytaster semispinosus* within the Azorean waters, though this species was never collected in the archipelago, but between the Azores and the European continental shores by RV 'Talisman' (Perrier 1894, as *Crenaster semispinosus*) and by RV 'Princesse Alice' (Koehler 1909, as *Dytaster parvulus*).

Family Ctenodiscidae Sladen, 1889

Genus *Ctenodiscus* Müller & Troschel, 1842

Erroneous – *Ctenodiscus crispatus* (Bruzelius, 1805)

2005. *Ctenodiscus crispatus* (Retzius, 1805); García-Diez *et al.*: 47.

2010. *Ctenodiscus crispatus* (Retzius, 1805); Micael & Costa: 322.

2012. *Ctenodiscus crispatus* (Retzius, 1805); Micael *et al.*: 5.

Type locality: ?Lund.

See: Shick *et al.* (1981); Clark & Downey (1992: 109–110, figs. 20a–b, d, pl. 28A–C).

Distribution: circumpolar Arctic, in the western Atlantic south in the cold current below the Gulf Stream to Cape Hatteras (though rare south of Cape Cod, Massachusetts) and in the east to Trondheim (Norway) and the cold area of the Faeroe Channel.

Depth: 10–1,890 m.

Habitat: deposit-feeder on soft sediments (mud, sand to clay).

Development: direct development.

Remarks: the report for the Azores is based on the assumption that the '*Asterias polaris* Gray' identified by Perrier (1896a) among the material collected by RV 'Hirondelle' in the Azores is a synonym of *Ctenodiscus crispatus*. Analysing the related bibliography, we disagree and thus consider the record of *C. crispatus* from the archipelago as erroneous (see remarks under *Asterias rubens* and *Leptasterias polaris*).

Family Porcellanasteridae Sladen, 1883

Genus *Thoracaster* Sladen, 1883

Erroneous – *Thoracaster cylindratus* Sladen, 1883

1992. *Thoracaster cylindratus* Sladen; Clark & Downey: 105–106, fig. 18f, pl. 26, figs. D–G.

Type locality: between the Canaries and Cabo Verde (N22°18' W21°02').

See: Madsen (1961: 82–92, figs. 10–11, pl. 5, pl. 6, figs. 1–7); Clark & Downey (1992).

Distribution: cosmopolitan, in the Atlantic, Pacific and Indian deep-waters; in the West Atlantic from the Gulf of Mexico and the Caribbean, southwards to Brazil; in the East Atlantic from SW of Ireland (Porcupine Seabight) southwards to off Liberia.

Depth: 2,540(?2,315)–5,990 m.

Habitat: soft bottoms, calcareous clay to *Globigerina* ooze**.**

Remarks: Clark & Downey (1992) have listed the Azores under the geographical range of *Thoracaster cylindratus*. However, this species was never collected within the Azorean EEZ. Perrier (1885c, 1894) identified a specimen of this species (= *Pseudaster cordifer*) among the material collected by RV 'Talisman' almost 500 km northeast of São Jorge Island (sta 134, 1883: N42°19' W23°36'). Later, Koehler (1909) reported this species on two of RV 'Princesse Alice' stations to the waters east and northeast of the Azores (sta 1306: N37°16'00" W20°11'45"; sta 753: N39°50'00" W17°57'45"). It is likely that *T. cylindratus* occurs in the Azores considering the wide distribution of this species in the Atlantic and the proximity of above mentioned records. The presence of this species within the archipelago's waters, however, is still to be confirmed.

Superorder Spinulosacea Blake, 1987
Order Spinulosida Perrier, 1884
Family Echinasteridae Verrill, 1867
Genus *Henricia* Gray, 1840

Erroneous – *Henricia sanguinolenta* (Müller, 1776)

1921b. *Henricia sanguinolenta* (O.F. Müller); Koehler: 31, fig. 23.
1927a. *Henricia sanguinolenta* (O.F. Müller); Mortensen: 118–121.
1938. *Henricia sanguinolenta* (O.F. Müller); Nobre: 39–40, fig. 14.

Type locality: south coast of Norway.

See: Madsen (1987: 209–218, figs. 1, 2a–b, 4–9); Clark & Downey (1992: 396–397, figs. 60o–p, pl. 93, fig. F, pl. 95, figs. H, I); Hernández *et al.* (2013: 491).

Distribution: Northeast Atlantic, from north boreal and arctic waters south to Northumberland (*c*. N55°) and Kattegat in the east and to Cape Cod in the west; reported elsewhere from the Canaries; possibly extending the North Pacific waters.

Depth: 0–200 m, though rarely below 50 m.

Habitat: mainly on hard substrata.

Development: lecithotrophic (brooder).

Remarks: in the historical literature, the inclusion of *Henricia sanguinolenta* in the Azorean marina fauna was based on the assumption that *H. oculata* was a junior synonymous of the former species (see remarks under *Henricia oculata*).

Subphylum Echinozoa Haeckel, 1896
Class Echinoidea Leske, 1778
Infraclass Carinacea Kroh & Smith, 2010
Superorder Calycina Gregory, 1900
Order Salenioida Delage & Hérouard, 1903
Family Saleniidae Agassiz, 1838
Genus *Salenocidaris* Agassiz, 1869

Erroneous – *Salenocidaris profundi profundi* (Duncan, 1877)

1927a. *Salenia profundi* (Duncan); Mortensen: 289, fig. 164.
1935. *Salenocidaris profundi* (Duncan); Mortensen: 354–357, pl. 85, figs. 1, 2, 29, 30, 35, 36, pl. 86, figs. 1, 2.
2005. *Salenocidaris profundi profundi* (Duncan 1877); García-Diez *et al.*: 50.
2014. *Salenocidaris profundi profundi* Duncan, 1877; Mironov: 123.

Type locality: ?Cape of São Vicente, Portugal.

See: Duncan (1877: 256–257, as *Salenia profundi*); Clark (1925: 66–67); Mortensen (1935).

Distribution: Northeast Atlantic, from Iceland (Faroe-Iceland banks) and the Bay of Biscay to the Canaries; reported elsewhere from Tristan da Cunha and Indonesia.

Depth: 1,700–3,470 m.

Habitat: soft sediments.

Remarks: the geographic distribution of *Salenocidaris profundi* in the Atlantic is poorly understood due to frequent misidentifications in the literature. Some authors such as Clark (1925) entertained the possibility of this species being conspecific with other Atlantic species, such as *S. varispina* and *S. hastigera*. Mortensen (1935) stated that the latter species was restricted to the Pacific and transferred all reports of *S. hastigera* in the Atlantic to *S. profundi*. Recently, Mironov (2006, 2014) confirmed the occurrence of *S. hastigera* in the Atlantic including the Azores. If all the reports for the archipelago are traced back to original records by Koehler (1895a, 1895b, 1898, 1909) no record of *S. profundi sensu stricto* remains in the archipelago. See remarks under *S. hastigera*.

Superorder Echinacea Claus, 1876

Order Arbacioida Gregory, 1900

Family Arbaciidae Gray, 1855a

Genus *Arbaciella* Mortensen, 1910

Erroneous – *Arbaciella elegans* Mortensen, 1910

non 1983. *Arbaciella elegans* Mortensen 1910 — Marques: 5. [misidentified juvenile of *A. lixula*]

non 1997. *Arbaciella elegans* Mortensen 1910 — Pereira: 334. [based on Marques 1983]

non 2008. *Arbaciella elegans* — Haddad & Barreiros: 9. [based on Marques 1983]

non 2010. *Arbaciella elegans* Mortensen 1910 — Micael & Costa: 322. [based on Marques 1983]

non 2012. *Arbaciella elegans* Mortensen 1910 — Micael *et al.*: 3. [based on Marques 1983]

Type locality: African west coast (Setté Cama, Gabon).

See: Mortensen (1910, 1935); Koehler (1914b).

Distribution: East Atlantic, Western tropical Africa from Cape Blanc to the Gulf of Guinea and Angola.

Depth: shallow-water.

Remarks: on erecting *Arbaciella elegans*, Mortensen (1910) observed the striking resemblance with young *Arbacia* species, particularly *A. lixula* and *A. lixula africana*, similar enough to cast doubts about the validity of this species (see also Mortensen 1935). Size at first sex maturity (presence of open gonopores), gross morphology, and colouration (which is strikingly colourful in comparison to that of juveniles of *A. lixula*) were the main features used to differentiate this taxon. Revising Azorean material (Museu Bocage – Natural History Museum, Lot no. 20743, Ponta Delgada harbour, São Miguel Island) identified by Marques (1980) as *Arbaciella elegans*, Kroh *et al*. (2011) employed genetic tools and re-visited the ontogeny development of *Arbacia lixula*. They found that *A. lixula* juveniles (the identity of which was confirmed by DNA analysis) are identical in morphology to what previous authors (*e.g.,* Gautier-Michaz 1955, 1958; Molinier & Picard 1956; Regis 1982) have considered as *Arbaciella elegans* in the Mediterranean and the Northeast Atlantic. Kroh *et al*. (2011) thus rejected the records of the *Arbaciella elegans* from these areas (including the Azores) as misidentifications of juveniles of *A. lixula,* reducing the distribution of *Arbaciella* *elegans* to its type area (tropical West African coasts). In addition, they cautioned that *Arbaciella elegans* as such may not be a distinct taxon and that it might turn out that all *Arbaciella* are juvenile *Arbacia* specimens (in the case of West Africa of *A. lixula africana*) upon DNA-analysis of material from the type region.

Order Camarodonta Jackson, 1912

Infraorder Echinidea Kroh & Smith, 2010

Family Echinidae Gray, 1825

Genus *Gracilechinus* Fell & Pawson, *in* Moore, 1966

Erroneous – *Gracilechinus elegans* (Düben & Koren, 1844)

1927a. *Echinus elegans* Düben and Koren; Mortensen: 303–304, fig. 139.

1938. *Echinus elegans* (Düben e Koren); Nobre: 116–117.

1943a. *Echinus elegans* Düben & Koren; Mortensen: 61–65, fig. 19, pl. 12, figs. 1–8, pl. 13, fig. 1, pl. 14, figs. 1–6.

1985. *Echinus elegans* Düben & Koren; Gage *et al.*: 185.

2006. *Echinus elegans* Düben & Koren 1846; Mironov: 110.

2010. *Echinus elegans* Düben & Koren 1846; Micael & Costa: 323.

2012. *Gracilechinus elegans* (Düben & Koren 1846); Micael *et al.*: 4.

Type locality: Bergen, Norway.

See: Düben & Koren (1846: 272-274, pl. 10, figs. 40-42, as *Echinus elegans*); Mortensen (1943a); Mironov (2006); Stevenson & Rocha (2012); Mecho *et al*. (2014: 286, fig. 5A).

Distribution: Mediterranean Sea and Northeast Atlantic; from Iceland and Scandinavia as far south as Cape Spartel, in the North African coast; also reported from the Antialtair Seamount.

Depth: 50–1,710 m.

Habitat: soft sediment; bioeroder (deep-water corals).

Type of Development: planktotrophic.

Remarks: Mortensen (1927a) listed the Azores under the geographical range of this species. However, no material belonging to *Gracilechinus elegans* was ever recorded from the Azores. Mortensen report seems to be a result of a mistake, which was repeated in later bibliography.

Family Parechinidae Mortensen, 1903

Genus *Psammechinus* Agassiz & Desor, 1846

Erroneous – *Psammechinus microtuberculatus* (Blainville, 1825)

1888. *Echinus microtuberculatus* Blainville — Barrois: 109.

1938. *Psammechinus microtuberculatus* (Blainville) — Nobre: 111–112.

1965. *Psammechinus microtuberculatus* (Blv.) — Tortonese: 333–335, fig. 159.

1983. *Psammechinus microtuberculatus* (Blainville, 1825) — Castro & Viegas: 24.

non 1983. *Psammechinus microtuberculatus* (Blainville, 1825) — Marques: 5. [juvenile *Paracentrotus lividus*]

1997. *Psammechinus microtuberculatus* (Blainville, 1825) — Pereira: 334.

2008. *Psammechinus microtuberculatus* — Haddad & Barreiros: 9.

2010. *Psammechinus microtuberculatus* (Blainville, 1825) Heller, 1868 — Micael & Costa: 323.

2012. *Psammechinus microtuberculatus* (Blainville, 1825) — Micael *et al*.: 4.

Type locality: Mediterranean Sea.

See: Mortensen (1943a: 139–147, figs. 56c, 58c, 59b, 60a, 61, 62, 63a, pl. 10, figs. 6–9, pl. 17, figs. 6–9, pl. 58, figs. 10, 16–18, 22); Harvey (1956: 51).

Distribution: restricted to the Mediterranean Sea.

Depth: 4–100 m.

Habitat: on rocky substrates and *Posidonia* prairies to muddy substrates where it feeds on animal matter.

Type of Development: planktotrophic.

Remarks: see remarks under *Psammechinus miliaris*.

Superfamily Odontophora Kroh & Smith, 2010
Family Echinometridae Gray, 1855a
Genus *Echinometra* Gray, 1825
Species *Echinometra lucunter* (Linnaeus, 1758)

Erroneous – *Echinometra lucunter lucunter* (Linnaeus, 1758)

1872. *Echinometra subangularis* Desml.; Agassiz: 234.

See: Mortensen (1943a: 357–368, figs. 172–175, pl. 41, figs. 1–5, pl. 42, figs. 12–14, pl. 43, figs. 1–13, pl. 44, fig. 9, pl. 64, figs. 17, 20–24); Schultz (2006: 212–213, figs. 395–400); Pawson (1978: 20–23, figs. 8–10).

Distribution: Atlantic, from North Carolina and Bermuda, southwards to Brazil, and eastwards from Cabo Verde to Angola; the subspecies *E. lucunter polypora* is restricted to Ascension and St. Helena islands.

Depth: 0–45 m.

Habitat: hard substrates (bioeroder).

Type of Development: planktotrophic.

Fossil record: *Ericichnus bromleyi*, a relatively recent described ichnospecies portraying groove-borings found in a Pliocene fossiliferous outcrop in Malbusca (Santa Maria Island) is thought to be made by the sea urchin *Echinometra lucunter* (see Santos *et al.* 2015).

Commercial value: edible.

Remarks: Agassiz (1872) listed the Azores under the geographical range of *Echinometra lucunter* (under the name *Echinometra subangularis*), which is clearly a misprint. The author never mentioned the archipelago again, whether listing the examined specimens' locations or discussing the distribution range for this species. This tropical species does not occur in the present-day shallow waters of the Azores and no specimens were ever reported from the area.

Order Echinothurioida Claus, 1880

Family Echinothuriidae Thomson, 1872b

Genus *Hygrosoma* Mortensen, 1903

Erroneous – *Hygrosoma luculentum* (Agassiz, 1879)

1895a. *Phormosomum luculentum* Agassiz; Koehler: 224.

1895b. *Phormosomum luculentum* Agassiz; Koehler: 228.

Type locality: Pacific.

See: Agassiz (1881: 97–99, pl. 9, figs. 1–2, pl. 10, figs. 1–4, pl. 10a, figs. 3–7, pl. 39, fig. 8, pl. 40, figs. 31–36, pl. 44, figs. 25–27, as *Phormosoma luculentum*); Clark (1925: 55–56, as *Echinosoma luculentum*); Mortensen (1935: 215–219, 123, 124, pl. 21, pl. 22, figs. 1–2, pl. 78, figs. 22–23).

Distribution: Pacific and Indian oceans.

Depth: 400–2,000 m.

Remarks: in his preliminary notes, Koehler (1895a: 224; 1895b: 228) identifies specimens taken in Azorean waters by RVs 'Hirondelle' and 'Princesse Alice' as the Indo-Pacific *H*. *luculentum*. Later, Koehler changed his previous determination first in 1889 to *P*. *uranus* (Koehler, 1898) and finally in 1909 to *Hygrosoma petersii* (see also remarks under *H. petersii*).

Infraclass Irregularia Latreille, 1825

Superorder Atelostomata Zittel, 1879

Order Holasteroida Durham & Melville, 1957

Family Calymnidae Mortensen, 1907

Genus *Calymne* Thomson, 1877

Erroneous – *Calymne relicta* Thomson, 1877

1881. *Calymne relicta*; Agassiz: 155–157, pl. 34, figs. 1–13, pl. 39, figs. 24–26, pl. 40, figs. 63–65, pl. 43, fig. 24, pl. 44, figs. 47, 48.

Type locality: North of the Bermuda.

See: Mortensen (1950: 129–131, fig. 115); Saucede *et al*. (2009).

Distribution: North Atlantic deep sea**,** North of the Bermuda, NW of Ampere Seamount and the Newfoundland Basin.

Habitat: on soft bottoms (muddy sand).

Depth: 3,720–4,860 m.

Remarks: on reviewing the material from RV ‘H.M.S. Challenger’, Clark (1925) noticed that the specimens reported by Agassiz (1881) as coming from Faial Island were mislabelled, being from Bermuda’s waters in reality.

Order Spatangoida Agassiz, 1840

Family Hemiasteridae Clark, 1917

Genus *Holanthus* Lambert & Thiéry, 1924

Erroneous – *Holanthus expergitus expergitus* (Lovén, 1874)

1881. *Hemiaster expergitus*; Agassiz: 186.
1907. *Hemiaster expergitus* Lovén; Mortensen: 97–107, figs. 16–18, pl. 2, figs. 1, 4, 18, 20, pl. 4, figs. 6–8, 10–12, pl. 15, figs. 9, 16–18, 24, 26, 30–31, 35, 38, 44–45, 47–48, 50.
1909. *Hemiaster expergitus*, Lovén; Koehler: 247.
1927a. *Hemiaster expergitus* Lovén; Mortensen: 323–324, figs. 186, 187.1.
1950. *Hemiaster expergitus* Lovèn; Mortensen: 387–389.
1985. *Hemiaster expergitus* Lovén, 1874; Gage *et al.*: 186.
2007. *Hemiaster expergitus* Lovén, 1874; Koukouras *et al.*: 82.

Type locality: Portugal (N38°07’ W9°18’).

See: Lovén (1874: 13–17); Mortensen (1907); Grieg (1932: 42, pl. 5, figs. 11–12); Serafy & Fell (1985: 23, fig. 36); Mironov (2014: 127).

Distribution: Mediterranean Sea and North Atlantic, from the Davis Strait to the Caribbean and eastwards from Iceland to Namibia, including Cabo Verde; other subspecies are reported from the Pacific and Indian oceans.

Depth: 380–4,833 m, though mainly at depths below than 1,000 m.

Habitat: buried about 12 cm from the surface of soft sediment (sand, mud to ooze).

Remarks: Lovén (1871) stated that he had found a new *Hemiaster* among the material collected at the Josephine Bank. Later, in the description of the species Lovén (1974) corrects to '*c*. Lisbon', Portugal (RV 'Josephine': N38°7' W9°18', 970 m). Agassiz (1881) commented that 'H.M.S. Challenger' also collected specimens of a *Hemiaster* near Lovén's type locality, which Agassiz referred to as 'near the Azores'. However, none of the two 'H.M.S. Challenger' stations were located near the archipelago, but in Canaries (sta 8, off Gomera) and Brazilian waters (sta 126: S10°46' W36°08') instead. In the species distributional overview Agassiz (1881) does not mention the Azores and place Lovén's and 'H.M.S. Challenger' specimens where they were originally recorded. Whether subsequent references to the archipelago are related with the initial misprint by Agassiz or to another (unreported) record, we were unable to verify.

Suborder Brissidina Stockley *et al*., 2005
Family Brissidae Gray, 1855b
Genus *Anabrissus* Mortensen, 1950

Erroneous – *Anabrissus damesi* (Agassiz, 1881)

1881. *Brissus damesi*, n. sp.; Agassiz: 197–200, pl. 30a, figs. 15–16.
1925. *Brissus damesi*; Clark: 218–219.

Type locality: Brazil (S9°05' to S9°10', W34°49' to W34°53').

See: Agassiz (1881); Clark (1925); Mortensen (1951b: 362–362, figs. 168–169, pl. 26, figs. 4–6, pl. 41, figs. 12, 13, 15).

Distribution: known only to Brazil.

Depth: 640 m.

Habitat: soft substrates (mud).

Remarks: in the batch of the original description of *Anabrissus damesi* (= *Brissus damesi*), Agassiz (1881) included a specimen from Faial Island ('H.M.S. Challenger', sta. 75: N38°37' W28°30', 92–824 m), which was described by Clark (1925) as a very small juvenile form (<10 mm) with no petals and no genital pores. The animal lacked important diagnostic characters and was later considered as unidentifiable by Mortensen(1951b)'s . Thus, the presence of this species in the archipelago is still to be confirmed and the known material of this species is still restricted to the type material from Brazil waters.

Superfamily Spatangidea Fischer, 1966

Family Spatangidae Gray, 1825

Genus *Spatangus* Gray, 1825

Erroneous – *Spatangus purpureus* Müller, 1776

1881. *Spatangus purpureus* — Agassiz: 171.
1892. *Spatangus purpureus* — Bell: 165–167, pl. 16, fig. 10.
1907. *Spatangus purpureus* O.F. Müller — Mortensen: 123–128, pl. 2, figs. 8, 12, 14, 16, pl. 16, figs. 1–2, 5–10, 22, 24–25, 27, 29, 31–32, 34.
1914b. *Spatangus purpureus* — Koehler: 279.
1917. *Spatangus purpureus* O.F. Müller 1776 — Clark: 234.
1921b. *Spatangus purpureus* O.F. Müller — Koehler: 129–130, figs. 89–90.
1927a. *Spatangus purpureus* O.Fr. Müller — Mortensen: 328–329, fig. 190.
1938. *Spatangus purpureus* O.F. Müller — Nobre: 127–128, fig. 55.
1956. *Spatangus purpureus* O. F. Müller — Harvey: 67.
2012. *Spatangus purpureus* O.F. Müller, 1776 — Micael *et al.*: 4.

See: Mortensen (1913: 14–17, figs. 14–15; 1927a; 1951a: 299–300; 1951b: 10–14); Schultz (2006: 427–428, figs. 802–804).

Distribution: Northeast Atlantic and Mediterranean Sea, from Iceland and Scandinavia along European and African coasts to Senegal; possibly also occurring in Cabo Verde and Angola.

Depth: 0–900 m.

Habitat: soft substrates, preferably on coarse sand or gravel, in which it lies wholly buried, feeds on all sorts of bottom particles and organisms.

Type of Development: planktotrophic (*c.* 3 weeks).

Remarks: Agassiz (1881) identified the species *Spatangus purpureus* among the material collected by 'H.M.S. Challenger' (sta 75: N38°37' W28°30', 92–165 m) in Azorean waters (no description was given). However, the existence of such specimen(s) could not be confirmed by Clark (1925) or Mortensen (1951b).

Furthermore, the only other 'H.M.S. Challenger' specimen identified by Agassiz (1881) as belonging to this species (off Bermuda) later proved to be a misidentification (see Mortensen 1907). Thus, the presence in the Azores of *S. purpureus* remains unconfirmed.

Erroneous – *Spatangus raschi* Lovén, 1869

1872. *Spatangus raschi*; Agassiz: 159.
1881. *Spatangus raschi*; Agassiz: 171.
1892. *Spatangus raschi*; Bell: 167–168, pl. 16, fig. 11.
1907. *Spatangus Raschi* Lovén; Mortensen: 129–130, pl. 1, figs. 4–5, pl. 2, fig. 19, pl. 16, figs. 17, 23, 28.
1917. *Spatangus raschi*; Clark: 235.
1927a. *Spatangus Raschi* Lovén; Mortensen: 329–330, figs. 192–193.
1932. *Spatangus raschi* Lovén; Grieg: 42–43.

Type locality: ?Norway.

See: Lovén (1869: 733–735, pl. 13); Mortensen (1927a; 1927b: 32); Gage *et al.* (1985: 186); Schultz (2006: 429, fig. 805).

Distribution: Northeast Atlantic, from Iceland and Scandinavia to Cap Bojador (NW Africa).

Depth: 146–1,500 m.

Habitat: surface deposit feeder on mud to detritic substrates.

Remarks: Agassiz (1872) reported *Spatangus raschi* from the archipelago based on a specimen present in the collection of the Breslau Museum. However, Mortensen (1951b) stated that there was no record of any *S. raschi* specimens from the Azores ever been housed at the museum. Thus, the presence of this species in the archipelago is still to be confirmed.

Family Maretiidae Lambert, 1905
Genus *Homolampas* Agassiz, 1874

Erroneous – *Homolampas fragilis* (Agassiz, 1869)

non 1949. *Homolampas fragilis* (Agassiz); Clark: 376, 377. [misidentified *A. atlantica*]

Type locality: Caribbean.

See: Mortensen (1950: 266–272, pl. 7, figs. 5–6, pl. 13, figs. 5, pl. 25, figs. 1,4, 13, 15–18); Pawson *et al.* (2009: 1200); Benavides-Serrato *et al.* (2012: 118).

Distribution: Western Atlantic, known only from the Gulf of Mexico and the Caribbean.

Depth: 550–3,550 m.

Habitat: infaunal, in soft bottoms.

Remarks: Clark (1949) reported this species from the Azores, based fragments of two medium-sized specimens retrieved by RV 'Atlantis', west of São Miguel Island (cruise 152, sta 20: N37°50'30" W26°00'00", 2,562 m). Later, Serafy (1974) re-examined one of the specimens and assigned it to his newly described species, *Araeolampas atlantica*. The second specimen of Clark was not mentioned by Serafy, but it seems likely that this also was an *Araeolampas*, since *H. fragilis* does not reach a size larger than 35 mm (Serafy 1974) and confirmed records of *H. fragilis* are restricted to the West Atlantic.

Class Holothuroidea de Blainville, 1834
Order Apodida Brandt, 1835
Family Synaptidae Burmeister, 1837
Genus *Synaptula* Örstedt, 1849

Erroneous – *Synaptula hydriformis* (Lesueur, 1824)

1923. *Synaptula hydriformis* Lesueur?; Hérouard: 147.
2005. *Synaptula hydriformis* (Lesueur, 1824); García-Diez *et al.*: 52.

Type locality: Guadalupe, Caribbean.

See: Lesueur (1824: 162–163, as *Holothuria hydriformis*); Deichmann (1954: 407); Laguarda-Figueras *et al.* (2001: 38–39, fig. 18A–D).

Distribution: Western Atlantic, from Brazil, northwards to Bermuda including the Gulf of Mexico and the Caribbean.

Depth: shallow-waters, 1–7 m.

Habitat: among algae, in mangrove swamps and reef lagoons.

Type of Development: viviparous.

Remarks: Hérouard (1923) tentatively attributed poorly preserved material (mainly muscle fragments, with no calcareous deposits) collected by RV 'Princesse Alice' in the Azores (sta 1349: N38°35'00" W28°05'45"), at a depth of 1,250 m to the tropical species *Synaptula hydriformis*. The depth distribution of this species is restricted to the first few meters, which makes the Azorean reported depth highly unlikely.

Order Elasipodida Théel, 1882

Family Elpidiidae Théel, 1882

Genus *Psychroplanes* Gebruk, 1988

Erroneous – *Psychroplanes obsoleta* (Hérouard, 1899)

1902. *Peniagone* [*Kolga*] *obsoleta* Hérouard; Perrier: 276.

Type locality: between the Azores and the European continent (N39°50’ W17°57’45”).

See: Hérouard (1899: 170, fig. 1; 1902: 41–42, pl. 6, figs. 11–15, pl. 8, figs. 16–18, as *Kolga obsoleta*); Hansen (1975: 134–135, fig. 56).

Distribution: known from the Mid-Atlantic near the equator and the deep-waters between the Azores and the European shores; reported elsewhere in the east of the Japanese Trench (Pacific).

Depth: 4,275–6,096 m.

Habitat: soft sediments.

Remarks: Perrier (1902) mentioned *Psychroplanes obsoleta* among the species reported by Hérouard from the Azores. However, Hérouard (1902) clearly states that the specimens came from waters between the Azores and the European mainland (RV ‘Princesse Alice’, sta 753: N39°50’00” W17°57’45”, 4,360 m). It is possible that *P. obsoleta* may occur in the abyssal waters of the Azores, considering the known geographical and bathymetric distribution of this species, but at present no records from the archipelago exist.

Family Laetmogonidae Ekman, 1926

Genus Laetmogone Théel, 1879

Erroneous – *Laetmogone wyvillethomsoni* Théel, 1879

non 1902. *Lætmogone Wyville-Thomsoni* (Théel); Hérouard: 31–32, pl. 4, figs. 10–16.

1927a. *Lætmogone Wyville-Thomsoni* Theel; Mortensen: 361.

1932. *Laetmogone wyvilli thomsoni* Théel; Grieg: 5, 46.

Type locality: off Chile, Southern Pacific Ocean.

See: Hansen (1975: 54–57, fig. 20); O’Loughlin (2002: 321).

Distribution: Southern Ocean and Antarctica.

Depth: 245–4,410 m.

Habitat: soft substrates.

Remarks: Hansen (1975) believed that all historical reports of *Laetmogone wyvillethomnsoni* from the Atlantic were misidentifications of closely similar species such as *L. violacea*. However, on re-examination of the specimens identified by Hérouard (1902) from the Azores, Hansen suggested that these animals belonged to a yet unnamed new species (see also remarks under *L. violacea*).

Order Holothuriida Miller *et al*., 2017

Family Holothuriidae Burmeister, 1837

Genus *Holothuria* Linnaeus, 1767

Subgenus *Holothuria* Linnaeus, 1767

Erroneous – *Holothuria (Holothuria) dakarensis* Panning, 1939

1969. *Holothuria dakarensis* Panning, 1939; Rowe: 153, 154.

1992b. *Holothuria* (*Holothuria*) *dakarensis* Panning, 1939; Pérez-Ruzafa *et al.*: 154–155.

1999. *Holothuria* (*Holothuria*) *dakarensis* Panning, 1939; Pérez-Ruzafa *et al.*: 57.

2002. *Holothuria* (*Holothuria*) *dakarensis* (Panning, 1939); Pérez-Ruzafa *et al.*: 287–288.

Type locality: Dakar (Senegal).

See: Cherbonnier (1950); Pawson & Shirley (1977); Borrero-Pérez *et al.* (2009); Pawson *et al.* (2010: 37–38, fig. 30); Prata *et al.* (2014).

Distribution: Atlantic, in the west from off Georgia south to the Gulf of Mexico and Rio Grande do Norte (Brazil) and in the east from Dakar (Senegal) and Cabo Verde to Angola.

Depth: 1–54 m.

Habitat: under rocks on sand or mud.

Type of Development: probably planktotrophic (inferred from the genus).

Remarks: in a review of the family Holothuriidae, Rowe (1969) listed the Azores under the geographical distribution of *Holothuria dakarensis*, a statement repeated by subsequent works. Pawson & Shirley (1977) believed that Rowe based his statement on material from Faial Island, deposited in the collection of the British Natural History Museum. On re-examination, the authors concluded the specimens belonged either to *H. mammata* or *H. tubulosa* rather than *H. dakarensis*. Furthermore, Borrero-Pérez *et al*. (2009) showed that *H. dakarensis* was historically confused with *H. mammata*, restricting the geographical range of *H. dakarensis* in the East Atlantic to southern latitudes of the African coasts, from Senegal and Cabo Verde to Angola.

Erroneous – *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791

1924. *Holothuria tubulosa* (Gmelin); Nobre: 89.
1930. *Holothuria tubulosa* (Gmelin); Nobre: 23.
1938. *Holothuria tubulosa* Gmelin; Nobre: 143–144, figs. 58.1, 69.1.
1977. *Holothuria* (*Holothuria*) *tubulosa* Gmelin; Pawson & Shirley: 915.
1983. *Holothuria tubulosa* Gmelin, 1790; Marques: 4, fig. 8.
1997. *Holothuria tubulosa* Gmelin, 1788; Pereira: 333.
1998. *Holothuria tubulosa;* Morton *et al.*: 98, 169, figs. 5.2T, 8.8R.
2009a. *Holothuria tubulosa*; Wirtz: 46.
2010. *Holothuria tubulosa* Gmelin, 1790; Micael & Costa: 323.
2010. *Holothuria tubulosa* Gmelin, 1790; Micael *et al.*: 329.
2012. *Holothuria (Holothuria) tubulosa* Gmelin, 1790; Micael *et al.*: 4.

Type locality: Mediterranean Sea.

See: Tortonese (1965: 53–56, figs. 16, 17); Borrero-Pérez *et al.* (2009).

Distribution: Mediterranean Sea.

Depth: 0–100 m.

Habitat: sand, mud to gravel, on sea grass prairies.

Type of Development: probably planktotrophic (inferred from the genus).

Commercial value: edible.

Remarks: see remarks under *H. mammata*.

Subgenus *Roweothuria* Thandar, 1988

Erroneous – *Holothuria* (*Rowethuria*) *arguinensis* Koehler & Vaney, 1906

1969. *Holothuria arguinensis* Koehler & Vaney, 1906; Rowe: 149, 150.
1992b. *Holothuria* (*Lessonothuria*) *arguinensis* Koehler & Vaney, 1906; Pérez-Ruzafa *et al.*: 152–153.

Type locality: Mauritania.

See: Koehler & Vaney (1906: 62–65, pl. 5, figs. 5–13, pl. 6, figs. 14–21); Pérez-Ruzafa *et al.* (1992b); Massin (1993: 399, fig. 1); González-Wangüemert & Borrero-Pérez (2012); Domínguez-Godino *et al.* (2015).

Distribution: East Atlantic, from Portuguese and Moroccan coasts to the north of Senegal, and Canaries; reported elsewhere in the north of the Alboran Sea (Mediterranean Sea).

Depth: 0–52 m.

Habitat: hard to soft substrates, macroalgal beds and seagrass meadows, tide pools.

Type of Development: planktotrophic, with a late non-feeding doliolaria stage (*c.* 18 days at 27–28 °C).

Commercial value: edible.

Remarks: in a review of the family Holothuriidae, Rowe (1969) listed the Azores under the geographical distribution of this species. We could not trace the original record and thus consider Rowe's statement as a mistake.

Family Mesothuriidae Smirnov, 2012

Genus *Mesothuria* Ludwig, 1894

Erroneous – *Mesothuria intestinalis* (Ascanius, 1805)

1902. *Allantis* (nov. gen.*) intestinalis*, (Asc. et Rathke) var. *Verrilli*, Théel; Hérouard: 18–21, pl. 1, figs. 3–6.

1927a. *Mesothuria intestinalis* (Ascanius); Mortensen: 381.

1938. *Mesothuria intestinalis* (Ascanius); Nobre: 150–152.

1954. *Mesothuria intestinalis* (Ascanius and Rathke); Deichmann: 385–386.

1965. *Mesothuria intestinalis* (Asc. Rathke); Tortonese: 69–70, fig. 26.

1992b. *Mesothuria intestinalis* (Ascanius et Rathke, 1767); Pérez-Ruzafa *et al*.: 144.

2010. *Mesothuria intestinalis* (Ascanius, 1805); Micael & Costa: 323.

2012. *Mesothuria intestinalis* (Ascanius, 1805); Micael *et al*.: 4.

Type locality: Norway.

See: Deichmann (1930: 94–95, pl. 6, figs. 9, 10, 1954: 385–386); Gebruk *et al.* (2012: 291–300, figs. 1, 9C–D).

Distribution: Mediterranean Sea and North Atlantic, from the Caribbean waters eastwards to the Gulf of Guinea, north to Scandinavian waters, including Canaries.

Depth: 20–2,480 m, infralitoral depths tend to be restricted to higher latitudes.

Habitat: muddy substrates, usually covers itself with shell fragments and other bottom material.

Type of Development: probably direct or lecithotrophic; hermaphroditic.

Remarks: historically, reports of *M. intestinalis* and *M. verrilli* are intermingled. For example, Hérouard (1902) considered *M. verrilli* as just a variety of *M. intestinalis*, and placed the material collected by RV 'Princesse Alice' under the later. Hérouard's decision led subsequent bibliography (*e.g.,* Mortensen 1927a; Nobre 1938) to include *M*. *intestinalis* in the Azorean fauna, disregarding the specific value of the variety. Later, Hérouard (1923) reconsidered *M. verrilli* as distinct species, an 'abyssal representative' of *M. intestinalis*. On reviewing *M. verrilli* historical material from the NE Atlantic (including the material taken by RV 'Talisman' in Azorean waters), Gebruk *et al*. (2012) discovered a second species, *M. milleri*. Additionally, by studying ontological changes in *M*. *milleri*, Gebruk recognized his new species in the *M*. *verrilli* descriptions by Marenzeller (1893) and Hérouard (1902, 1923). Coincidently, such age dependent variation is very close as well of what is known for *M. intestinalis*, leading to the possibility of both species being present among the material collected in the Azores by RVs 'Princesse Alice' and 'Hirondelle'. Conversely, Gebruk *et al*. (2012) also remarked that *M. intestinalis* is easily distinguished from other *Mesothuria* species by having a sequential hermaphrodite gonad. This particularity was acknowledged by Hérouard (1923) at the time and used this diagnosing character to further substantiate the promotion of *M. verrilli* to a distinct species. Marenzeller (1893) described RV 'Hirondelle' specimens as gonochoristic. Thus, the presence of *M*. *intestinalis* is still to be confirmed in the Azores in spite of its widespread distribution in the North Atlantic (see remarks under *M. milleri*).

Erroneous – *Mesothuria verrilli* (Théel, 1886b)

1893. *Holothuria Verrilli*, Théel; Marenzeller: 7–9, pl. 1, fig. 2, pl. 2, fig. 2.
1902. *Allantis* (nov. gen.*) intestinalis*, (Asc. et Rathke) var. *Verrilli*, Théel; Hérouard: 18–21, pl. 1, figs. 3–6.
1902. *Mesothuria Verrillii*, Théel, Östergren; Perrier: 307–312, figs. 3–4, pl. 16, figs. 22–31.
1923. *Mesothuria Verrilli*, Théel; Hérouard: 10–13.
1927a. *Mesothuria Verrilli* (Théel); Mortensen: 381–382, figs. 224.4–5.
1930. *Mesothuria verrilli* (Théel); Deichmann: 93–94, pl. 6, figs. 1–8.
1938. *Mesothuria verrilli* (Théel); Nobre: 152.
1988. *Mesothuria verrilli* (Théel, 1886); Harvey *et al*.: 184.
1992b. *Mesothuria verrilli* (Théel, 1886); Pérez-Ruzafa *et al*.: 144.

2005. *Mesothuria verrilli* (Théel, 1886); García-Diez *et al*.: 51.

Type locality: off Ambergris Cay, Caribbean.

See: Théel (1886b: 6; as *Holothuria verrilli*); Deichmann (1930); Gebruk *et al.* (2012: 268–274, fig. 2).

Distribution: reliable records are restricted to Caribbean waters.

Depth: 700–2,683 m.

Habitat: soft bottoms.

Remarks: in the original description for this species, Théel (1886b) included diagnostic characteristics that could encompass other closely related species such as *M. intestinalis* and *M. milleri*. As a consequence, this species originally described for the Caribbean soon found its geographical range extended to the entire North Atlantic. Later reviews, such as Gebruk *et al.* (2012) have concluded that *M*. *verrilli* is restricted to the western Atlantic, and NE Atlantic records are most probably confusions with either *M. intestinalis* or *M. milleri*. Thus, reports of this species from the Azores should be dismissed as misidentifications.

Order Persiculida Miller *et al*., 2017

Family Molpadiodemidae Miller *et al*., 2017

Genus *Molpadiodemas* Heding, 1935

Erroneous – *Molpadiodemas atlanticus* (Perrier, 1898)

1930. *Pseudostichopus atlanticus* Perrier; Deichmann: 87–88.

Type locality: between the Azores and European waters (N42°19’00” W21°15’46”).

See: Perrier (1902: 333–337, pl. 17, figs. 15–20, as *Pseudostichopus atlanticus*); O’Loughlin & Ahearn (2005: 153, figs. 3a, b, 4a–d, 6a, b); Bohn (2006: 16–19, figs. 9A, 10).

Distribution: cosmopolitan, Atlantic and Pacific deep-waters; from the Caribbean north to west of Greenland, east to the West European Basin and south to Southern Africa.

Depth: 2,610–5,415 m.

Habitat: mud.

Remarks: see remarks under *Molpadiodemas villosus.*

Erroneous – *Molpadiodemas villosus* (Théel, 1886a)

1902. *Pseudostichopus villosus*, Théel; Hérouard: 11–13, pl. 2, fig. 1–3, pl. 7, fig. 3.

1932. *Pseudostichopus villosus* Théel; Grieg: 4.

2005. *Pseudostichopus villosus* Théel, 1886; García-Diez *et al.*: 51.

Type locality: off Japan, Pacific (N35°22’ E169°53’).

See: Théel (1886a: 170–171, as *Pseudostichopus villosus*); O’Loughlin & Ahearn (2005: 164–165, figs. 2a, e, 7d–f, 8q–t, 12a–d).

Distribution: cosmopolitan; in the Atlantic from the North American Basin south to the Scotia Sea and Antarctica.

Depth: 681–5,304 m.

Habitat: soft sediments, from mud to ooze.

Type of Development: a probable brooder.

Remarks: Théel (1886a) remarked that among the material collected by RV ‘H.M.S. Challenger’ off Chilean waters there were specimens closely resembling his newly described species *Molpadiodemas villosus* (= *Pseudostichopus villosus*), but which lacked tube feet. Perrier (1902) believed that those specimens belonged to his newly described species, *M. atlanticus*. More recently, O’Loughlin & Ahearn (2005) re-examined the material in question and confirmed Perrier’s assumption. In the same year of Perrier’s publication, Hérouard (1902) reported *Molpadiodemas villosus* (= *Pseudostichopus villosus*) from the archipelago based on the material collected by RV ‘Princesse Alice’ (sta 652: N36°55’00” W22°22’45”, 4,261 m). Coincidently, Hérouard’s description and figures presented an animal with a smooth surface, likewise close to the Chilean material taken by ‘H.M.S. Challenger’ but not to *M. villosus*, which has a hairy like body surface. Deichmann (1930) compared her specimens of *M. atlanticus* from the Caribbean with Hérouard figures and concluded that they were identical. Perrier (1902) believed the distribution of ossicles could be used as a diagnostic character of *M. atlanticus* since *M. villosus* completely lacks ossicles in its tegument. RV ‘Princesse Alice’ specimens completely lacked ossicles, except in the gonads. On the other hand, it is not uncommon for ossicles to dissolve during preservation, a problem Deichmann (1930) noted in her own *M*. *atlanticus* specimen. She attributed this to the acidic nature of the alcohol used to preserve her material. Moreover, in O’Loughlin & Ahearn (2005)’s review stated that ossicles are not always present in this species.

Conversely, Deichmann (1930) omitted data on the internal anatomy, probably because her own specimen had almost no internal organs, due to evisceration. The striking difference that separates RV 'Princesse Alice' material from *M. atlanticus* is its simple non-branching sac-like gonad structure. The genus *Molpadiodemas* as it was re-diagnosed by O'Loughlin & Ahearn (2005) encompasses only holothurians with branching gonads, with tubules arising from a common source at end of a gonoduct, thus excluding *M. atlanticus* and invalidating Deichmann's (1930) suggestion. In contrast, O'Loughlin (2002) believed RV 'Princesse Alice' *M*. *villosus* belonged to the highly variable species *Pseudostichopus peripatus*, a close similar species known to occur in the Azores. Unlike *M. atlanticus* the unbranching gonad structure poses no diagnostic problem. However, O'Loughlin (2002) noted that Hérouard's description encompassed far too large individuals (up to 170 mm), with no distinctive lateroventral margin, and as result the author marked the record as uncertain. Regardless, and in spite of the presence of both *M*. *atlanticus* and *M*. *villosus* in the vicinity of the Azorean, the presence of both species in the archipelago is still to be confirmed.

Family Pseudostichopodidae Miller *et al*., 2017

Genus *Pseudostichopus* Théel, 1882

Erroneous – *Pseudostichopus occultatus* Marenzeller, 1893

1902. *Pseudostichopus occultatus* Marenzeller; Hérouard: 14–15, pl. 2, figs. 4–14. [misidentified *P*. *peripatus*]
1938. *Pseudostichopus occultatus* Marenzeller; Nobre: 156–157. [based on Hérouard 1902]
2005. *Pseudostichopus occultatus* Marenzeller, 1893; García-Diez *et al.*: 51. [based on Hérouard 1902]

Type locality: Mediterranean Sea.

See: O'Loughlin (2002: 307, as *Meseres occultatus*); O'Loughlin & Ahearn (2005: 173–174); Mecho *et al.* (2014: 288–289, figs. 8A–D).

Distribution: Mediterranean Sea, reported also from Cape Finisterre, Galicia (NE Atlantic).

Depth: 363–2,250 m.

Habitat: mud.

Remarks: Hérouard (1902) reported *Pseudostichopus occultatus* based on the material collected by RV 'Princesse Alice' at two stations in Azorean waters (sta 527: N38°08'00" W23°15'45"; sta 650: N36°54'00" W20°46'15"). Later, Hérouard (1923) transferred these specimens to two newly described species *P. lapidus* (sta 527) and *P. marenzelleri* (sta 650). Both species are considered synonyms of *P. peripatus*.

ACKNOWLEDGEMENTS

We would like to gratefully and sincerely thank João Paulo Constância (Museu Carlos Machado, Ponta Delgada, Azores), Nuno Lourenço (EMEPC, Paço d'Arcos, Portugal), Felipe Porteiro (DOP, University of the Azores, Horta, Azores), and Alexandra Cartaxana (MB-NMHN, Lisbon, Portugal) for access to the collections and for the loan of specimens. We are also grateful to Max Whissak for the providing us with additional photographs by manned submersible *LULA 1000*. We thank all the participants of the several workshops and expeditions that through the years help convey the rich material that is now part of the echinoderm reference collection of the Department of Biology (University of the Azores). The authors would like to thank Biodiversity Heritage Library (BHL, http://www.biodiversitylibrary.org/) and Internet Archive (https://archive.org/) for the extensive and comprehensive digital resources that considerably ease access to scientific literature. We gratefully acknowledge funding by the Austrian Science Fund (FWF) grant P29508-B25 ("Phylogeny an evolution of edible sea urchins"). Patrícia Madeira benefited from PhD grant SFRH/BD/61146/2009 (FCT – Fundação para a Ciência e Tecnologia, Portugal) and from the SYNTHESYS Project (AT-TAF-2563; AT-TAF-0260; BE-TAF-404), which is financed by European Community Infrastructure Action under the FP6 and FP7 programmes (http://www.synthesys.info/). Ricardo Cordeiro benefited from PhD grant SFRH/BD/60366/2009 (FCT – Fundação para a Ciência e Tecnologia, Portugal). Sérgio Ávila acknowledges his IF/00465/2015 research contract funded by Fundação para a Ciência e a Tecnologia (Portugal). This work was also funded by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE and by National Funds through FCT – Foundation for Science and Technology under the UID/BIA/50027/2013, POCI-01-0145-FEDER- and by regional funds through DRCT-M1.1.a/005/Funcionamento-C-/2016 (CIBIO-A). This work was also financed by FEDER in 85% and by Azorean Public funds by 15% through Operational Program Azores 2020, under the project AZORESBIOPORTAL –PORBIOTA (ACORES-01-0145-FEDER-000072).

5.5. References

Agassiz, A. (1863) List of the echinoderms sent to different Institutions in exchange for other specimens, with annotations. *Bulletin of the Museum of Comparative Zoölogy at Harvard College,* 1(2), 17–28.

Agassiz A. (1869) Preliminary report on the echini and star–fishes dredged in deep-water between Cuba and the Florida Reef, by L. F. de Pourtalès, Assist. U.S. Coast Survey. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 1(9), 253–308.

Agassiz, A. (1872–1874) Revision of the Echini. *Illustrated catalogue of the Museum of Comparative Zoölogy at Harvard College*, 7(1–4), 762 pp.

Agassiz, A. (1879) Preliminary Report on the Echini of the Exploring Expedition of H.M.S. Challenger, Sir C. Wyville Thomson Chief of Civilian Staff. *Proceedings of the American Academy of Arts and Sciences*, 14, 190–212.

Agassiz, A. 1880. Preliminary report on the Echini. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea in 1878–79, and along the Atlantic Coast of the United States during summer of 1880, by the U.S. Coast Survey Steamer “Blake”. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 8, 69–84.

Agassiz, A. (1881) Report on the Echinoidea dredged by H.M.S. Challenger 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger, Zoology*, 3, 1–321.

Agassiz, A. (1904) The Panamic Deep Sea Echini. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 31, x(10)+243 pp.

Agassiz, L. (1836) Prodrome d’une Monographie des Radiaires ou Echinodermes. *Mémoires de la Société des Sciences naturelles de Neuchâtel*. 1, 168–199.

Agassiz, L. (1838) Échinites. Famille des Cidarides. Première Monographie. Des Salénies. *Monographies d’Échinodermes vivans et fossiles.* L. Agassiz, Neuchâtel, 1–132+2 pp.

Agassiz, L. (1840) *Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. Sequuntur characteres diagnostici generum novorum vel minus cognitorum*. Oliv. Petitpierre, Neuchâtel, 20 pp.

Agassiz, L. & Desor, P.J.E. (1846) Catalogue raisonné des familles, des genres, et des espèces de la classe des échinodermes. *Annales des Sciences Naturelles, Troisième Série, Zoologie*, 6, 305–374.

Alva, V. & Vadon, C. (1989) Ophiuroids from the western coast of Africa (Namibia and Guinea-Bissau). *Scientia Marina*, 53, 827–845.

Alves, F.M.A., Chicharro, L.M., Serrão, E. & Abreu, A.D. (2001) Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). *Scientia Marina*, 65, 383–392.

Améziane, N., Bourseau, J.P., Heinzeller, T. & Roux, M. (1999) Les genres *Cyathidium* et *Holopus* au sein des Cyrtocrinida (Crinoidea; Echinodermata). *Journal of Natural History*, 33, 439–470.

Améziane, N. (2007) Echinodermata of New Caledonia. *In*: Payri, C. & Richer De Forges, B. (Eds.) Compendium of marine species of New Caledonia. *Documents Scientifiques Techniques* IRD, Nouméa, 2nd edition, II7, 337–347.

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Blazewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandćo, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.-Y., Cheng, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J.F., Dawson, M.N., De Clerck, O., Decock, W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M.A., Turon, X., Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G.C., Wilson, S.P. & Costello, M.J. (2012) The Magnitude of Global Marine Biodiversity – Supplemental Information. *Current Biology*, 22, 1–91.

Arendt, Y.A. (1974) The sea lilies. Cyrtocrinids. *Transactions of the Palaeontological Institute, Academy of Science of the USRR*, 144, 1–251.

Ascanius, P. (1805) *Icones Rerum Naturalium, ou figures enluminées d'histoire naturelle du Nord*. Möller et fils, Copenhagen, 5, 1–8.

Ávila, S.P., Madeira, P., Silva, C.M. da, Cachão, M., Landau, B., Quartau, R. & Martins, A.M.F. (2008) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science*, 23, 777–785.

Ávila, S.P., Madeira, P., Zazo, C., Kroh, A., Kirby, M., Silva, C.M. da, Cachão, M. & Martins, A.M.F. (2009) Palaeocology of the Pleistocene (MIS 5.5) outcrops of Santa Maria Island (Azores) in a complex oceanic tectonic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274, 18–31.

Ávila, S. P., Rebelo, A., Medeiros, A., Melo, C., Gomes, C., Bagaço, L., Madeira, P., Borges, P.A., Monteiro, P., Cordeiro, R., Meireles, R. & Ramalho, R. (2010) *Os fósseis de Santa Maria (Açores). 1. A jazida da Prainha*. OVGA, Observatório Vulcanológico e Geotérmico dos Açores, Lagoa, 103 pp.

Ávila, S.P., Medeiros, A., Martins, A.M.F., Silva, A., Melo, C., Gomes, C., Michielsen, G., Madeira, J., Bagaço, L., Silva, L., Fernandes, M., Silva, M., Madeira, P., Cordeiro, R., Meireles, R. & Prieto, R. (2011) *Lajes do Pico "À ban-baxe-muro"*, Editora Publiçor, Ponta Delgada, 345 pp.

Ávila, S.P., Melo, C. Silva, L., Ramalho, R., Quartau, R., Hipólito, A., Cordeiro, R., Rebelo, A.C., Madeira, P., Rovere, A., Hearty, P.J., Henriques, D., Silva, C.M. da, Martins, A.M.F. & Zazo, C. (2015a) A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews*, 114, 126–148.

Ávila, S.P., Ramalho, R., Habermann, J., Quartau, R., Kroh, A., Berning, B., Johnson, M., Kirby, M., Zanon, V., Titschack, J., Goss, A., Rebelo, A.C., Melo, C., Madeira, P., Cordeiro, R., Meireles, R., Bagaço, L., Hipólito, A., Uchman, A., Silva, C.M. da, Cachão, M. & Madeira, J. (2015b) Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores, NE Atlantic Ocean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 430, 57–73.

Ávila, S.P., Ramalho, R.S., Habermann, J.M. and Titschack, J. (2018) The marine fossil record at Santa Maria Island (Azores). *In*: Kueppers U., Beier C. (eds) *Volcanoes of the Azores*. Springer, Berlin, Heidelberg, pp. 155–196.

Augier H. (1985) Premier contribution a l'etude et a la cartigraphe des biocenoses marines benthiques de l'ile de Madere. *Boletim do Museu Municipal do Funchal (Hist. Nat.)*, 37(168), 86–129.

Bacallado, J.J., Moreno, E. & Pérez-Ruzafa, A. (1985) Echinodermata (Canary Islands) provisional Check-list. *In*: Keegan, B.F. & O'Connor, B.D.S. (Eds.) *Echinodermata; Proceedings of the 5th International Echinoderm Conference, Galway, September 1984*. A.A. Balkema, Rotterdam. pp. 149–151.

Bashmachnikov, I., Lafon, V. & Martins, A. (2004) Sea surface temperature distribution in the Azores region. Part II: space-time variability and underlying mechanisms. *Arquipélago*. *Life and Marine Sciences*, 21A, 19–32.

Barrois, T. (1888) Liste des Echinodermes recueillis aux Açores durant les mois d'Août et September 1887. *Revue Biologique du Nord de la France*, 1, 31–33, 69–75, 109–115.

Bartsch, I. (1987) Notes on Ophiuroidea (Echinodermata) from the northeastern Atlantic Ocean. I. Ophiacanthidae. *Spixiana*, 10, 115–130.

Bartsch, I. (2008) Notes on ophiuroids from the Great Meteor Seamount (Northeastern Atlantic). *Spixiana*, 31(2), 233–239.

Bather, F. A. (1899) A phylogenetic classification of the Pelmatozoa. *Report of the Sixty-eighth meeting of the British Association for the Advancement of Science held at Bristol in September 1898, Transactions of Section D*, 916–923.

Bell, F.J. (1892) *Catalogue of the British echinoderms in the British Museum (Natural History)*. Trustees of the British Museum, London, xvii(17)+202 pp.

Benavides-Serrato, M., Borrero-Pérez, G.H. & Diaz-Sanchez, C.M. (2011) *Equinodermos del Caribe colombiano I: Crinoidea, Asteroidea y Ophiuoridea.* Serie de Publicaciones Especiales de Invemar, Santa Marta, 22, 384 pp.

Benavides-Serrato, M., Borrero-Pérez, G.H. & Diaz-Sanchez, C.M. (2012) *Equinodermos del Caribe colombiano II: Echinoidea y Holothuroidea*. Serie de Publicaciones Especiales de Invemar, Santa Marta. 30, 250 pp.

Bernasconi, I. (1962) *Ceramaster patagonicus fisheri*, nueva sub especie de California. *Anales del Instituto de Biologia*, 33(1–2): 287–291.

Bianchi, C.N., Morri, R.H.C., Sartoni, G. & Wirtz, P. (1998) Sublittoral epibenthic communities around Funchal (Ilha da Madeira, NE Atlantic). *Boletim do Museu Municipal do Funchal* (*História Natural*), supplement 5, 59–80.

Billett, D.S.M. (1988) *The ecology of deep-sea holothurians*. PhD thesis (unpublished), University of Southampton, Southampton, xi(11)+398.

Bisoll, P.M., Costa, R. & Sibuet, M. (1984) Ecological and genetical survey on two deep-sea holothurians: *Benthogone rosea* and *Benthodytes typica*. *Marine Ecology, Progress* Series, 15, 275–281.

Blainville, H.M. de (1825) Oursin, Echinus (Actinozoaires). *In*: Levrault, F.G. (Ed.) *Dictionnaire des sciences naturelles*. Le Normat, Paris, 37, 59–98.

Blainville, H.M. de (1830) Mollusques, Vers et Zoophytes. *In*: Levrault, F.G. (Ed.) *Dictionnaire des sciences naturelles*. Le Normat, Paris, 60, 548 pp.

Blainville, H.M. de (1834) Manuel d'Actinologie ou de Zoophytologie. F.G. Levrault, Strasbourg, 1, viii(8)+694;

Blake, D.B. (1987) Classification and phylogeny of post-Paleozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History*, 21, 481–528.

Bohn, J.M. (2004) Remarks on some Holothuroidea described by Heller from the eastern Adriatic Sea. *In*: Heinzeller, T. & Nebelsick, J.H. (Eds.) *Echinoderms: München. Proceedings of the 11th international echinoderm conference*, Munich, Germany, 6–10 October 2003. A.A. Balkema Publishers, Leiden, pp. 517–519.

Bohn, J.M. (2006) Crinoidea and Holothuroidea (Echinodermata) of the abyssal Angola Basin—Results of the DIVA–1 expedition of FS "Meteor" (Cruise M48/1). *Zootaxa*, 1276, 1–31.

Boissin, E., Hoareau, T. B., Féral, J. P., & Chenuil, A. (2008a). Extreme selfing rates in the cosmopolitan brittle star species complex *Amphipholis squamata*: data from progeny-array and heterozygote deficiency. *Marine Ecology Progress Series*, 361, 151–159.

Boissin, E., Féral, J.P. & Chenuil, A. (2008b) Defining reproductively isolated units in a cryptic and syntopic species complex using mitochondrial and nuclear markers: the brooding brittle star, *Amphipholis squamata* (Ophiuroidea). *Molecular Ecology*, 17(7), 1732–1744.

Bölsche, W. (1866) Ueber *Actinometra Bennettii* und eine neue *Comatula* Art (*Antedon Dübenii*). *Archiv für Naturgeschichte*, 32(1), 90–92.

Borges, M. & Amaral, A.C.Z. (2007) Ophiuroidea (Echinodermata): quatro novas ocorrências para o Brasil. *Revista Brasileira de Zoologia*, 24(4), 855–864.

Borges, M., Monteiro, A.M.G. & Amaral, A.C.Z. (2002) Taxonomy of Ophiuroidea (Echinodermata) from the continental shelf and slope of the Southern and Southeastern Brazilian Coast. *Biota Neotropica*, 2(2), 1–69.

Borges, M. & Campos, L.S. (2011) *Ophiomusium acuferum* (Ophiolepididae) and *Ophiomisidium pulchellum* (Ophiuridae) (Ophiuroidea: Echinodermata), redescription based on the Brazilian specimens. *Zoologia*, 28(2), 219–225.

Borrero-Pérez, G.H., Benavides-Serrato, M., Solano, Ó. & Navas, G.R. (2008) Brittle stars (Echinodermata: Ophiuroidea) from the continental shelf and upper slope of the Colombian Caribbean. *Revista de Biología Tropical*, 56(Suppl. 3), 169–204.

Borrero-Pérez, G.H., Pérez-Ruzafa, A., Marcos, C. & González-Wangüemert, M. (2009) The taxonomic status of some Atlanto-Mediterranean species in the subgenus *Holothuria* (Echinodermata: Holothuroidea: Holothuriidae) based on molecular evidence. *Zoological Journal of the Linnean Society*, 157, 51–69.

Borrero-Pérez G.H., Gómez-Zurita, J., González-Wangüemert, M., Marcos, C., Pérez-Ruzafa, A. (2010) Molecular systematics of the genus Holothuria in the Mediterranean and Northeastern Atlantic and a molecular clock for the diversification of the Holothuriidae (Echinodermata: Holothuroidea). *Molecular Phylogenetics and Evolution*, 57, 899–906.

Borrero-Pérez, G.H., González-Wangüemert, M., Marcos, C., Pérez-Ruzafa, A. (2011) Phylogeography of the Atlanto-Mediterranean sea cucumber *Holothuria* (*Holothuria*) *mammata*: the combined effects of historical processes and current oceanographical pattern. *Molecular Ecology*, 20(9), 1964–1975.

Brady, G.S. & Robertson, D. (1871) Descriptions of two new species of British Holothurioidea. *Proceedings Zoological Society of London*. 1871, 690–692.

Brandt, J.F. (1835) *Prodromus Descriptionis Animalium ab H. Mertensio in Orbis Terrarum Circumnavigatione Observatorum*. Petropoli, Leipzig, 1, 75 pp.

Bronn, H.G. (1860) *Die Klassen und Ordnungen der Strahlenthiere: wissenschaftlich dargestellt in Wort und Bild Band Zweiter (Actinozoen)*. C.F. Winter'sche Verlagshandlung, Leipzig & Heidelberg, 434 pp.

Bronstein, O., Georgopoulou, E., & Kroh, A. (2017). On the distribution of the invasive long-spined echinoid Diadema setosum and its expansion in the Mediterranean Sea. *Marine Ecology Progress Series*, 583, 163–178.

Bruguière J.G. (1791) T*ableau Encyclopédique et Méthodique des trois Règnes de la Nature: vers, coquilles, mollusques et polypes divers*. Mme Agasse widow, Imprimeur-Libraire, Paris, 180 pp.

Bruzelius, N. (1805) *Dissertatio sistens species cognitas asteriarum, quam, sub praesidio A.J. Retzii. exhibet N. Bruzelius*. Lundae, 37 pp.

Burmeister, H. (1837) *Handbuch der Naturgeschicht*. Enslin, Berlin, 2, xii(12)+pp. 369–858.

Cadenat, J. (1938) Liste des echinodermes recueillis pendant la cinquieme croisiere du navire de recherches President-Theodore-Tissier. *Revue des Travaux de l'Institut des Peches Maritimes*, 11, 349–375.

Cardigos, F., Colaço, A., Dando, P.R., Ávila, S.P., Sarradin, P.-M., Tempera, F., Conceição, P., Pascoal, A. & Santos, R.S. (2005) Shallow-water hydrothermal vent field fluids and communities of the D. João de Castro Seamount (Azores). *Chemical Geology*, 224, 153–168

Carpenter, P.H. (1883a) Note on *Democrinus Parfaiti*. *Annals and Magazine of Natural History*, 11(5), 334–336.

Carpenter, P.H. (1883b) The Stalked Crinoids of the Caribbean Sea. *Bulletin of the Museum Comparative Zoölogy at Harvard College*, 10(4), 165–181.

Carpenter P.H. (1884) Report on the Crinoidea collected during the voyage of H.M.S. Challenger, during the years 1873–1876. Part I. The Stalked Crinoids. *Report on the Scientific Results of the Voyage of H.M.S. Challenger, Zoology*, 11(32), xii (12)+442 pp.

Carpenter, W.B. & Jeffreys, J.G. (1871) Report on deep sea research carried out during the months of July, August and September 1870, in H.M. surveying-ship 'Porcupine'. *Proceedings of the Royal Society of London*, 19(125), 146–220.

Castro, M.L. & Viegas, M.C. (1983) Estudo dos povoamentos de algas fotófilas da ilha de S. Miguel (Açores). *Arquipélago, Série Ciências da Natureza*, 4, 7–30.

Chapman, G. (1955) Aspects of the Fauna and Flora of the Azores, IV: Echinodermata. *Annals and Magazine of Natural History*, 12(8), 398–400.

Cherbonnier, G. (1941) Etude anatomique et biogeographique sur deux cucumaria abyssaux, *C. abyssorum* Theel et *C. albatrossi* n. sp. *Bulletin Muséum National Histoire Naturelle*, Paris. 2ª série, 13, 93–103.

Cherbonnier, G. (1950) Note sur *Holothuria dakarensis* Panning. *Bulletin Muséum National Histoire Naturelle*, Paris, 2 série, 22 (1), 102–108.

Cherbonnier, G. (1957) Une Ophiure nouvelle de Méditerranée: *Amphiura apicula* nov. sp. *Vie et Milieu*, 8(2), 200–204.

Cherbonnier, G. (1958) Holothuries des cotes de Sierra Leone (5e et dern. note). *Bulletin Muséum National Histoire Naturelle*, Paris, 2 série, 30, 371–378.

Cherbonnier, G. (1959) Echinides: *Expédition Océanographique Belege dans les Eaux Cotiérs Africaines de l'Atlantique Sud. 1948–1949. Institut Royal des Sciences Naturelles de. Belgique, Résultats Scientifiques*, 3(6), 37–59.

Cherbonnier, G. (1965) Holothurides. *Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique Sud (1948–1949): résultats scientifiques*, Brussels, 3(2), 23 pp.

Cherbonnier, G. (1969) Échinodermes récoltés par la «Thalassa» au large de côtes d'espagne et du Golfe de Gascogne (3–12 AOUT 1967). *Bulletin Muséum National Histoire Naturelle Paris*, 2 série, 41(1), 343–361.

Cherbonnier, G. (1970) Échinodermes récoltés par la «Thalassa» au large de côtes d'espagne et du Golfe de Gascogne (18–25 AOUT 1968). *Bulletin Muséum National Histoire Naturelle*, Paris, 2ª série, 41(5), 1266–1277.

Cherbonnier G. & Guille, A. (1972) Sur une espece actuelle de Crinoide cretacique de la famille Holopodidae: *Cyanthidium foresti* nov. sp. *Comptes rendus hebdomadaires des séances de l'Académie des sciences. Série D, Sciences Naturelles*, 274, 2193–2196.

Cherbonnier G. & Sibuet, M. (1972) Résultats scientifiques de la campagne Noratlante: Astérides et Ophiurides. *Bulletin du Muséum National D'histoire Naturelle*, 102(76), 1333–1394.

Chesher, R. H. (1966) The R/V Pillsbury deep-sea biological expedition to the Gulf of Guinea, 1964–1965, 10: report on the Echinoidea collected by the R/V Pillsbury in the Gulf of Guinea. *Studies in Tropical Oceanography*, 4(1), 209–223.

Chesher, R.H. (1968) The Systematics of Sympatric Species in West Indian Spatangoids: A Revision of the Genera Brissopsis, Plethotaenia, Paleopneustes, and Saviniaster. *Studies in Tropical Oceanography*, 7, 168 pp.

Clark A.H. (1908) New genera of unstalked crinoids. *Proceedings of the Biological Society of Washington*, 21, 125–136.

Clark, A.H. (1911a) The recent crinoids of the coasts of Africa. *Proceedings of the U.S. National Museum*, 40, 1–51.

Clark, A.H. (1914) Echinoderma II: Crinoidea. *In*: Michaelsen, W. *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. L. Friederichsen & Co. Hamburg, 1(2), 305–318.

Clark A.H. (1923b) A revision of the recent representatives of the crinoid family Pentacrinidae, with the diagnoses of two new genera. *Journal of the Washington Academy of Sciences*, 13, 8–12.

Clark, A.H. (1939) Echinoderms (other than holothurians) collected on the presidential cruise of 1938. *Smithsonian Miscellaneous Collections*, 98(11): 19 pp.

Clark, A.H. (1948) Some interesting starfishes and brittle stars dredged by the Atlantis in mid-Atlantic. *Journal of The Washington Academy of Sciences*, 38, 75–78.

Clark, A.H. (1949) Echinoderms from the mid-Atlantic dredged by lhe Atlantis in the summer of 1948. *Journal of the Washington Academy of Sciences*, 39, 371–377.

Clark, A.H. & A.M. Clark (1967) A Monograph of the Existing Crinoids. Part 5 Suborders Oligophreata (concluded) and Macrophreata. *United States National Museum Bulletin*, 82, 1–860.

Clark, A.M. (1951) Some echinoderms from South Africa. *Transactions of the Royal Society of South Africa*, 33(2), 193–221.

Clark, A.M. (1953) A revision of the genus *Ophionereis* (Echinodermata, Ophiuroidea). *Proceedings of the Zoological Society of London*, 123(1), 65–94.

Clark, A.M. (1970) Notes on the family Amphiuridae (Ophiuroidea). *Bulletin of the British Museum (Natural History) Zoology*, 19(1), 1–81.

Clark, A.M. (1973) Some new taxa of recent stalked Crinoidea. *Bulletin of the British Museum (Natural History), Zoology*, 25(7), 267–288.

Clark, A.M. (1974) Notes on some echinoderms from Southern Africa. *Bulletin of the British Museum (Natural History) Zoology*, 26(6), 421–487, plates 1–3.

Clark, A.M. (1977) Notes on deep-water Atlantic Crinoidea. *Bulletin of the British Museum (Natural History) Zoology*, 31(4), 159–186.

Clark, A.M. (1980) Crinoidea collected by the Meteor and Discovery in the NE Atlantic. *Bulletin of the British Museum (Natural History)*, *Zoology*, 38(4), 187–210.

Clark, A.M. (1981) Notes on Atlantic and other Asteroidea. 1. Family Benthopectinidae. *Bulletin of the British Museum (Natural History)*, *Zoology*, 41(3), 91–135.

Clark, A.M. (1982a) Notes on Atlantic Asteroidea. 2. Luidiidae. *Bulletin of the British Museum (Natural History) Zoology*, 42(3), 157–184.

Clark A.M. (1982b) Inter-relationships of the recent stalked non–isocrinid Crinoidea. *Australian Museum Sydney Memoir*, 16, 121–128.

Clark A.M. & Rowe, F.W.E. (1971) Monograph of shallow-water Indo-West Pacific echinoderms. British Museum (Natural History), 690, 1–238.

Clark, A.M. & Downey, M.E. (1992) *Starfishes of the Atlantic*. Natural History Museum Publications. Ed. Chapman & Hall, London, 794 pp.

Clark, H.L. (1901) *The Echinoderms of Porto Rico*. Bulletin of the United States Fish Commission, 20(1), 231–263.

Clark, H.L. (1907) The apodous holothurians. A monograph of the Synaptidae and Molpadiidae. *Smithson Contributions to Knowledge*, 35, 1–231.

Clark, H.L. (1909) Notes on some Australian and Indo-Pacific echinoderms. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 52, 107–135.

Clark, H.L. (1911b) North Pacific Ophiurans in the collection of the United States National Museum. *Smithsonian Institution United States National Museum Bulletin*. 75, 1–302.

Clark, H.L. (1915) Catalogue of recent ophiurans. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 25 (4), 165–376.

Clark, H.L. (1917) Hawaiian and other Pacific Echini. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 46, 85–283.

Clark, H.L. (1918) Brittle stars, New and Old. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 62, 265–338.

Clark, H.L. (1921a) The echinoderm fauna of Torres Strait: its composition and its origin. *Department of Marine Biology of the Carnegie Institute*, 10, vi+223.

Clark, H.L. (1921b) Report on the Echinoidea Collected by the Barbados–Antigua Expedition from the University of Iowa in 1918. *University of Iowa Studies in Natural History*, 9(5), 103–121.

Clark, H.L. (1922) The holothurians of the genus Stichopus. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 65(3), 39–74.

Clark, H.L. (1923a) The Echinoderm fauna of South Africa. *Annals of the South African Museum*. 13(7), 8–23.

Clark, H.L. (1925) *A catalogue of the Recent sea urchins (Echinoidea) in the British Museum (Natural History)*. Trustees of the British Museum, London. The Oxford University Press, London, 1–250 pp.

Clark, H.L. (1933) A Handbook of the Littoral Echinoderms of Porto Rico and the Other West Indian Islands. *Scientific Survey of Porto Rico and the Virgin Islands, New York Academy of Sciences*, 16(1), 1–147.

Clark, H.L. (1941) Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The echinoderms (other than Holothurians). *Memorias de la Sociedad cubana de Historia natural, "Felipe Poey"*, 15(1), 1–154.

Claus, C.F.W. (1876) *Grundzüge der Zoologie.* N.G. Elwert'sche Universitätsbuchhandlung, Marburg & Leipzig, 3rd Ed, ixii+1254 pp.

Claus, C.F.W. (1880) Grundzüge der Zoologie. 4th Edition. N.G. Elwertsche Universitatsbuchhandlung, Marburg & Leipzig, 1, vii (7)+821 pp.

Cooke, C.W. (1942) Cenozoic irregular echinoids of the Eastern United States. *Journal of Paleontology*, 16, 1–62.

Copley J.T.P., Tyler, P.A., Sheader, M., Murton, B.J. & German, C.R. (1996) Megafauna from sublittoral to abyssal depths along the Mid-Atlantic Ridge south of Iceland. *Oceanologica Acta*, 19(5), 549–559.

Crump, R.G. & Emson R.H. (1983) The natural history, life history and ecology of the two British species of Asterina. *Field Studies*, 5 (5), 867–882.

Cutress, B.M. (1996) Changes in Dermal Ossicles During Somatic Growth in Caribbean Littoral Sea Cucumbers (Echinoidea: Holothuroidea: Aspidochirotida). *Bulletin of Marine Science*, 58 (1), 44–116.

Cuvier, G. (1817) Le règne animal distribé d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparee. Deterville, Paris, 2, xviii (18)+528.

Dambach, M. (1969) Die Reaktion der Chromatophoren des Seeigels *Centrostephanus longispinus* auf Licht. *Zeitschrift für vergleichende Physiologie*, 64, 400–406.

Danielssen, D.C. & Koren, J. (1883) Fra den norske Nordhavsexpedition. *Nyt magazin for naturvidenskaberne*, 27, 267–299.

David, B. & Laurin, B. (1996) Morphometrics and cladistics: measuring phylogeny in the sea urchin *Echinocardium*. *Evolution*, 50(1), 348–359.

David, J., Roux, M., Messing, C.G. & Ameziane, N. (2006) Revision of the pentacrinid stalked crinoids of the genus *Endoxocrinus* (Echinodermata, Crinoidea), with a study of environmental control of characters and its consequences for taxonomy. *Zootaxa*, 1156, 1–50.

Deichmann, E. (1930) The Holothurians of the Western Part of the Atlantic Ocean. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 71, 43–236.

Deichmann, E. (1954) The Holothurians of the Gulf of Mexico. *Bulletin of the U.S. Department of the Interior, Fish and Wildlife Service*, 89, 381–410.

Deichmann, E. (1957) The Littoral Holothurians of the Bahama Islands. *American Museum Novitates*, 1821, 1–20.

Deichmann, E. (1958) The Holothurioidea collected by the Velero III and IV during the years 1932 to 1954. Part II. Aspidochirota. *Allan Hancock Pacific Expedition (Reports)*, 11, 249–349.

Delage, Y. & Hérouard, E. (1903) Les Échinodermes. *Traité de zoologie concrète*. Schleicher, Paris, 3, x(10)+495.

Delavault, R. & Cognetti, G. (1961) L'hermaphrodisme chez *Marthasterias glacialis* L. *Comptes Rendus Académie des Sciences Paris*, 253, 2771–2772.

Delle Chiaje, S. (1823) Descrizione zoologica ed anatomica di alcune specie di Oloturie. *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*, Societa Tipographica, Napoli, 1, 77–116.

Delle Chiaje, S. (1827) *Memoire sulla storia e notomia degli animali senza vertebre del regno di Napoli.* Societa Tipographica, Napoli, 2, 1–444.

Delle Chiaje, S. (1828) *Memoire sulla storia e notomia degli animali senza vertebre del regno di Napoli. Societa Tipographica*, Napoli, 3, 1–232.

Demand, J., Fabriol, R., Gerard, F. Lundt, F. & Chovelon, P. (1982) Prospection géothermique, íles de Faial et de Pico (Açores). Rapport géologique, geochimique et gravimétrique. Technical report, BRGM 82 SGN 003 GTH.

Desbruyères D.l., Segonzac M. & Bright, M. (2006) Handbook of Deep-Sea Hydrothermal Vent Fauna. Second Edition. *Denisia*, 18, 544 pp.

Desor, E. (1855–1858) *Synopsis des échinides fossiles*. Reinwald, Paris, lxviii (68)+490 pp.

Devaney, D.M. (1970) Studies on Ophiocomid Brittlestars. I. A New Genus (*Clarkcoma*) of Ophiocominae with a Reevaluation of the Genus Ophiocoma. *Smithsonian Contributions to Zoology*, 51, 41 pp.

Dilman A.B. (2006) Asteroid fauna of the Reykjanes Ridge. *In*: Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*, KMK Scientific Press, Russian Academy of Sciences, P.P. Shirshov Institute of Oceanology, Moscow, pp. 177–192.

Dilman, A.B. (2008) Asteroid fauna of the northern Mid-Atlantic Ridge with description of a new species *Hymenasterides mironovi* sp. nov. *Marine Biology Research*, 4, 1–2, 131–151.

Dilman, A.B. (2013) Asteroid fauna of the northern Mid-Atlantic Ridge: additional records. *Marine Biology Research*, 9(5–6), 563–586.

Dilman A.B. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Asteroidea. *Invertebrate Zoology*, 11(1), 25–42.

Djakonov, A.M. (1950) Starfish of the Soviet Union. *Tableaux analytiques de la faune de l'URSS*, 34, 1–203. [not seen]

Döderlein, L. (1912) Die gestielten Crinoiden der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition "Valdivia" 1898–1899*, 17(1), 1–34.

Döderlein, L. (1917) Die Asteriden der Siboga-Expedition. 1. Die Gattung *Astropecten* und ihre Stammesgeschichte. *Siboga Expedition*, 46a, 1–190.

Döderlein, L. (1920) Die Asteriden der Siboga-Expedition. 2. Die Gattung *Luidia* und ihre Stammesgeschichte. *Siboga Expedition*, 46, 193–291.

Domanski, P.A. (1984) Giant larvae: prolonged planktonic larval phase in the asteroid *Luidia sarsi*. *Marine Biology*, 80, 189–195.

Domenico, F. de, Giacobbea S. & Rinelli, P. (2009) The genus *Antedon* (Crinoidea, Echinodermata) in the Strait of Messina and the nearby Tyrrhenian Sea (Central Mediterranean. *Italian Journal of Zoology*, 76 (1), 70–75.

Domínguez-Godino, J., Slater, M., Colin, H. & González-Wangüemert, M. (2015) A new species for sea cucumber ranching and aquaculture: Breeding and rearing of *Holothuria arguinensis*. *Aquaculture*, 438, 122–128.

Downey, M.E. (1968) *Catalog of Recent Echinoid Type Specimens in the U.S. National Museum Smithsonian Institution and the Museum of Comparative Zoology Harvard University*. Smithsonian Institution Press Washington, D.C. vi(6)+99 pp.

Downey, M.E. (1969) Catalog of Recent Ophiuroid Type Specimens in Major Collections in the United States. *United States National Museum Bulletin*, 293, 239 pp.

Downey, M.E. (1970) Zorocallida, new order, and *Doraster constellatus*, new genus and species, with notes on the Zoroasteridae. *Smithsonian Contributions to Zoology*, 64, 1–18.

Downey, M.E. (1973) *Starfishes from the Caribbean and the Gulf of Mexico*. Smithsonian Contributions to Zoology, 126, 1–158.

Downey, M.E. (1986) Revision of the Atlantic Brisingida (Echinodermata: Asteroidea), with description of a new genus and family. *Smithsonian Contributions to Zoology*, 435, 1–57.

Drouët, H. (1861) *Elément de la Faune açoréenne*. J.B. Bailliere & Fils, Lubaires de L'Academie de Médicine, Paris, 245 pp.

Düben, M.W. (1844) Norriges Hafsfauna. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1(1), 110–116.

Düben, M.W. & Koren, J. (1846) Öfversigt af Skandinaviens Echinodermer. *Kungl. Svenska Vetenskapsakademiens Handlingar 1844*, 229–328.

Duncan, P.M. (1877) On the Saleniidae. Observations on the morphology of Recent Saleniae and description of a new species. *Annals and Magazine of Natural History*, 20, 245–257.

Duncan, P.M. (1878) On the identity of the Ophiuran genera *Ophiopleura*, Danielssen and Koren, and Lütkenia, Duncan, with notes on the species. *Annals and Magazine of Natural History*, 2(9), 266–268.

Duncan, P.M. (1889) A revision of the genera and great groups of the Echinoidea. *Journal of the Linnean Society, Zoology*, 23, 1–311.

Durham, J.W. & Melville, R.V. (1957) A classification of echinoids. *Journal of Paleontology*, 31, 242–272.

Egea, E., David, B., Choné, T., Laurin, B., Féral, J.P. & Chenuil, A. (2016) Morphological and genetic analyses reveal a cryptic species complex in the echinoid *Echinocardium cordatum* and rule out a stabilizing selection explanation. *Molecular phylogenetics and evolution*, 94, 207–220.

Ekman, S. (1926) Systematisch-phylogenetische Studien uber Elasipoden und Aspidochiroten. *Zoologische Jahrbücher. Abteilung für allgemeine Zoologie und Physiologie der Tiere*. 47, 429–540. [not seen]

Emlet, R. B. (1995) Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution*, 49(3), 476–489.

Eschscholtz, F. (1829) *Zoologischer Atlas; enthaltend Abbildungen und Beschreibungen neue Thierarten während der Flottcapitains von Kotzebue zweiter reise um die Welt 1823–26*. Reimer, Berlin, 2, 13 pp.

Falconetti, C., Fredj-Reygrobaliet, D. & Fredj, G. (1976) Sexualité et fissiparite concomitants chez l'astérie *Sclerasterias richardi*: premières données. *Marine Biology*, 34, 247–257.

Falconetti, C., Fredj-Reygrobaliet, D. & Fredj, G. (1977) Induction de l'émission des gamètes et premiers stades du développement larvaire chez l'astérie fissipare *Sclerasterias richardi*. *Marine Biology*, 39, 171–178.

Farran, G.P. (1913) The deep-water Asteroidea, Ophiuroidea and Echinoidea of the West Coast of Ireland. *Department of Agriculture and technical instruction for Ireland, fisheries branch, scientific investigations*, 1912, 6, 1–66.

Fasmer, H. (1930) On the genus Anthophiura. *Videnskabelige meddelelser fra Dansk naturhistorisk forening i Kjøbenhavn*, 90, 1–7.

Fechter, H. (1973) *Cyathidium mereorensis* spec. nov., ein neuer Crinoide aus der Familie Holopodidae. *Helgolander wissenschajiliche* Meeresuntersuchungen, 25, 162–169.

Fell, H.B. (1945) A Revision of the Current Theory of Echinoderm Embryology. *Transactions of the Royal Society of New-Zealand*, 75(2), 20–38.

Fell, H.B & Pawson, D.L. (1966) Echinacea. Systematic descriptions. *In*: Moore, R.C. (Ed.) *Treatise on Invertebrate Paleontology, U. Echinodermata*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 3 (2), U367–U440.

Fell, F.J. (1975) The echinoid genus *Centrostephanus* in the South Pacific Ocean with a description of a new species. *Journal of the Royal Society of New Zealand*, 5, 179–193.

Fenaux, L. (1970) Maturation of the gonads and seasonal cycle of the planktonic larvae of the ophiuroid *Amphiura chiajei* Forbes. *The Biological Bulletin*, 138, 262–271.

Féral, J.P., Poulin, E., Oubelkheir, K. (1998) Geographic and Genetic Differentiation of *Echinocardium cordatum* (Pennant). The Current State of a Complex Questions: The Status of *Echinocardium fenauxi* (Péquignat). *In*: Mooi, R. & Telford, M (Eds.) *Proceedings of the 9th International Echinoderm Conference, San Francisco*. Balkema, Rotterdam, pp. 647–649.

Filander, Z., Samyn, Y. & Griffiths, C. (2019) Four notable additions to the South African echinoid fauna (Echinodermata, Echinoidea). *ZooKeys*, 831, p. 71.

Fisher, W.K. (1906) The starfishes of the Hawaiian islands. *Bulletin of the United States Fish Commission*, 23, 987–1130.

Fisher, W.K. (1910) New genera of starfishes. *Annals and magazine of Natural History*, 8(5), 171–173.

Fisher, W.K. (1911) Asteroidea of the North Pacific and adjacent waters. 1. Phanerozonia and Spinulosida. *Bulletin of the US National Museum*, 76, xiii+420 pp.

Fisher, W.K. (1923) A preliminary synopsis of the Asteriidæ, a family of sea stars. *Annals and Magazine of Natural History*, 12(9), 247–258.

Fisher, W.K. (1928) Asteroidea of the North Pacific and adjacent waters. Part 2: Forcipulata (part). *Bulletin of the United States National Museum*, 76, 1–245.

Fisher, W.K. (1930) Asteroidea of the North Pacific and Adjacent Waters, Part. 3: Forcipulata (concluded). *Bulletin of the United States National Museum*, 76, 1–356.

Fischer, A.G. (1966) Spatangoids. *In*: R.C. Moore (Ed.) *Treatise on Invertebrate Paleontology, Part U. Echinodermata*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 3 (2), pp. U543–U628.

Fonseca, P., Abrantes, F., Aguilar, R., Campos, A., Cunha, M., Ferreira, D., Fonseca, T.P., Henriques, V., Machado, M., Mechos, A., Pérez, S., Relvas, P., Rodrigues, C.F., Salgueiro, E., Vieira, R.P., Weetman, A. & Castro, M. (2014) A deep-water crinoid *Leptometra celtica* bed off the Portuguese south coast. *Marine Biodiversity,* 44(2), 223–228.

Fontaine, A.R. (1962) The colours of *Ophiocomina nigra* (Abildgaard, 1789). I. The colour variation and its relation to distribution. *Journal of the Marine Biological Association of the United Kingdom*, 42, 1–8.

Forbes, E. (1839) On the Asteriadae of the Irish Sea. *Memoirs of the Wernerian Natural History Society*, 8, 114–128.

Forbes, E. (1841) *A history of British Starfishes and other animals of the class Echinodermata*. John Van Woorst, London, 267 pp.

Forbes, E. A. (1843) On the radiata of the eastern Mediterranean. *Transactions of the Linnean Society of London*, 19, 143–153.

Fréminville, C.P. (1811) Mémoire sur un nouveau genre de Zoophytes de l'ordre des Radiaires. *Nouveau Bulletin des Sciences, par la Société Philomathique*, *Paris,* 2, 349–350.

Gage, J.D. & Tyler, P.A. (1982) Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson. *Oceanologica Acta*, 5, 73–83.

Gage, J.D., Billett, D.S.M., Jensen, M. & Tyler, P.A. (1983) Echinoderms of the Rockall Trough and adjacent areas. I. Crinoidea, Asteroidea and Ophiuroidea. *Bulletin of the British Museum* (*Natural History*)*, Zoology*, 45, 263–308.

Gage, J.D., Billett, D.S.M., Jensen, M. & Tyler, P.A. (1985) Echinoderms of the Rockall Trough and adjacent areas. 2. Echinoidea and Holothurioidea. *Bulletin of the British Museum* (*Natural History*)*, Zoology*, 48(4), 173–214.

Gage, J.D., Anderson, R.M., Tyler, P.A., Chapman, R. & Dolan, E. (2004) Growth, reproduction and possible recruitment variability in the abyssal brittle star *Ophiocten hastatum* (Ophiuroidea: Echinodermata) in the NE Atlantic. *Deep-Sea Research I*, 51(6), 849–864.

García-Diez, C., Porteiro, F.M., Meirinho, A., Cardigos, F. & Tempera, F. (2005) Taxonomic review of selected invertebrate groups collected during the Campaigns of the Prince Albert I of Monaco in the Azorean waters. *Arquipélago. Life and Marine Sciences*, 22A, 35–59.

Garrido, M.J., Hernández, M., Espino, F., Herrera, R. & Tavío, O. (2004) *Hacelia superba* H.L. Clark, 1921 and *Chaetaster longipes* Retzius, 1805 (Echinodermata: Echinodea) new records for Canary Islands. *Arquipélago, Life and Marine Sciences*, 21A, 87–88.

Gautier-Michaz, M. (1955) Sur la présence de l'échinide *Arbaciella elegans* Mortensen en Méditerranée occidentale. *Bulletin de la Station d'Aquiculture et de Pêche de Castiglione*, 1955, 293–295.

Gautier-Michaz, M. (1958) Resultats scientifiques des campagnes de la Calypso. VII. Etudes sur le seuil Siculo-Tunisien. 5. Echinodermes. *Annales Institut Océanographique*, Monaco, 34, 145–155.

Gebruk, A.V. (1988) New taxa of abyssal sea cucumbers of the family Elpidiidae (Elasipoda). *Zoologicheskii Zhurnal*, 67(6), 914–922. [not seen]

Gebruk, A.V. (2008) Holothurians (Holothuroidea, Echinodermata) of the northern Mid-Atlantic Ridge collected by the G.O. Sars MAR–ECO expedition with descriptions of four new species, *in*: Gebruk, A.V. (Ed.) (2008). Benthic fauna of the northern Mid-Atlantic Ridge: results of the MAR–ECO expedition. *Marine Biology Research*, 4(1–2), pp. 48–60.

Gebruk, A.V., Solis-Marin, F.A., Billett, D.S.M., Rogacheva, A.V. & Tyler, P.A. (2012) Review of the genus *Zygothuria* Perrier, 1898 and the Atlantic group of species of the genus *Mesothuria* Ludwig, 1894 (Synallactidae: Holothuroidea) with description of the new species *Mesothuria milleri* sp. nov. *Journal of Natural History*, 46(5–6), 265–348.

Gebruk, A.V., Rogacheva, A.V., Pawson, D.L., Hamel, J.-F., Macisaac, K.G. & Mercier, A. (2013) *Penilidia desbarresi* sp. nov. (Echinodermata: Holothuroidea: Elasipodida) from the upper slope of Newfoundland and re-description of *P. ludwigi* (von Marenzeller, 1893). *Marine Biology Research*, 9(10), 1029–1036.

Gebruk, A. V., Smirnov, A.V. & Rogacheva, A.V. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Holothuroidea. *Invertebrate Zoology*, 11(1), 156–180.

Gebruk, A.V., Tyler, P.A. & Billett, D.S.M. (1997) Pelagic juveniles of the deep-sea elasipodid holothurians: New records and review. *Ophelia*, 46(2), 153–164.

George, S. B. (1990). Population and seasonal differences in egg quality of *Arbacia lixula* (Echinodermata: Echinoidea). *Invertebrate Reproduction & Development*, 17(2), 111–121.

Gislén T (1924) Echinoderm studies. *Zoologiska Bidrag från Uppsala*, 9, 330 pp.

Gislén, T. (1951) Crinoidea with a survey of the bathymetric distribution on the deep-sea crinoids. *Reports of the Swedish Deep Sea Expedition, Zoology,* 2 (4), 49–55.

Glück, F.U., Stöhr, S., Bochert, R. & Zettler, M.L. (2012) Brittle stars (Echinodermata: Ophiuroidea) from the continental shelf off Angola and Namibia. *Zootaxa*, 3475, 1–20

Gmelin, J.F. (1791) Vermes. *In:* Gmelin J.F. (Ed.) *Caroli a Linnaei Systema Naturae per Regna Tria Naturae,* Ed. 13, G.E. Beer, Lipsiae, Tome 1(6), 3021–3910.

Gondim, A.I., Christoffersen, M.L. & Dias, T.L.P. (2014) Taxonomic guide and historical review of starfishes in northeastern Brazil (Echinodermata, Asteroidea). *ZooKeys*, 449, 1–56.

González-Wangüemert, M. & Borrero-Pérez, G.H. (2012) A new record of *Holothuria arguinensis* colonizing the Mediterranean Sea. *Marine Biodiversity Records*, 5, 1–4.

Gras, H. & Weber, W. (1977) Light-induced alterations in cell shape and pigment displacement in chromatophores of the sea urchin *Centrostephanus longispinus*. Cell and Tissue Research, 182, 165–176.

Gray, *I.E.*, Downey, M.E. & Cerame-Vivas, M.J. (1968) Sea stars of North Carolina. *Fishery Bulletin*, 67(1), 127–163.

Gray, J.E. (1825) An attempt to divide the Echinida, or Sea Eggs, into natural families. *Annals of Philosophy, new series*, 10, 423–431.

Gray, J.E. (1835) On the genera distinguishable in *Echinus* Lamarck. *Proceedings of the Zoological Society of London*, 3, 57–59.

Gray J.E. (1840) A synopsis of the genera and species of the class Hypostoma (*Asterias* Linnaeus). *Annals of the Magazine of Natural History*, 6, 175–184, 275–290.

Gray J.E. (1855a) An arrangement of the Families of Echinida, with Descriptions of some New Genera and Species. *Proceedings of the Zoological Society of London*, 23, 35–39.

Gray J.E. (1855b) *Catalogue of the Recent Echinida, or Sea Eggs, in the Collection of the British Museum. Part I. Echinida Irregularia*. Woodfall & Kinder, London, 69 pp.

Gray J.E. (1866) *Synopsis of the species of starfish in the British museum*. J. Van Voorst, London, iv+17 pp.

Gregory, J.W. (1900) The Echinoidea. *In*: Bather, F.A., Gregory, J.W. & Goodrich, E.S. (Eds.) *A Treatise on Zoology. Part III. The Echinoderma.* A.&C. Black, London, pp. 282–332.

Grieg, J.A. (1932) Echinodermata. *Report of the scientific results of the Michael Sars North Atlantic deep sea expedition 1910*, 3(2), 1–47.

Grube, A.E. (1840) *Actinien, Echinodermen und Wuermer des adriatischen und Mittelmeers, nach eigenen Sammlungen beschreiben*. J.H Bon, Koenigsberg, 92 pp.

Guille, A. (1982) A new genus and species of ophiacanthid brittlestar (Echinodermata: Ophiuroidea) from the Kerguelen Islands, with new taxonomic, biogeographic and quantitative data on the echinoderm fauna. *Australian Museum Memoir*, 16, 67–87.

Haddad Jr, V. & Barreiros, J.P. (2008) *Dangerous Azorean Marine Animals: a field guide*. Blu Edições, Terceira, Açores, 60 pp.

Haeckel, E. (1896) Systematische Phylogenie. Entwurf eines Natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte. Georg Reimer, Berlin, 2, xviii(18)+720.

Haesaerts, D., Jangoux, M. & Flammang, P. (2006) Adaptations to Benthic Development: Functional Morphology of the Attachment Complex of the Brachiolaria Larva in the Sea Star *Asterina gibbosa*. *Biological Bulletin*, 211(2), 172–182.

Halpern, J.A. (1970) Goniasteridae (Echinodermata: Asteroidea) of the Straits of Florida. *Bulletin of Marine Science*, 20(1), 193–286.

Halpern, J.A. (1972) Pseudarchasterinae (Echinodermata, Asteroidea) of the Atlantic. *Proceedings of the Biological Society of Washington*, 85(30), 359–384.

Hamel, J.F. & Mercier, A. (1995) Prespawning behavior, spawning, and development of brooding starfish *Leptasterias polaris*. *Biological Bulletin*, 188(1), 32–45.

Hansen, B. (1956) Holothurhoidea from depths exceeding 6000 Meters. *Galathea*, 2, 33–54.

Hansen, B. (1975) Systematics and biology of the deep-sea holothurians: Elasipoda. Galathea report: scientific results of the Danish deep-sea expedition round the world 1950–1952. *Galathea*, 13, 262 pp.

Hartlaub, C. (1890) Beitrag zur Kenntniss der Comatuliden-Fauna des indischen Archipels. *Nachrichten von der Königlichen Gesellschaft der Wissenschaften und der Georgs-August-Universität zu Göttingen*, 5, 168–187.

Harvey, E.B. (1956) *The American Arbacia and other sea urchins*. Princeton University Press. Princeton, viii(8)+298.

Harvey, R., Gage, J.D., Billett, D.S.M., Clark, A.M. & Paterson, G.L.J. (1988) Echinoderms of the Rockall Trough and adjacent areas. 3. Additional records. *Bulletin British Museum Natural History, Zoology*, 54, 153–198.

Heding, S.G. (1935) Holothurioidea, Part 1: Apoda, Molpadioidea, Gephyrothurioidea. *The Danish Ingolf Expedition*, Hagerup, Copenhagen, 4 (9), 1–84.

Heding, S.G. (1942) Holothurioidea, Part 2: Aspidochirota, Elasipoda, Dendrochirota. *The Danish Ingolf Expedition*, Hagerup, Copenhagen, 4(13), 1–39.

Heinzeller, T. & Fechter, H. (1995) Microscopical Anatomy of the Cyrtocrinid *Cyathidium meteorensis* (sive *foresti*) (Echinodermata, Crinoidea). *Acta Zoologica*, 76(1), 25–34.

Heinzeller, T., Fechter, H., Améziane-Cominardi, N. & Welsch, U. (1997) Development of *Cyathidium foresti* (Echinodermata: Crinoidea, Cyrtocrinida) from early attached larvae to adult-like juveniles. *Journal of Zoological Systematics and Evolutionary Research*, 35, 11–21.

Heller, C. (1863) Untersuchungen über die Litoralfauna des adriatischen Meeres. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 46, 415–448.

Heller, C. (1868) Die zoophyten und Echinodermen des Adriatischen Meeres. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft von Wien*, 18, 1–88.

Hernández J.C., Clemente S., Tuya F., Pérez-Ruzafa, A., Sangil, C., Moro-Abad, L. & Bacallado-Aránega J.J (2013) Echinoderms of the Canary Islands, Spain. *In*: Alvarado J.J., Solis-Marin F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*. Springer Berlin Heidelberg, pp. 471–510.

Hernández-Herrejón, L.A., Solís-Marín, F.A. & Laguarda-Figueras, A. (2008) Ofiuroideos (Echinodermata: Ophiuroidea) de las aguas mexicanas del golfo de México. *Revista Biología Tropical, Internacional Journal of Tropical Biology and Conservation*, 56(3), 83–167.

Hérouard, E. (1896) Note preliminaire sur les Holothuries provenant des dragages du Yacht Princesse-Alice. [Premiere Note.]. Bulletin de la Société Zoologique de France, 21, 163–168.

Hérouard, E. (1899) Troisieme note préliminaire sur les Holothuries provenant des dragages du yacht Princesse-Alice. Révision de la sous-familie des Elpidiinae et description de nouvelles èspeces. *Bulletin de la Société Zoologique de France*, 24, 170–175.

Hérouard, E. (1902) Holothuries Provenant Des Campagnes De La Princesse-Alice (1892–1897). *Résultats Campagnes Scientifiques Prince de Monaco*, 62 pp.

Hérouard, E. (1912) Holothuries nouvelles des campagnes du yacht Princesse Alice. *Bulletin de l'Institut Océanographique*, 239, 1–9.

Hérouard, E. (1923) Holothuries provenant des campagnes des yachts Princesse-Alice et Hirondelle ii. (1898–1915). *Résultats Campagnes Scientifiques Prince de Monaco*, 66, 1–161.

Hertz, M. (1927) Die Ophiuriden der Deutschen Tiefsee–Expedition I. *Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition "Valdivia"*, 22(3), 59–120.

Higgins, R.C. (1974) Specific status of *Echinocardium cordatum*, *E. australe* and *E. zealandicum* (Echinoidea: Spatangoida) around New Zealand, with comments on the relation of morphological variation to environment. *Journal of Zoology*, 173, 451–475.

Higgins, R.C. (1975) Observations on the morphology of *Echinocardium cordatum* (Echinoidea: Spatangoida) from diverse geographical areas. *Journal of Zoology*, 177, 507–515.

Hörstadius, S. (1938) Über die Entwicklung von *Astropecten aranciacus* L. *Pubblicazioni della Stazione Zoologica di Napoli*, 17: 221–312.

Howell, K.L., Billett, D.S.M. & Tyler, P.A. (2002) Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. *Deep-Sea Research I*, 49, 1901–1920.

Howell, K.L., Pond, D.W., Billett, D.S.M. & Tyler, P.A. (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. *Marine Ecology Progress Series*, 255, 193–206.

Instituto Hidrográfico, 2000. *Roteiro da Costa de Portugal: Arquipélago dos Açores*, 2nd ed., Instituto Hidrográfico, Lisbon.

Jackson, R.T. (1912) Phylogeny of the Echini with a revision of Palaeozoic species. *Memoirs of the Boston Society of Natural History*, 7, 1–491.

Jaeger, G.F. (1833) *De Holothuriis*. Gessnerianis, Turici. 40 pp.

Janies, D.A. (1995) *Reconstructing the evolution of morphogenesis and dispersal among velatid asteroids*. Ph.D. thesis (unpublished), University of Florida, Gainesville.

Jesus, D. & Abreu, A.D. (1998) Contribution to the knowledge of the soft bottom echinoderms of Madeira Island. *Boletim do Museu Municipal do Funchal* (*História Natural*), 50(286), 59–69, 4 figs.

Jesus, D.C. & Fonseca, L.C. (1999) First records of 13 echinoderm species on the southwest coast of Portugal. *Boletín Instituto Español de Oceanografía*, 15 (1–4), 343–349.

John, G. (1889) Ueber bohrende *Seeigel. Archiv für Naturgeschichte*, 55(1), 268–302.

John, D.D. & Clark, A.M. (1954) The "Rosaura" expedition. 3. The echinodermata. *Bulletin of the British Museum (Natural History) Zoology*, 2, 139–162.

Johnson, J. & Stevens, I. (2000) A fine resolution model of the eastern North Atlantic between the Azores, the Canary Islands and the Gibraltar Strait. *Deep-Sea Research I*, 47, 875–899.

Jones, D.O.B., Walls, A., Clare, M., Fiske, M.S., Weiland, R.J., O'Brien, R. & Touzel, D.F. (2014) Asphalt mounds and associated biota on the Angolan margin. *Deep-Sea Research I*, 94, 124–136.

Jullien, J. (1878) Description d'un nouveau genre des Stéllérides, de la Famille des Astériadées. *Société Zoologique de France*, 3, 141–148.

Kasyanov, V.L., Kryuchkova, G.A., Kulikova, V.A. & Medvedeva, L.A. (1998) *Larvae of marine bivalves and echinoderms*. Smithsonian Institution Libraries, Washington D.C., 288 pp.

Klein, B., & Siedler, G. (1989) On the origin of the Azores Current. *Journal of Geophysical Research: Oceans*, 94(C5), 6159–6168.

Knorr, G.W. (1766–1777) *Deliciae naturae selectae oder auserlesenes Naturalien-Cabinet, welches aus den drey Reichen der Natur zeiget, was von curiösen Liebhabern aufbehalten und gesammlet zu werden verdienet*. Matthäus Berdier de la Blaquiere, Nürnberg, viii+132 pp.

Koehler, R. (1895a) Note préliminaire sur les échinides recueillis pendant les campagnes de l'Hirondelle. *Bulletin de la Société Zoologique de France*, 20, 223–227.

Koehler, R. (1895b) Note préliminaire sur les échinides des premières campagnes de la Princesse Alice. *Bulletin de la Société Zoologique de France*, 20, 227–233.

Koehler, R. (1895c) Dragages profonds executes a bord du Caudan dans le Golfe de Gascogne. Rapport préliminaire sur le Échinodermes. *Revue biologique du Nord de la France*, 7, 439–496.

Koehler, R. (1896a) Note preliminaire sur les Ophiures recueillies pendant les campagnes de "L'Hirondelle". *Memoires. Societe Zoologique de France*, 9, 203–213.

Koehler, R. (1896b) Note preliminaire sur les Ophiures des premières campagnes de la "Princesse Alice". *Memoires. Societe Zoologique de France*, 9, 241–253.

Koehler, R. (1896c) Échinodermes. Résultats scientifiques de la Campagne du "Caudan" dans le Golfe de Gascogne. *Annales de l'Université de Lyon*, 26, 33–127.

Koehler, R. (1897a) Echinodermes recueillis par "l'Investigator" dans l'Ocean Indien. I. Les Ophiures de mer profonde. *Annales Sciences Naturelles Zoologie et Paleontologie*, 4, 273–372.

Koehler, R. 1897b. *Sperosoma Grimaldii*, nouveau genre d'Echinothuride. *Zoologischer Anzeiger*, 20, 302–307.

Koehler, R. (1898) Echinides et Ophiures provenant des campagnes du yacht Hirondelle (Golfe de Gascogne, Açores, Terre-Neuve). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 12, 78 pp.

Koehler, R. (1901) Note préliminaire sur quelques Ophiures nouvelles provenant des campagnes de la Princesse Alice. *Bulletin de la Société Zoologique de France*, 26, 222–231.

Koehler, R. (1906a) Description des ophiures nouvelles recueillies par le Travailleur et le Talisman. *Mémoires de la Société Zoologique de France*, 19, 5–34.

Koehler, R. (1906b) Ophiures. *Expeditions Scientifiques du Travailleur et du Talisman*, 8, 245–311.

Koehler R. (1907a) Note préliminaire sur quelques Astéries et Ophiures provenant des campagnes de la Princesse Alice. *Bulletin de l'Institut Océanographique de Monaco*, 99, 1–47.

Koehler, R. (1907b) Revision de la collection des Ophiures du Museum d'histoire Naturelle Paris. *Bulletin Sciences de la France et de la Belgique*, 41, 279–351.

Koehler, R. (1909) Echinodermes provenant des campagnes du yacht Princesse-Alice (Astéries, Ophiures, Echinides et Crinoïdes). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 34, 1–317.

Koehler, R. (1914a) A Contribution to the Study of Ophiurans of the United States National Museum. *Bulletin of the United States National Museum*, 84, 1–173.

Koehler, R. (1914b) Echinoderma I: Asteroidea, ophiuroidea et Echnoidea. *In*: Michaelsen, W. *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. L. Friederichsen & Co., Hamburg. 1(2), 127–303.

Koehler, R. (1921a) Echinodermes (Asteries, Ophiures, Echinides et Crinoides) des dernieres campagnes de la Princesse-Alice et de l' Hirondelle II. *Bulletin de l'Institut Océanographique de Monaco*, 396, 1–8.

Koehler, R. (1921b) Echinodermes. *Faune de France*, 1. Librairie de la Faculte des Sciences, Paris, 216 pp.

Koehler, R. (1922) Ophiurans of the Philippine Seas and adjacent waters. *Smithsonian Institution United States National Museum Bulletin*, 100(5), 1–486.

Koehler, R. (1923) Sur quelques Ophiures des Côtes de l'Angola et du Cap. *Meddelanden från Göteborgs musei zoologiska avdelning*, 18, 1–17.

Koehler, R. (1924) *Les échinodermes des mers d'Europe. Encyclopédie Scientifique, Tome I*. Libraire Octave Doin, Paris, France, XIII+361 pp.

Koehler, R. & Vaney, M.C. (1906) Mission des Pêcheries de la Côte occidentale d'Afrique. II. Echinodermes. *Actes Société Linnéenne, Bordeaux*, 60, 58–66.

Koehler, R. & Vaney, M.C. (1910) Note préliminaire sur les Crinoïdes du Travailleur et du Talisman. *Bulletin du Muséum d'Histoire naturelle*, Paris. 16, 26–32.

Kölliker, A. von (1880) Report on the Pennatulida dredged by H.M.S. Challenger during the years 1873–1876. *Reports of Science Research Voyage of H.M.S. Challenger, Zoology*, 1(2), 1–41.

Koukouras, A., Sinis, A.I., Bobori, D., Kazantzidis, S. & Kitsos, M.-S. (2007) The echinoderm (Deuterostomia) fauna of the Aegean Sea, and comparison with those of the neighbouring seas. *Journal of Biological Research*, 7, 67–92.

Kroh, A. & Smith, A.B. (2010) The phylogeny and classification of post-Palaeozoic echinoids. Journal of Systematic Palaeontology, 8(2), 147–212.

Kroh, A. & Mooi, R. (2018) World Echinoidea database. Available from http://www.marinespecies.org/echinoidea/ at VLIZ. Accessed 2018-01-11. doi: 10.14284/170.

Kroh, A., Madeira, P. & Haring, E. (2011) Species distribution: virtual or real – the case of *Arbaciella elegans* (Echinoidea: Arbaciidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 99–105.

Laguarda-Figueras, A., Solís-Marín, F.A., Durán-González, A. Hernández-Pliego, P. & Del Valle-García, R. (2001) Holoturoideos (Echinodermata: Holothuroidea) of the Mexican Caribbean: Puerto Morelos, Quintana Roo, México. *Avicennia*, 14, 7–46.

Lahaye, M. & Jangoux, M. (1988) Morphologie external et comportement des larves doliolaria d'*Antedon bifida* (Echinodermata, Crinoidea). *Annales de la Société royale zoologique de Belgique*, 118(2), 183–189.

Lamarck, J.-B. (1801) *Système des animaux sans vertèbres, ou tableau general des classes, des orders et des genres de ces animaux*. Published by the author and Deterville, Paris, viii (8)+432 pp.

Lamarck, J.-B. (1816) *Histoire naturelle des animaux sans vertèbres. Tome second.* Verdière, Paris, 568 pp.

Lambert, J. (1896) Notes sur quelques Échinides Créracés de Madagascar. *Bulletin de la Société Géologique de France, série 3*, 24, 313–332.

Lambert, J. (1900) Etude sur quelques Echinides de l'Infra-Lias et du Lias. *Bulletin de la Société des Sciences Historiques et Naturelles de l'Yonne, 1899*, 52, 3–57.

Lambert, J. (1905) Notes sur quelques Échinides éocéniques de l'Aude et de l'Hérault. *In*: Doncieux, L. (Ed.) *Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Première Partie. Montagne Noire et Minervois. Annales de l'Université de Lyon, Nouvelle Série, I. Sciences, Médecine*, 17, 129–164.

Lambert, J. & Thiéry, P. (1914) *Essai de Nomenclature Raisonnée des Echinides*. L. Ferrière, Chaumont, 6–7, 385–512.

Lambert, J. & Thiéry, P. (1924) *Essai de Nomenclature Raisonnée des Echinides*. L. Ferrière, Chaumont, 4, 241–320.

Lares, M.T. & McClintock, J.B. (1991) The effects of temperature on the survival, organismal activity, nutrition, growth, and reproduction of the carnivorous, tropical sea urchin *Eucidaris tribuloides*. *Marine Behaviour and Physiology*, 19(2), 75–76.

Latreille, M. (1825) *Familles naturelles du règne animal*. J.-B. Bailliére, Paris, 570 pp.

Laurin, B., David, B., Féral, J.P. & Derelle, E. (1994) Polytypism in the spatangoid sea urchin Echinocardium: A morphological vs molecular approach. *In*: Guille, F. & Roux, M. (Eds.) *Echinoderms through time*, Balkema, Rotterdam, pp. 739–745.

Lawrence, J.M. (1996) Mass mortality of echinoderms from abiotic factors. *In*: Jangoux, M. & Lawrence, J.M. (Eds.), *Echinoderm Studies*, 5, 103–137.

Lawrence, J.M. (2007) *Edible Sea Urchins: Biology and Ecology*. Elsevier, 380 pp.

Leske, N.G. (1778) *Jacobi Theodori Klein naturalis dispositio echinodermatum et lucubratiunculam de aculeis echinorum marinorum*. Ex Officlna Gleditschiana, Leipzig, xx(20)+214.

Lessios, H.A., Kessing, B.D., Robertson, D.R. & Paulay, G. (1999) Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution*, 53, 806–817.

Lessios, H.A., Kessing, B.D. & Pearse, J.S. (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55, 955–975.

Lesueur, C.A. 1824. Description of several new Species of Holothuria. *Journal Academy Natural Sciences of Philadelphia*, 4, 155–163.

Levitan, D.R. (2000) Optimal egg size in marine invertebrates: theory and phylogentic analysis of the critical relationship between egg size and development time in echinoids. *The American Naturalist*, 156, 175–192.

Lieberkind, I. (1935) Asteroidea. I. Porcellanasteridae. *The Danish Ingolf Expedition, Hagerup, Copenhagen*, 4(10), 1–37.

Linnaeus, C. (1758) *Systema Naturae*. 10th Edition, Holmiae, Stockholm,1, 824 pp.

Linnaeus, C. (1767) Systema Naturae. 12th Edition, Holmiae, Stockholm, 1(2), 533–1327 pp.

Ljungman, A.V. (1865) Tillägg till kännedom af Skandinaviens Ophiurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1863, 21(7), 359–367.

Ljungman, A.V. (1866) Om några nya arter af Ophiurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1866, 23(6), 163–166.

Ljungman, A.V. (1867) Ophiuroidea viventia huc usque cognita enumerat. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1866, 23(9), 303–336.

Ljungman, A.V. (1872) Förteckning öfver uti Vestindien af Dr A. Goës samt under korvetten Josefinas expedition i Atlantiska Oceanen samlade Ophiurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1871, 28(5), 615–658.

Loriol P. de (1882) Animaux invertébrés, Terrain jurassique. *Paléontologie française, ou description des fossiles de la France*, Sér. 1, 11(1), 1–627.

Loriol, P. de (1900) Notes pour servir à l'étude des Echinodermes. *Revue Suisse de Zoologie*, 8, 55–96.

Lovén, S. 1869. En ny art af slägtet *Spatangus* från Nordsjön. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 9, 733–735.

Lovén, S. (1871) Om Echinoideernas byggnad. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 28(5), 1065–1111.

Lovén, S. (1874) Etudes sur les Echinoidees. *Handlingar (Kunglia Vetenskaps-Akademiens) Ny följd*, 11(7), 1–91.

Ludwig, H. (1875) Beiträge zur Kenntniss der Holothurien. *Arbeiten Zoologische Zootomischen Institut Würzburg,* 2(2), 77–120.

Ludwig, H. (1893) Vorlaufiger Bericht uber die erbeuteten Holothurien. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 24(4), 105–114.

Ludwig, H. (1894) Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer Albatross, during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding, xii. The Holothurioidea. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 17(3), 1–183.

Ludwig, H. (1897) Die Seesterne des Mittelmeeres. *Zoologischen Station zu Neapel*, 24, viii(8)+491.

Ludwig H. (1907) Diagnosen neuer Tiefsee-Seesterne aus der Familie der Porcellanasteriden. *Zoologischer Anzeiger*, 31, 312–319.

Ludwig, H. (1910) *Notomyota*, eine neue Ordnung der Seesteine. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 23, 435–466.

Lütken, C.F. (1855) Bidrag til Kundskab om Slangestjernerne. I. Forelöbig Oversigt over Grönlandshavets Ophiurer. *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn 1854*, 6, 95–104.

Lütken, C.F. (1856) Bidrag til kundskab om Slangestjernerne. II. Oversigt over de vestindiske Ophiurer. *Videnskabelige Meddelelser fra den Naturhistorisk Förening i Kjøbenhavn 1856*, 8, 1–19.

Lütken, C.F. (1858) Additamenta ad historiam Ophiuridarum. Förste Afdelning. *Det kongelige danske Videnskabernes Selskabs Skrifter. Femte Raekke, Naturvidenskabelig og mathematisk Afdelning*, 5, 1–74.

Lütken, C.F. (1859) Additamenta ad historiam Ophiuridarum. Anden Afdelning. *Det kongelige danske Videnskabernes Selskabs Skrifter. Femte Raekke, Naturvidenskabelig og mathematisk Afdelning,* 5, 177–271.

Lütken, C.F. (1869) Additamenta ad historiam Ophiuridarum. Tredie Afdelning. *Det kongelige danske Videnskabernes Selskabs Skrifter. Femte Raekke, Naturvidenskabelig og mathematisk Afdelning,* 8, 20–109.

Lütken, C.F. & Mortensen, T. (1899) Reports on an exploration off the west coasts of Mexico, Central and Southern America and off the Galapagos Islands. XXV. The Ophiuridae. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 23(2), 97–208.

Lyman, T. (1865) Ophiuroidae and Astrophytidae. *Illustrated Catalogue of the Museum of Comparative Zoölogy at Harvard College*, 1, 200 pp.

Lyman, T. (1869) Preliminary report on the Ophiuridae and Astrophytidae dredged in deep-water between Cuba and the Florida Reef, by L. F. de Pourtales. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 1(10), 309–354.

Lyman, T. (1874) On the species of *Ophiothrix* from the Waters of Western Europe and of the Mediterranean. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 3, 240–252.

Lyman, T. (1875) Zoological Results of the Hassler Expedition. 2. Ophiuridae and Astrophytidae. *Illustrated catalogue of the Museum of Comparative Zoölogy at Harvard College*, 8(2), 1–34.

Lyman, T. (1878) Ophiuridae and Astrophytidae of the “Challenger” expedition. Part I. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 5(7), 65–168.

Lyman, T. (1879) Ophiuridae and Astrophytidae of the “Challenger” expedition. Part II. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 6(2), 17–83.

Lyman, T. (1882) Report on the Ophiuroidea. *Report on the Scientific Results of the Voyage of H.M.S. Challenger 1873–1876, Zoology*, 5(14), 1–386.

Lyman, T. (1883) Report on the Ophiuroidea. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea (1878–79), and on the east coast of the United States, during the summer of 1880, by the U.S. coast survey steamer “Blake”, commander J.R. Bartlett, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 10(6), 227–287.

MacBride, E.W. (1907) The Development of *Ophiothrix fragilis*. *Quarterly Journal of Microscopical Science*, 2(51), 557–606.

Maciel, P.C. & J.M. Gonçalves (1998) Distribuição dos ouriços-do-mar de espinhos curtos *Sphaerechinus granularis* na costa da ilha do Faial, Açores, no Verão de 1996. III Simpósio Fauna e Flora das Ilhas Atlânticas, 21–25 September, Universidade dos Açores, Ponta Delgada, p. 182.

Macurda, D.B. & Roux, M. (1981) The Skeletal Morphology of the Isocrinid Crinoids *Annacrinus wyvillethomsoni* and *Diplocrinus maclearanus*. *Contributions from the Museum of Paleontology*, University of Michigan, 25(9), 169–219.

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61(3), 243–264.

Madeira, P., Kroh, A., Melo, C., Cordeiro & Ávila, S.P. (2017a) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic). *In*: Ávila, S.P. & Melo, C. (Eds.). RCANS *2017 - 6th Regional Committee on Neogene Atlantic Stratigraphy, Ponta Delgada, São Miguel Island, Azores, July, 10-13, University of the Azores (Abstract Book)*, p. 44.

Madeira, P., Frias Martins, A.M. & Ávila, S.P. (2017b) First record of the Mediterranean asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) in the Azores Archipelago (NE Atlantic Ocean). *Arquipelago*. *Life and Marine Sciences*, 35, 11–18.

Madsen, F.J. (1947) The Echinoderms collected by the “Skagerak” Expedition in the Eastern Atlantic 1946. *Meddelanden från Göteborgs Kungliga Vetenskaps- och Vitterhets- Samhälles Handlingar, sjätte följden*, Serie B. 5(7), 1–16.

Madsen, F.J. (1950) The echinoderms collected by the Atlantide Expedition, 1945–46. 1. Asteroidea. *Atlantide Reports*, 1, 167–222.

Madsen, F.J. (1957) On a new species of *Meoma*, and on a few other echinoids from tropical West Africa. *Bulletin de l'Institut Français d'Afrique Noire, Série A, Sciences Naturelles*, 19, 474–481.

Madsen, F.J. (1961) The Porcellanasteridae. A monographic revision of an abyssal group of sea stars. *Galathea Reports*, 4, 33–174.

Madsen, F.J. (1970) West African Ophiuroids. *Atlantidae Report*, 11, 151–243.

Madsen, F.J. 1973. The Ophiodermatidae. *Galathea Report*, 11, 133–143.

Madsen, F.J. (1977) The Ophioleucidae (Ophiuroidea). *Galathea Report*, 14, 109–122.

Madsen, F.J. (1987) The *Henricia sanguinolenta* complex (Echinodermata, Asteroidea) of the Norwegian Sea and adjacent waters. A re-evaluation, with notes on related species. *Steenstrupia*, 13(5), 201–268.

Mah, C.L. (2017) *World Asteroidea database*. Available from http://www.marinespecies.org/asteroidea at VLIZ. Accessed 2017-01-15. doi:10.14284/170.

Mah, C.L. & Blake, D.B. (2012) Global Diversity and Phylogeny of the Asteroidea (Echinodermata). *PLoS One*, 7(4), 1–22, doi: 10.1371/journal.pone.0035644.

Mah, C.L., Mercier, A., Hamel, J.-F. & Nizinski, M. (2012) Range Extensions and Taxonomic Notes on Atlantic Myxasteridae (Velatida, Asteroidea). *Zootaxa*, 3572, 55–62.

M'Andrew, R. & Barrett, L. (1857) List of the Echinodermata dredged between Drontheim and the North Cape. *Annals and Magazine of Natural History*, 20(2), 43–44.

Marenzeller, E. von (1892) Note preliminaire sur les Holothuries provenant des campagnes du yacht l'Hirondelle. *Bulletin Société Zoologique France*, 17, 64–66.

Marenzeller, E. von (1893) Contribution à l'étude des Holothuries de l'Atlantique N'ord (Golfe de Gascogne, Iles Açores). *Résultats Campagnes Scientifiques du Prince de Monaco*, 6, 32 pp.

Markov, A.V. & Solovjev, A.N. (2001) Echinoids of the family Paleopneustidae (Echinoidea, Spatangoida): morphology, taxonomy, phylogeny. Geos-Trudy Paleontologicheskogo Instituta, Rossikaia Akademia Nauk, 280, 1–108.

Marques, V.M. (1980) Echinodermes recueillis pedant la mission «Hesperides 76» du N/O Jean Charcot. *Arquivo do Museu Bocage*, *2ª série*, 7(7), 95–107.

Marques, V.M. (1983) Peuplements benthiques de Açores, 1 — echinoderms. *Arquivo do Museu Bocage*, AII (I), 1–7.

Marques, V.M. (1984) Effects of *Arbacia lixula* (L.) (Echinoidea) on the algal communities of São Miguel and Graciosa islands (Azores archipelago: Portugal). *Arquivos do Museu Bocage*, Série B, 2(13), 103–108.

Martynov, A. (2010) Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. *Zootaxa*, 2697, 1–154.

Martynov, A.V. & Litvinova, N.M. (2008) Deep-water Ophiuroidea of the northern Atlantic with descriptions of three new species and taxonomic remarks on certain genera and species. *Marine Biology Research*, 4, 76–11.

Massin, C. (1993) The Holothurioidea (Echinodermata) collected during the Tyro Mauritania-II expedition 1988. *Zoologische Mededelingen*, Leiden, 67, 397–429.

Massin, C. & Hendrickx, M.E. (2011) Deep-water Holothuroidea (Echinodermata) collected during the TALUD cruises off the Pacific coast of Mexico, with the description of two new species. *Revista Mexicana de Biodiversidad*, 82, 413–443.

Mastrototaro, F. & Mifsud, C. (2008) Some observations on the morphology of *Sclerasterias richardi* a rarely encountered Mediterranean Sea star (Echinodermata: Asteriidae). *Mediterranean Marine Science*, 9(2), 103–109.

Matsumoto, H. (1915) A new classification of the Ophiuroidea: with description of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68, 43–92.

McEdward, L.R. & Miner, B.G. (2001) Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology*, 79, 1125–1170.

McKenzie, J.D. (1991) The taxonomy and natural history of north European dendrochirote holothurians (Echinodermata). *Journal of Natural History*, 25, 123–171.

Mecho, A., Billett, D.S.M., Ramírez-Llodra, E., Aguzzi, J., Tyler, P.A. & Company, J.B. (2014) First records, rediscovery and compilation of deep-sea echinoderms in the middle and lower continental slope of the Mediterranean Sea. *Scientia Marina*, 78 (2), 281–302.

Mecho, A., Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J. & Company, J.B. (2015) Reproductive biology of the seastar *Ceramaster grenadensis* from the deep north-western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 95, 805–815.

Meijere, J.C.H. de (1903) Vorläufige Beschreibung der neuen, durch die Siboga-Expedition gesammelten Echiniden.*Tijdschrift der Nederlandsche Dierkundige Vereeniging, 2de serie*, 8(1), 1–16.

Messing, C.G. (1978) *Pentametrocrinus atlanticus* (Perrier) (Crinoidea: Echinodermata): a review. *Journal of Natural History*, 12(6), 699–708.

Messing, C.G. & Dearborn, J.H. (1990) Marine Flora and Fauna of the Northeastern United States Echinodermata: Crinoidea. *NOAA/National Marine Fisheries Service, NOAA Technical Report NMFS*, 90, 29 pp.

Metaxas, A. & Giffin, B. (2004) Dense beds of the ophiuroid *Ophiacantha abyssicola* on the continental slope off Nova Scotia, Canada. *Deep-Sea Research I*, 51, 1307–1317.

Micael, J., Azevedo, J.M.N. & Costa, A.C. (2006) Biological characterisation of a subtidal tunnel in S. Miguel island (Azores). *Marine, Freshwater, and Wetlands Biodiversity Conservation*, 4, 307–316.

Micael, J., Alves, M.J., Costa, A.C. & Jones, M.B. (2009) Exploitation and Conservation of Echinoderms. *Oceanography and Marine Biology: An Annual Review*, 47, 191–208.

Micael, J. & Costa A.C. (2010) Echinodermata. *In*: Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P. & Vieira, V. (Eds.) *A list of the terrestrial and marine biota from the Azores*. Princípia, Oeiras, pp. 321–323.

Micael, J., Alves, M.J., Jones, M.B. & Costa A.C. (2010) Quantitative sampling of sub-tidal echinoderms. *Vie et Milieu – Life and Environment*, 60(4), 327–333.

Micael, J., Alves, M.J., Jones, M.B. & Costa, A.C. (2012) Diversity of shallow-water asteroids (Echinodermata) in the Azorean Archipelago. *Marine Biodiversity Records*, 5 (e49), 1–5, doi: 10.1017/S1755267211000534.

Micael, J., Alves, M.J. & Costa, A.C. (2013) The population dynamics of *Ophidiaster ophidianus* (Echinodermata: Asteroidea) in the Azores, at the north-western periphery of its distribution. *Journal of the Marine Biological Association of the United Kingdom*, 93(4), 1087–1095.

Micael, J., Rodrigues, A.S., Barreto, M.C., Alves, M.J., Jones, M.B. & Costa, A.C. (2011) Allocation of nutrients during the reproductive cycle of *Ophidiaster ophidianus* (Echinodermata: Asteroidea). *Invertebrate Reproduction & Development*, 55(4), 205–216.

Micael, J., Rodrigues, P., Costa, A.C. & Alves, M.J. (2014) Phylogeography and genetic diversity of *Ophidiaster ophidianus* (Echinodermata: Asteroidea)—evidence for a recent range expansion in the Azores. *Journal of the Marine Biological Association of the United Kingdom*, 94, 1475–1484.

Mifsud, C., Taviani, M. & Stöhr, S. (2009) Remarks on Echinodermata from the South Central Mediterranean Sea based upon collections made during the MARCOS cruise (10 to 20th April, 2007). *Mediterranean Marine Science*, 10(2), 63–71.

Miller, A.K., Kerr, A.M., Paulay, G., Reich, M., Wilson, N.G., Carvajal, J.I. & Rouse, G.W. (2017). Molecular phylogeny of extant Holothuroidea (Echinodermata). *Molecular Phylogenetics and Evolution*, 111, 110–131.

Miller, J.E. & Pawson, D.L. (1979) A new subspecies of *Holothuria lentiginosa* Marenzeller from the western Atlantic Ocean (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, 91(4), 912–922.

Miller, J.E. & Pawson, D.L. (1984) Holothurians (Echinodermata: Holothuroidea). *Memoirs of the Hourglass Cruises*, 7(1), 1–79.

Miller, J.E. & Pawson, D.L. (1990) Swimming sea cucumbers (Echinodermata: Holothuroidea): a survey with analysis of swimming behavior in four bathyal species. *Smithsonian Contributions to the Marine Sciences*, 35, 1–18.

Miller, J.S. (1821) *A natural history of the Crinoidea or lily-shaped animals, with observations on the genera Asteria, Euryale, Comatula, and Marsupites*. C. Frost, Bristol, 150 pp.

Milne-Edwards, A. (1882) Rapport sur les travaux de la commission chargée par M. Le Ministre de l'Instruction Publique d'étudier la faune sous-marine dans les grandes profondeurs de la Méditerranée et de l'océan Atlantique. *Archives des Missions Scientifiques et Littéraires, troisieme serie*, 9, 1–63.

Minderlein, R. & Wirtz, P. (2014) A sea urchin (*Diadema africanum* Rodriguez *et al.*, 2013) and a pipe fish (*Syngnathus phlegon* Risso, 1827) – two new records for the Azores. *Arquipelago, Life and Marine Sciences*, 31, 3 pp.

Minin, K.V (2012) Vertical trends in morphological variability of sea urchins of the genus Echinus from the Northeast Atlantic and Arctic. *Paleontological Journal*, 46(8), 927–935.

Mironov, A.N. (1978) [The most deep-sea species of sea urchins (Echinoidea, Pourtalesiidae)]. *Zoologicheskii Zhurnal*, 57, 721–726 [in Russian, English summary].

Mironov, A.N. (2006) Echinoids from seamounts of the North-Eastern Atlantic, onshore/offshore gradients in species distribution. *In*: Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*, KMK Scientific Press, Russian Academy of Sciences, P.P. Shirshov Institute of Oceanology, Moscow. Pp. 96–133.

Mironov, A.N. (2008) Pourtalesiid sea urchins (Echinodermata: Echinoidea) of the northern Mid-Atlantic Ridge. *Marine Biology Research*, 4, 3–24.

Mironov, A.N. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Echinoidea. *Invertebrate Zoology*, 11(1), 120–129.

Mironov, A.N., Améziane, N. & Eléaume, M.P. (2014) Deep-sea fauna of European seas: An annotated speciescheck-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Crinoidea. *Invertebrate Zoology*, 11(1), 112–119.

Mironov, A.N. & Krylova, E.M. (2006) Origin of the fauna of the Meteor Seamounts, nort-east Atlantic. *In:* Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*. KMK Scientific Press, Russian Academy of Sciences, P.P. Shirshov Institute of Oceanology, Moscow, pp. 22–57.

Mironov, A.N. & Sagaidachny, A.Y. (1984) [Morphology and distribution of the recent echinoids of the genus Echinocyamus (Echinoidea: Fibulariidae)]. *Trudy Instituta Okeanologii AN*, *USSR*, 119, 179–204 [in Russian, English summary].

Mladenov, P.V. (1985) Development and metamorphosis of the brittle star *Ophiocoma pumila*: evolutionary and ecological implications. *Biological Bulletin*, 168, 285–295.

Molinier R. & Picard J. (1956) Aperçu bionomique sur les peuplements marins littoraux des côtes rocheuses méditerranéennes de l'Espagne. *Bullettin des travaux publiés par la Station d'aquiculture et de pêche de Castiglione N.S.*, 8, 251–268.

Montagu, G. (1803). *Testacea Britannica or Natural History of British Shells, Marine, Land, and Fresh-Water, Including the Most Minute: Systematically Arranged and Embellished with Figures*. J. White, London, 2, 293–606.

Moore, R.C., Lalicker, C.G. & Fischer, A.G. (1952) *Invertebrate fossils*. McGraw-Hill, New York, 766 pp.

Moreno-Batet, E. & Bacallado, J.J. (1980) Sur une collection d'astéries del'Archipel des Canaries *In*: M. Jangoux (Ed.), *Proceedings of the European colloquium on Echinoderms, Brussels, 3–8th September 1979*, Amsterdam, A.A. Balkema, pp. 123–126.

Mortensen, T. (1903) Echinoidea (Part 1). *The Danish Ingolf–Expedition 1895–1896,* Bianco Luno, Copenhagen, 4(1), 1–198.

Mortensen, T. (1907) Echinoidea (Part 2). *The Danish Ingolf–Expedition 1895–1896*, Bianco Luno, Copenhagen, 4(2), 1–200.

Mortensen, T. (1910) *Arbaciella elegans*. Eine neue Echiniden-Gattung aus der Familie Arbaciidae. *Mitteilungen des Naturhistorischen Museum Hamburg*, 27, 327–334.

Mortensen, T. (1913) On the development of some British echinoderms. *Journal of the Marine Biological Association of the United Kingdom*, 10 (1), 1–18.

Mortensen, T. (1920) Notes on some Scandinavian Echinoderms with descriptions of two new Ophiuroids. *Videnskabelige Meddelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, 72, 45–79.

Mortensen, T. (1921) Studies of *the Development and Larval Forms of Echinoderms*. G.E.C. Gad, Copenhagen, 294 pp.

Mortensen, T (1924) Echinoderms of New Zealand and the Auckland-Campbell Islands. II. Ophiuroidea. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, C. A. Reitzel, Copenhagen, 77, 91–177.

Mortensen, T. (1925) Echinodermes du Maroc et De Mauritanie. *Bulletin de la Société des sciences naturelles du Maroc*, 5(4–5), 178–187.

Mortensen, T. (1927a) *Handbook of the echinoderms of the British Isles*. Oxford University Press, viii (8) + 471 pp.

Mortensen, T. (1927b) Sur les échinides recueillis par l'expédition du "Travailleur" et du "Talisman." *Archives du Muséum d'Histoire Naturelle*, 2(6), 21–34.

Mortensen, T. (1928) *A Monograph of the Echinoidea. I. Cidaroidea.* C.A. Reitzel & Oxford University Press, Copenhagen & London, 551 pp.

Mortensen, T. (1933a) Ophiuroidea. *The Danish Ingolf Expedition*, 4(8), 1–121.

Mortensen, T. (1933b) Echinoderms of South Africa (Asteroidea and Ophiuroidea). Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening*, 93, 215–400.

Mortensen, T. (1933c) The echinoderms of St. Helena (Other than crinoids). Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening*, 93, 401–473.

Mortensen, T. (1934) New Echinoidea. Preliminary Notice. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København, 98, 161–167.

Mortensen, T. (1935) *A Monograph of the Echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta*. C.A. Reitzel & Oxford University Press, Copenhagen & London, 647 pp.

Mortensen, T. (1936) Echinoidea and Ophiuroidea. *Discovery Reports*, 12, 199–348.

Mortensen, T. (1939) New Echinoida (Aulodonta). Preliminary Notice. Videnskabelige Meddelelser fra Danks naturhistorisk Forening i København. 103, 547–550.

Mortensen, T. (1940a) *A Monograph of the Echinoidea. III, 1. Aulodonta, with Additions to Vol. II (Lepidocentroida and Stirodonta)*. C.A. Reitzel, Copenhagen, 370 pp.

Mortensen, T. (1940b) Contributions to the Biology of the Philippine Archipelago and adjacent regions. Report on the Echinoidea collected by the United States fisheries streamer "Albatross" during the Philippine Expedition, 1907–1910. Part II. The Echinothuriidae, Saleniidae, Arbaciidae, Aspidodiadematidae, Micropygidae, Diadematidae, Pedinidae, Temnopleuridae, Toxopneustidae, and Echinometridae. *Bulletin of the Smithsonian Institution*, U.S. National Museum, 100 (14.1), 1–52.

Mortensen, T. (1943a) *A Monograph of the Echinoidea. III, 3. Camarodonta. II. Echinidæ, Strongylocentrotidæ, Parasaleniidæ, Echinometridæ*. C.A. Reitzel, Copenhagen, 446 pp.

Mortensen, T. (1943b) *A Monograph of the Echinoidea. III, 2. Camarodonta. I. Orthopsidæ, Glyphocyphidæ, Temnopleuridæ and Toxopneustidæ*. C.A. Reitzel, Copenhagen, 553 pp.

Mortensen, T. (1948) A *Monograph of the Echinoidea. IV, 2. Clypeasteroida. Clypeasteridæ, Arachnoidæ, Fibulariidæ, Laganidæ and Scutellidæ.* C.A. Reitzel, Copenhagen, 471 pp.

Mortensen, T. (1950) *A Monograph of the Echinoidea. V, 1. Spatangoida I. Protosternata, Meridosternata, Amphisternata I. Palæopneustidæ, Palæostomatidæ, Aëropsidæ, Toxasteridæ, Micrasteridæ, Hemiasteridæ*. C.A. Reitzel, Copenhagen, 432 pp.

Mortensen, T. (1951a) Report on the Echinoidea collected by the "Atlantide" Expedition. *Atlantide Report*, 2, 293–303.

Mortensen, T. (1951b) *A Monograph of the Echinoidea. V, 2. Spatangoida II. Amphisternata II. Spatangidæ, Loveniidæ, Pericosmidæ, Schizasteridæ, Brissidæ*. C.A. Reitzel, Copenhagen, 593 pp.

Morton, B. & Britton, J.C. 2000. The origins of the coastal and marine flora and fauna of the Azores. *Oceanography and Marine Biology*, 38, 13–84.

Morton, B., Britton, J.C. & Martins, A.F.M. (1998) *Ecologia costeira dos Açores*. Sociedade Afonso Chaves, Ponta Delgada, 249 pp.

Moyse, J. & Tyler, P.A. (1995) Sea urchins, starfish and sea cucumbers (Phylum Echinodermata). *In*: Hayward, P.J. & Ryland, J.S. (Eds.) *Handbook of the marine fauna of North-West Europe*. Oxford University Press, pp. 662–686.

Müller, O.F. (1776) *Zoologiae Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*. Typiis Hallageriis, Copenhagen, xxii+274 pp.

Müller O.F. (1789) *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia. Volumen tertium*. N. Mölleri et Filii, Copenhagen, 71 pp.

Müller, J. (1841). Über die Gattungen und Arten der Comatulen. *Archiv für Naturgeschichte*, 7(1), 139–148.

Müller, J. & Troschel, F.H. (1840a) Ueber die Gattungen der Ophiuren. *Archiv für Naturgeschichte*, 6(1), 326–330, 367–368.

Müller, J. & Troschel, F.H. (1840b) Ueber die Gattungen der Asterien. *Archiv für Naturgeschichte*, 6(1), 318–326.

Müller, J. & Troschel, F.H. (1842) *System der Asteriden*. Vieweg und Sohn, Braunschweig, xxx(30)+134 pp.

Murillo, F.J., Serrano, A., Kenchington, E. & Mora, J. (2015) Epibenthic assemblages of the tail of the grand bank and Flemish cap (northwest Atlantic) in relation to environmental parameters and trawling intensity. *Deep Sea Research Part I: Oceanographic Research Papers*, 109, 99–122.

Muths, D., Jollivet, D., Gentil, F. & Davoult, D. (2009) Large-scale genetic patchiness among NE Atlantic populations of the brittle star *Ophiothrix fragilis*. Aquatic Biology, 5, 117–132.

Narasimhamurti, N. (1933) The development of *Ophiocoma nigra*. *Quarterly Journal of Microscopical Science*, 76, 63–88.

Nardo, J.D. (1834) De Asteriis. Isis von Oken, Encyclopaedische Zeitun, 27, 716–717.

Nataf, G. & Cherbonnier, G. (1975) Troisieme contribution a la connaissance des Asterides de la cote occidentale d'Afrique. *Bulletin du Museum National D'Histoire Naturelle*, *3ª série, Zoologie*, Paris, 311(218), 813–834, 3 pls.

Nichols, D. (1959) Changes in the Chalk heart-urchin *Micraster* interpreted in relation to living forms: *Royal Society of London, Philosophical Transactions, Series B*, 242, 347–437.

Nichols, D. (1994) Reproductive seasonality in the comatulid crinoid *Antedon bifida* (Pennant) from English Channel. *Philosophical Transactions of the Royal Society of London B*, 343, 113–134.

Nobre, A. (1924) Contribuições para a Fauna dos Açores. *Anais do Instituto de Zoologia da Universidade do Porto*, 1, 41–90.

Nobre, A. (1930) *Materiais para o estudo da fauna dos Açores*. Instituto de Zoologia da Universidade do Porto, Porto, 108 pp.

Nobre, A. (1938) *Equinodermes de Portugal*. 3rd Edition. Companhia Editora do Minho, Barcelos, 215 pp.

Nordsieck F. (1975) Conchiglie delle Isole Canarie. Parte 2. *La Conchiglia*, 75–76, 3–7, 22. [not seen]

Norman A.M. (1865) On the genera and species of British Echinodermata. 1, Crinoidea, Ophiuroidea, Asteroidea. *Annals and Magazine of Natural History, series 3*, 15, 98–129.

Norman, A.M. (1905) On *Cucumaria Montagui*, Fleming. *Annals and Magazine of Natural History*, 16, 352–359.

O’Hara, T. & Stöhr, S. (2006) Deep-water Ophiuroidea (Echinodermata) of New Caledonia: Ophiacanthidae and Hemieuryalidae. *Mémoire du Muséum national d’Histoire naturelle*. 193, 33–141

O'Hara, T.D.;, Hugall, A.F., Thuy, B., Stöhr, S., Martynov, A.V. (2017) Restructuring higher taxonomy using broad-scale phylogenomics: The living Ophiuroidea. *Molecular Phylogenetics and Evolution*. 107: 415–430.

O'Hara, T.D., Stöhr, S., Hugall, A.F., Thuy, B. and Martynov, A. (2018) Morphological diagnoses of higher taxa in Ophiuroidea (Echinodermata) in support of a new classification. *European Journal of Taxonomy*, 416: 35 pp., doi.org/10.5852/ejt.2018.416.

Okanishi, M. & Fujita, T. (2014) A taxonomic review of the genus *Astrodia* (Echinodermata: Ophiuroidea: Asteronychidae). *Journal of the Marine Biological Association of the United Kingdom*, 94, 187–201.

O’Loughlin, P.M. (2002) Report on selected species of Banzare and Anare Holothuroidea, with reviews of *Meseres* Ludwig and *Heterocucumis* Panning (Echinodermata). *Memoirs of Museum Victoria*, 59(2), 297–325.

O’Loughlin, P.M. & Ahearn C. (2005) A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific ocean. *Memoirs of Museum Victoria*, 62(2), 147–179.

O’Loughlin, P.M., Paulay, G., Vandenspiegel, D. & Sam, Y. (2007) New Holothuria species from Australia (Echinodermata: Holothuroidea: Holothuriidae), with comments on the origin of deep and cool holothuriids. *Memoirs of Museum Victoria*, 64, 35–52.

Örstedt, A.S. (1849) *Synaptula vivipara*. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening, København,* 1849–1850, 7.

Orton, J.H. (1914) On some Plymouth holothurians. *Journal of the Marine Biological Association of the United Kingdom*, 10 (2), 211–235.

Östergren, H. (1898) Das system der Synaptiden. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 55(2), 111–120.

Östergren, H. (1907) Zur Phylogenie und Systematik der Seewalzen. *In*: *Zoologiska Studier Tillägnade Prof. T. Tullberg [Utg.: Naturvet. Studentsällsk.]*, Almqvist & Wiksell, Upsala, pp. 191–215.

Otto, A.W. (1823) Beschreibung einiger neueu Mollusken und Zoophyten. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosum, 11 (2), 273–314.

Panning, A. (1939) Holothurien von den Kanaren und von Dakar. *Videnskabelige Meddelelser Dansk Naturhistorik Forening, København*, 103, 523–546.

Parenzan, P. (1934) Revisione delle specie mediterranee del genere *Astropecten*. *Bolletino di Zoologia*, 5(1), 201–223.

Paterson, G.L.J. (1985) The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History), Zoology Series*, 49(1),1–162.

Paterson, G.L.J., Tyler, P.A. & Gage, J.D. (1982) The taxonomy and zoogeography of the genus *Ophiocten* (Echinodermata: Ophiuroidea) in the North Atlantic Ocean. *Bulletin of the British Museum (Natural History)*, *Zoology*, 43(3), 109–128.

Pawson, D.L. (1965) Some echinozoans from north of New Zealand. *Transactions of the Royal Society of New Zealand, Zoology*, 5, 197–224.

Pawson, D.L. (1978) The Echinoderm Fauna of Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to the Marine Sciences*, 2, 31pp.

Pawson, D.L. (1982) Deep-sea echinoderms in the Tongue of the Ocean, Bahama Islands: a survey, using the research submersible Alvin. *Australian Museum Memoir*, 16, 129–145.

Pawson, D.L. (2007) Phylum Echinodermata. *Zootaxa*, 1668, 749–764.

Pawson, D.L. & Miller, J.E. (1981) Western Atlantic sea cucumbers of the genus *Thyone*, with descriptions of two new species (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, 94(2), 391–403.

Pawson, D.L. & Miller, J.E. (1983) Systematics and Ecology of the Sea urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans. *Smithsonian Contributions to the Marine Sciences*, 20, 1–15.

Pawson, D.L., Pawson, D.J. & King, R.A. (2010) A taxonomic guide to the Echinodermata of the South Atlantic Bight, USA: 1. Sea cucumbers (Echinodermata: Holothuroidea). *Zootaxa*, 2449, 1–48.

Pawson, D.L. & Shirley, T.C. (1977) Occurrence of the subgenus *Holothuria* (*Holothuria*) in the Gulf of Mexico (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, 90(4), 915–920.

Pawson, D.L., Vance, D.J., Messing, C.G., Solís-Marin, F.A. & Mah, C.L. (2009) Echinodermata of the Gulf of Mexico. *In*: Felder D.L. & Camp, D.K. (Eds.) *Gulf of Mexico: origin, waters, and biota, vol. 1, Biodiversity.* Texas A & M University Press, College Station, pp. 1177–1204.

Pearse, A. S. & Williams, L. G. (1951) The biota of the reefs off the Carolinas. *Journal of the Elisha Mitchell Scientific Society*, 67(1), 133–161.

Pearson, J. (1914) Proposed re-classification of the genera *Mülleria* and *Holothuria*. *Spolia Zeylan*, 9, 163–172.

Pennant, T. (1777) *British Zoology, vol. IV. Crustacea. Mollusca. Testacea*. Benj. White, London, 154 pp.

Péquignat, E. (1963) Sur un nouvel *Echinocardium* de Ligurie et de Provence: *Echinocardium fenauxi* n. sp. *Doriana.* 3 (138), 1–9.

Pereira, M. (1997) Checklist of the littoral echinoderms of the Azores. *Açoreana*, 8(3), 331–337.

Pérès, J.M. (1964) Contribution à l'étude des peuplements benthiques du golfe Ibéro–Marocaine. Campagne de la Calypso en mer d'Alboran et dans la Baie Ibéro–Marocaine (1958), XX. *Annales de l'Institut Oceanographique*, 41, 3–30.

Pérès, J.M. (1992) Le bathyscaphe français Archimède aux Açores: étude bionomique et écologique du benthos profond. *Açoreana*, suplemento, 237–264.

Pérez-Portela, R., Villamor, A., & Almada, V. (2010) Phylogeography of the sea star *Marthasterias glacialis* (Asteroidea, Echinodermata): deep genetic divergence between mitochondrial lineages in the north-western mediterranean. *Marine Biology*, 157(9), 2015–2028.

Pérez-Ruzafa, A., Marcos, C. & Bacallado, J.J. (1992a) Holoturias (Echinodermata: Holothlroidea) de las Islas Canarias: II. Ordenes Dendrochirotida, Elasipodida, Apodida y Molpadida. *Revista de la Academia Canaria de Ciencias*, 3–4, 163–185.

Pérez-Ruzafa, A., Marcos, C. & Bacallado, J.J. (1992b) Holoturias (Echinodermata: Holothuroidea) de las Islas Canarias: I. Consideraciones Generales y Orden Aspidochirotida. *Revista de la Academia Canaria de Ciencias*, 4(3–4), 139–162.

Pérez-Ruzafa, A., Entrambasaguas, L. & Bacallado, J.J. (1999) Fauna de equinodermos (Echinodermata) de los fondos rocosos infralitorales del archipielago de Cabo Verde. *Revista de la Academia Canaria de Ciencias*, 11 (3–4), 43–62.

Pérez-Ruzafa, A., Entrambasaguas, L., Espejo, C., Marcos, C. & Bacallado, J.J. (2002) Fauna de equinodermos (Echinodermata) de los fondos rocosos infralitorales del archipiélago de Salvajes (Océano Atlantico). *Revista de la Academia Canaria de Ciencias*, 14 (3–4), 277–296.

Pérez-Ruzafa, A., Aránega, J.J.B., García, I.A. & Díaz, J.R.D. (2003) División Echinodermata. *In*: Moro, L., Martìn, J.L., Garrido, M.J. & Izquierdo, I. (Eds.) *Lista de especies marinas de Canarias (algas, hongos, plantas y animales)*, Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias, Tenerife, 112–113 pp.

Pérez-Ruzafa, A., Alvarado, J.J., Solís-Marín, F.A., Hernández, J.C., Morata, A., Marcos, C., Abreu-Pérez, M., Aguilera, O., Alió, J., Bacallado-Aránega, J.J., Barraza, E., Benavides-Serrato, M., Benítez-Villalobos, F., Betancourt-Fernández, L., Borges, M., Brandt, M., Brogger, M.I., Borrero-Pérez, G.H., Buitrón-Sánchez, B.E., Campos, L. S., Cantera, J.R., Clemente, S., Cohen-Renfijo, M., Coppard, S.E., Costa-Lotufo, L., Valle-García, R. del, Díaz de Vivar, M.E., Díaz-Martínez, J.P., Díaz, Y., Durán-González, A., Epherra, L., Escolar, M., Francisco, V., Freire, C.A., García-Arrarás, J.E., Gil, D. G., Guarderas, P., Hadel, V.F., Hearn, A., Hernández-Delgado, E.A., Herrera-Moreno, A., Herrero-Pérezrul, M.D., Hooker, Y., Honey-Escandón, M.B.I., Lodeiros, C., Luzuriaga, M., Manso, C.L.C., Martín, A., Martínez, M.I., Martínez, S., Moro-Abad, L., Mutschke, E., Navarro, J.C., Neira, R., Noriega, N., Palleiro-Nayar, J., Pérez, A.F., Prieto-Ríos, E., Reyes, J., Rodríguez-Barreras, R., Rubilar, T., Sancho-Mejías, T.I., Sangil, C., Silva, J. R.M.C., Sonnenholzner, J.I., Ventura, C.R.R., Tablado, A., Tavares, Y., Tiago, C.G., Tuya, F., Williams, S.M. (2013) Latin America Echinoderm Biodiversity and Biogeography: Patterns and Affinities. *In*: Alvarado, J.J. & Solis-Marin, F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*, 511–542.

Perrier, M.E. (1875) *Révision de la collection de stellérides du Museum d'Histoire naturelle de Paris*. Reinwald, Paris, 384 pp.

Perrier, M.E. (1881) Description sommaire des espèces nouvelles d'Astéries. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 9, 1–31.

Perrier, M.E. (1883a) Sur des *Eudiocrinus* de l'Atlantique, et sur la nature de la faune des grandes profondeurs. *Comptes Rendus Académie des Sciences*, Paris, 96, 725–728.

Perrier, M.E. (1883b) On a new attached Crinoid, *Democrinus Parfaiti*, from the dredgings of the 'Travailleur'. *Annals and Magazine of Natural History*, 11(5), 223–224.

Perrier, M. E. (1884) Mémoire sur les étoiles de mer recueillis dans la Mer des Antilles et la Golfe de Mexique. *Nouvelle Archives Museum d'Histoire naturelle de Paris*, 6(2), 127–276.

Perrier, M.E. (1885a) Les Encrines vivantes. *Revue Scientifique (revue rose)*, Paris, 35, 690–693.

Perrier, M.E. (1885b) Sur les stellérides recueillis durant la mission du Talisman. *Comptes-rendus Hébdomadaires des Seances de l'Académie des Sciences* (Paris), 101, 884–887.

Perrier, M.E. (1885c) Premiére note préliminaire des les Echinodermes, recueillis durant les campagnes de dragages sous-marines du Travailleur et du Talisman. *Annales des Sciences Naturelles, Zoologie*, 22(8), 1–72.

Perrier, M.E. (1885d) Sur Ies Brisingidae de la mission du Talisman. *Comptes-rendus Hébdomadaires des Seances de l'Académie des Sciences* (Paris), 101, 441–444.

Perrier, M.E. (1891) Stellérides nouveaux provenant des campagnes du yacht l'Hirondelle. *Mémoires de la Société zoologique de France*, 4, 258–271.

Perrier, M.E. (1893) *Traité de zoologie par Edmond Perrier. Première Partie. Zoologie Générale, Protozoaires et Phytozoaires Arthropodes*. Masson, Paris, 1352 pp.

Perrier, M.E. (1894) Stellérides. *Expéditions Scientifiques du Travailleur et du Talisman*. Masson, Paris, 1–431.

Perrier, M.E. (1896a) Contribution à l'étude des stellérides de l'Atlantique Nord (Golfe de Gascogne, Açores, Terre-Neuve). *Resultats Des Campagnes Scientifiques Accomplies Par Le Prince Albert I. Monaco*, 11, 1–571.

Perrier, R. (1896b) Sur les Elasipodes recueillis par le Travailleur et le Talisman. *Comptes Rendus Académie Sciences*, Paris, 123, 900–903.

Perrier, R. (1898) Sur les Holothuries recueillies par le Travailleur et le Talisman. *Comptes Rendus Académie Sciences*, Paris, 126, 1664–1666.

Perrier, R. (1899) Diagnose des especes nouvelles d'Holothuries draguees par le du Travailleur et le Talisman. Deuxieme note. *Bulletin Muséum National Histoire Naturelle*, Paris, 5, 299–303.

Perrier, R. (1900) Diagnose des Espèces Nouvelles D'Holoturies Draguées par le Travailleur et le Talisman (troisième et dernière note). *Bulletin du Muséum d'Histoire Naturelle*, 6, 116–119.

Perrier, R. (1902) Holothuries. *In*: *Expéditions Scientifiques du Travailleur et du Talisman pendant les Années 1880, 1881, 1882, 1883.* Ouvrage publié sous les auspices du ministère de l'instruction publique sous la direction de A. Milne-Edwards de 1888 à 1890 et continué par E. Perrier. vol. 7. Masson et Cie, Editeurs, Paris, pp. 273–554.

Peters, W. (1855) Über die an der Küste von Mossambique beobachteten Seeigel und insbesondere über die Gruppe der Diademen. *Abhandlungen der preussischen Akademie der Wissenschaften 1854*, 101–119.

Phelsum, M. von (1774) *Brief aan den wel-eerwaardigen en zeer geleerden heere Cornelius Nozeman*. Arrenberg, Rotterdam, 145 pp.

Philippi, R.A. (1837) Ueber die mit *Asterias aurantiaca* verwandten und verwechselten Asterien der sicilianischen Küste. *Archiv für Naturgeschichte*, 3, 193–194.

Philippi, R.A. (1845) Beschreibung einiger neuer Echinodermen nebst kritischen Bemerckungen über einige weniger bekannte Arten. *Archiv für Naturgeschichte*, 11, 344–359.

Picton, B. (1993) *A field guide to the shallow-water echinoderms of the British Isles*. IMMEL Publishing Lda, London, 96 pp.

Pomel, A. (1883) *Classification méthodique et Genera des Échinides vivantes et fossiles*. Thèses présentées à la Faculté des Sciences de Paris pour obtenir le Grade de Docteur ès Sciences Naturelles 503, Adolphe Jourdan, Alger, 131 pp.

Pourtalès, L.F. de (1874) On a new species of *Rhizocrinus* from Barbados. *In*: Agassiz, A. & Pourtalès. Zoological Results of the Hassler Expedition: Echini, Crinoids, and Corals. *Illustrated catalogue of the Museum of Comparative Zoölogy at Harvard College*, 8, 27–31.

Prata J., Dias, T.L.P. & Christoffersen, M.L. (2014) Occurrence of *Holothuria* (*Holothuria*) *dakarensis* (Holothuroidea: Echinodermata) in the South-western Atlantic, with notes on distribution and ecology. *Marine Biodiversity Records*, 7, 1–6.

Purcell, S.W., Samyn, Y. & Conand, C. (2012) Commercially important sea cucumbers of the world. *FAO Species Catalogue for Fishery Purposes*, Rome, 6, 150 pp.

Quartau, R., Hipólito, A., Romagnoli, C., Casalbore, D., Madeira, J., Tempera, F., Roque, C. & Chiocci, F.L. (2014) The morphology of insular shelves as a key for understanding the geological evolution of volcanic islands: insights from Terceira Island (Azores). *Geochemistry, Geophysics, Geosystems*, 15, 1801–1826.

Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Thomas, C., Quartau, R., Hipólito, A., Rovere, A., Hearty, P.J. & Ávila, S.P. (2017) The emergence and evolution of Santa Maria Island (Azores) – the conundrum of uplifting islands revisited. *Geological Society of America Bulletin*. doi:10.1130/B31538.1.

Ramirez-Llodra, E., Tyler, P. & Billett, D. (2002) Reproductive biology of porcellanasterid asteroids from three abyssal sites in the northeast Atlantic with contrasting food input. *Marine Biology*, 140(4), 773–788.

Ramón, M., Lleonartb, J. & Massutía, E. (2010) Royal cucumber (*Stichopus regalis*) in the northwestern Mediterranean: Distribution pattern and fishery. *Fisheries Research*, 105, 21–27.

Rasmussen H.W. (1978) Articulata. *In*: Moore, R.C. & Teichert, C. (Eds.) *Treatise on Invertebrate Paleontology. Pt. T, Echinodermata*. Geological Society of America and University of Kansas Press, 2(3), T813–T928.

Regis, M.B. (1982) Donnes microstructurales et validite du genre *Arbaciella* Mrtsn (Echinodermata-Echinoidea). *Memoires sur le Biologie Marine et Oceanographique*, 12, 5–26.

Retzius, A.J. (1783) Anmärkningar vid Asteriae genus. *Kungliga Svenska Vetenskapsakademiens handlingar*, 4, 234–244.

Ridder, C. de, Jangoux, M., Vos, L. de (1987) Frontal ambulacral and peribuccal areas of the spatangoid echinoid *Echinocardium cordatum* (Echinodermata): a functional entity in feeding mechanism. *Marine Biology*, 94(4), 613–624.

Ringvold, H. (1999) Starfishes (Echinodermata, Asteroidea) new for the Faroe Islands, collected by "BIOFAR". *Sarsia*, 84, 469–472.

Rochebrune, A.T. (1881) Matériaux pour la faune de l'Archipel du Cap Vert. *Nouvelle Archives du Museum National d'Histoire Naturelle, Paris, series 2*, 4, 215–340.

Rochette, R., Hamel, J.-F. & Himmelman, J.H. (1994) Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status. *Marine Ecology Progress Series*, 106, 93–100.

Rodrigues, C.F., Paterson, G. Cabrinovic, A. & Cunha, M.R. (2011) Deep-sea ophiuroids (Echinodermata: Ophiuroidea: Ophiurida) from the Gulf of Cadiz (NE Atlantic). *Zootaxa*, 2754, 1–26.

Rodríguez, A., Hernández, J.C., Clemente, S. & Coppard, S.E. (2013) A new species of *Diadema* (Echinodermata: Echinoidea: Diadematidae) from the eastern Atlantic Ocean and a neotype designation of *Diadema antillarum* (Philippi, 1845). *Zootaxa*, 3636(1), 144–170.

Rogacheva, A., Cross, I.A. & Billett, D.S.M. (2009) Psychropotid holothurians (Echinodermata: Holothuroidea: Elasipodida) collected at abyssal depths from around the Crozet Plateau in the southern Indian Ocean. *Zootaxa*, 2096, 460–478.

Rogacheva, A., Gebruk, A. & Alt, C.H.S. (2012) Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge. *Zoosymposia*, 7, 213–224.

Rogacheva, A., Gebruk, A. & Alt, C.H.S. (2013) Holothuroidea of the Charlie Gibbs Fracture Zone area, northern Mid-Atlantic Ridge. *Marine Biology Research*, 9(5–6), 587–623.

Roux, M. (1980) Les crinoïdes pédonculés (Échinodermes) photographiés sur les dorsales océaniques de l'Atlantique et du Pacifique. Implications biogéographiques. *Comptes Rendus de l'Académie des Sciences, Série D*, Paris, 291(11), 901–904.

Roux, M. (1985) Les crinoïdes pédonculés (Echinodermes) de l'Atlantique N.E.: Inventaire, écologie et biogéographie. *In*: Laubier, L. & Monniot, C. (Eds.), *Peuplements profonds du golfe de Gascogne, Campagnes BIOGAS*. IFREMER, pp. 479–489.

Roux, M., Messing, C.G. & Ameziane, N. (2002) Artificial keys to the genera of living stalked crinoids (Echinodermata). *Bulletin of Marine Science*, 70 (3), 799–830.

Rowe, F.W.E. (1969) A review of the family Holothuriidae (Holothurioidea: Aspidochirotida). *Bulletin of the British Museum (Natural History). Zoology*, 18(4), 119–170.

Rowe, F.W.E. (1970) A Note on the British Species of Cucumarians, Involving the Erection of Two New Nominal Genera. *Journal of the Marine Biological Association of the United Kingdom*, 50(3), 683–687.

Sabine, E. (1924) Marine Invertebrate Animals. *A supplement to the Appendix of Captain Parry's Voyage for the Discovery of a North-West Passage in the years 1819–20.* John Murray, London, 219–239.

Santos, A., Mayoral, E., Dumont, C.P., da Silva, C.M., Ávila, S.P., Gudveig Baarli, B., Cachão, M., Johnson, M.E., Ramalho, R.S. (2015) Role of environmental change in rock-boring echinoid trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 432, 1–14.

Sars, G.O. (1872) Nye Echinodermer fra den norske kyst. *Videnskabelige Selskabets Forhandlinger 1871*, 1–31.

Sars, G.O. (1875) *On Some Remarkable Forms of Animal Life From the Great Deeps off the Norwegian Coast. II. Researches on the Structure and Affinity of the genus Brisinga Based on the study of a New Species, Brisinga coronata.* Christiana University, Christiania, 112 pp.

Sars, M. (1859) Bidrag til Kundskaben om Middelhavets Littoral-Fauna. *Nyt Magazin för Naturvidenskaberne*, 10, 1–99.

Sars, M. (1861) Oversigt af Norges Echinodermer. *Videnskabsselskabet i Christiana*, Christiana, 160 pp.

Saucede, T., Mironov, A.N., Mooi, R. & David, B. (2009) The morphology, ontogeny, and inferred behaviour of the deep-sea echinoid *Calymne relicta* (Holasteroida). *Zoological Journal of the Linnean Society*, 155, 630–648.

Say, T. (1825) On the species of the Linnaean genus Asterias inhabiting the coast of the U.S. *Journal of the Academy of natural sciences of Philadelphia*, 5, 141–154.

Schipper, C.A., Dubbeldam, M., Feist, S.W., Rietjens, I.M.C.M. & Murk, T.A.J. (2008) Cultivation of the heart urchin *Echinocardium cordatum* and validation of its use in marine toxicity testing for environmental risk assessment. *Journal of Experimental Marine Biology and Ecology*, 364(1–2), 11–18.

Schoener, A. (1972) Fecundity and possible mode of development of some deep-sea ophiuroids. *Limnology and Oceanography*, 17(2), 193–199.

Schultz, H. (2006) *Sea Urchins – a guide to worldwide shallow-water species*. Heinke & Peter Schultz Partner Scientific Publications, 3rd edition, 484 pp.

Selenka, E. (1867) Beitrage zur Anatomie und Systematik der Holothurien. *Der Philosophischen Facultat zu Gottingen in December 1866, als Dissertation vorgelegt*. Verlag Von Wilhelm Engelmann, Leipzig, 291–374.

Serafy, D.K. (1971) Intraspecific variation in the brittle star *Ophiopholis aculeata* (Linnaeus) in the northwestern Atlantic (Echinodermata: Ophiuroidea). *The Biological Bulletin*, 140, 323–333.

Serafy, D.K. (1974) A new heart-urchin, *Araeolampas atlantica*, new genus, new species, from the North Atlantic and notes on the closely related *Homolampas*. *Proceedings of the Biological Society of Washington*, 87, 41–48.

Serafy, D.K. & Fell, F.J. (1985) Marine Flora and Fauna of the Northeastern United States. Echinodermata: Echinoidea. *NOAA Technical Report NMFS*, 33, 27 pp.

Shick, J.M., Taylor, W.F. & Lamb, A.N. (1981) Reproduction and genetic variation in the deposit-feeding sea star *Ctenodiscus crispatus*. *Marine Biology*, 63(1), 51–66.

Sicuro, B. & Levine, J. (2011) Sea Cucumber in the Mediterranean: A Potential Species for Aquaculture in the Mediterranean. *Reviews in Fisheries Science*, 19(3), 299–304.

Sieverts-Doreck, H. (1952) Articulata. *In*: Ubaghs, G. (Ed.), Classe de Crinoides. *Traité de Paléontologie*, 3, 658–773.

Sibuet, M. (1972) Echinodermes recoltes lors de la mission du Bathyscaphe Archimède aux Açores en 1969. *Publications du Centre national pour l'exploitation des océans. Résultats des campagnes à la mer*, 3, 121–123.

Sibuet, M. (1975) Astérides abyssales de l'Atlantique sud. (Résultats de la campagne Walda, juin–juillet–août 1971). *Bulletin du Muséum National d'Histoire Naturelle*, 3(289), 281–297.

Sibuet, M. (1976) The genus *Hymenaster* (Asterids) in the Atlantic ocean. *Bulletin du Museum National d'Histoire Naturelle (Museum National d'Histoire Naturelle)*, 368 (256), 305–324.

Sibuet, M. (1977) *Ophidiaster reyssi* nouvelle espèce d'Astéride bathyale de l'oéean Atlantique. *Bulletin du Muséum national d'histoire naturelle*. 3e série, 343 (494), 1085–1090.

Silva, H.M. da & Pinho, M.R. (2007) Small-scale fishing on seamounts. *In*: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N. & Santos, R.S. (Eds.) *Seamounts: Ecology, Fisheries & Conservation*. Wiley-Blackwell, pp. 335–360.

Simroth H. (1888) Zur kenntnis der Azorenfauna. *Archiv für Naturgeschichte*, Berlin, 54 (1), 179–234.

Sladen, W.P. (1879) On *Astrophiura permira*, an echinoderm-form intermediate between Ophiuroidea and Asteroidea. *Proceedings of the Royal Society of London*, 27, 456–457.

Sladen, W.P. (1882) The Asteroidea of H.M.S. Challenger Expedition. Part I, Pterasteridae. *Journal of the Linnean Society of London*, 16, 189–246.

Sladen, W.P. (1883) The Asteroidea of H.M.S. Challenger Expedition. Part II, Astropectinidae. *Journal of the Linnean Society. Zoology*, 17, 214–269.

Sladen, W.P. (1889) Report on the Asteroidea collected by H.M.S. Challenger during the years 1873–1876. *Challenger series of reports, Zoology*, 30, 893 pp.

Sladen, W.P. (1891) Report on a collection of echinodermata from the south-west coast of Ireland, dredged in 1888 by a committee appointed by the Royal Irish Academy. *Proceedings of the Royal Irish Academy*, *third series*, 1, 687–704.

Sluiter, C.P. (1901) Neue Holothurien aus der Tief-See des Indischen Archipels gesammelt durch die Siboga-Expedition. *Tijdschrift Nederlandsche Dierkundige Vereeniging*, 7(1), 1–28.

Smirnov, A.V. (2012) System of the class Holothuroidea. *Paleontological Journal*, 46(8), 793–832.

Smirnov, I.S., Piepenburg, D., Ahearn, C. & Juterzenka, K.V. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Ophiuroidea. *Invertebrate Zoology*, 11(1), 192–209.

Smith, A.B. (1981) Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. Palaeontology, 24, 779–801.

Smith, A.B. (1984) *Echinoid Palaeobiology*. Allen & Unwin, London, x (10)+ 190 pp.

Smith, A.B. & Wright, C.W. (1990) British Cretaceous echinoids. Part 2, Echinothurioida, Diadematoida and Stirodonta (1, Calycina). *Monographs of the Palaeontographical Society*, 143 (583), 101–198.

Sneli, J.-A. (1999) Echinodermata, Asteroidea in the Faroe region. *Fróðskaparrit*, 47, 229–259.

Sponer, R. & Roy, M.S. (2002) Phylogeographic analysis of the brooding brittle star *Amphipholis squamata* (Echinodermata) along the coast of New Zealand reveals high cryptic genetic variation and cryptic dispersal potential. *Evolution*, 56(10), 1954–67.

Stevenson, A. & Rocha, C. (2012) Evidence for the bioerosion of deep-water corals by echinoids in the Northeast Atlantic. *Deep-Sea Research I*, *Oceanographic Research Papers*, 71, 73–78.

Steenstrup, J.J.S. (1847) Gebirgsarten und Versteinerungen vom Museum der Kopenhagener Universität. *Amtlicher Bericht über die 24. Versammlung Deutscher Naturforscher und Aerzte in Kiel 1846. Akademische Buchhandlung*, *Kiel,* 117–119.

Stimpson, W. (1862). On new genera and species of starfishes of the family Pycnopodidae (*Asteracanthion* Mueller & Troschel). *Proceedings of the Boston Society of Natural History*, 8, 261–273.

Stockley, B., Smith, A.B., Littlewood, T., Lessios, H.A., Mackenzie-dodds, J.A. (2005) Phylogenetic relationships of spatangoid sea urchins (Echinoidea): taxon sampling density and congruence between morphological and molecular estimates. *Zoologica Scripta*, 34, 447–468.

Stöhr, S. (2005) Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society*, 143, 543–576.

Stöhr, S. (2011) New records and new species of Ophiuroidea (Echinodermata) from Lifou, Loyalty Islands, New Caledonia. *Zootaxa*, 3089, 1–50.

Stöhr, S. & M. Segonzac (2005) Deep-sea ophiuroids (Echinodermata) from reducing and non-reducing environments in the North Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 84, 4722/1–20.

Stöhr, S., Boissin, E. & Chenuil, A. (2009) Potential cryptic speciation in Mediterranean populations of *Ophioderma* (Echinodermata: Ophiuroidea). *Zootaxa*, 2071, 1–20.

Stöhr, S., O'Hara, T. & Thuy, B. (2012) Global diversity of Ophiuroidea. *PloS One*, 7(3), 1–14.

Storm, V. (1881) Bidrag til Kundskab om Throndhjemsfjordens Fauna III. *Kongelige Norske videnskabers selskabs skrifter*, 1881, 73–96.

Studer, T. (1883) Über der Asteriden, welche während der Reise SMS Gazelle um die Erde gesammelt wurden. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1883(8), 128–132.

Sumida, P.Y.G., Tyler, P.A., Cage, J.D. & Nørrevang, A. (1998) Postlarval development in shallow and deep-sea ophiuroids (Echinodermata: Ophiuroidea) of the NE Atlantic Ocean. *Zoological Journal of the Linnean Society*, 124, 267–300.

Sumida, P.Y.G., Tyler, P.A & Billett, D.S.M (2001) Early juvenile development of deep-sea asteroids of the NE Atlantic Ocean, with notes on juvenile bathymetric distributions. *Acta Zoologica*, 82 (1), 11–40.

Thandar, A.S. (1988) A new subgenus of *Holothuria* with a description of a new species from the south-east Atlantic Ocean. *Journal Zoology*, London. 215, 47–54.

Thandar, A.S. (1999) Deep-Sea holothuroids taken by the R. V. Africana II in 1959, from off the West Coast of the Cape Peninsula, South Africa. *Annals of the South African Museum*, 105, 363–409.

Thandar, A.S. & Mjobo, S. (2014). On some sea cucumbers from Ghana (Echinodermata: Holothuroidea) with descriptions of a new genus and one new species. *Zootaxa*, 3900(2), 243–254.

Théel, H. (1879) Preliminary report on the Holothuridae of the Exploring voyage of H.M.S. Challenger. *Bihang till Kungliga Svenska Vetenskaps Akademien Handlingar*, 5(19), 1–24.

Théel, H. (1882) Report on the Holothuroidea dredged by H.M.S. Challenger during the years 1873–76. Part I. *Challenger Reports, Zoology*, 4, 176 pp.

Théel, H. (1886a) Report on the Holothuroidea dredged by H.M.S. Challenger during the years 1873–76. Part II. *Challenger Reports, Zoology*, 14(39), 290 pp.

Théel, H. (1886b) Report on the Holothurioidea. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U. S. Coast Survey Steamer "Blake", Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 13(1), 1–21.

Theroux, R.B. & Wigley, R.L. (1998) Quantitative Composition and Distribution of the Macrobenthic Invertebrate Fauna of the Continental Shelf Ecosystems of the Northeastern United States. *NOAA Technical Report, National Fisheries Marine Service*, U.S. Department of Commerce, 140, 50 pp.

Thomas, L.P. (1973) Western Atlantic brittlestars of the genus *Ophionereis*. Biological Results of the University of Miami Deep-Sea Expeditions. *Bullentin of Marine Science*, 23(3), 585–599.

Thomson, W. (1872a) On the crinoids of the "Porcupine" deep-sea dredging expedition. *Proceedings of the Royal Society of Edinburgh*, 7(1869–1872), 764–773.

Thomson, W. (1872b) On the Echinoidea of the Porcupine Dredging Expeditions. *Proceedings of the Royal Society of London*, 2, 719–756.

Thomson, W. (1873) *The depths of the sea*. Macmillan, London. 527 pp.

Thomson, W. (1876) Notice of new living crinoids belonging to the Apiocrinidae. *Journal of the Linnean Society of London, Zoology*, 13, 47–55.

Thomson, W. (1877) *The voyage of the "Challenger": the Atlantic*. Macmillan, London 1, 424 pp.

Thomson, W. & Murray, J. (1885) Report on the scientific results of the voyage of H.M.S. "Challenger" during the years 1875–1876. Narrative, 1(1–2), i–liv+1110 pp.

Tommasi, L.R. & Oliveira, E. de (1976) Equinodermes do Brasil. V. Sobre algumas espécies coletadas durante viagens do N/Oc. "Prof. W. Besnard". *Boletim Instituto Oceanografica*, São Paulo, 25 (1), 77–100.

Tortonese, E. (1955) Notes on Asteroidea. *Annals and Magazine of Natural History*, 8, 675–684.

Tortonese, E. (1965) *Fauna D'Italia – Echinodermata*. Edizioni Calderini, Bologna, 422 pp.

Tortonese, E. & Clark, A.M. (1956) On the generic position of the asteroid *Goniodiscus placenta* Müller & Troschel. *Annals and Magazine of Natural History*, 9 (12), 347–352.

Troschel, F.H. (1872) Die Familie der Echinocidariden. *Archiv für Naturgeschichte*, 38, 293–356.

Tuya, F., Boyra, A., Sanchez-Jerez, P., Barbera, C. & Haroun, R. (2004) Can one species determine the structure of the benthic community on a temperate rocky reef? The case of the long-spined sea urchin Diadema antillarum (Echinodermata: Echinoidea) in the eastern Atlantic. *Hydrobiologia*, 519, 211–214.

Tyler, P.A. & Billett, D.S.M. (1987) The reproductive ecology of elasipodid holothurians from the N. E. Atlantic. *Biological Oceanography*, 5(4), 273–296.

Tyler P.A., Billet, D.S.M. & Gage, J.D. (1990) Seasonal reproduction in the seastar *Dytaster grandis* from 4000 m in the North-East Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 70, 173–180.

Tyler, P.A., Emson, R.H., Sumida, P. & Howell, K. (2005) Ophiuroid distribution at sublittoral and bathyal depths round the Faroe Islands, NE Atlantic Ocean. *BIOFAR Proceedings*, 175–194.

Tyler, P.A., Muirhead, A., Gage, J.D. & Billett, D.S.M. (1985a) Gametogenic strategies in deep-sea echinoids and holothurians from the NE Atlantic. *In:* Keegan, B.F. & O'Connor, B.D.S. (eds.) *Proceedings of the 5th International Echinoderm Conference, Galway, September 1984*. Balkema, Amsterdam, p. 135–140.

Tyler, P.A., Gage, J.D. & Billett, D.S.M. (1985b) Life-history biology of *Peniagone azorica* and *P. diaphana* (Echinodermata: Holothurioidea) from the north-east Atlantic Ocean. *Marine Biology*, 89 (1), 71–81.

Tyler, P.A., Muirhead, A., Billett, D.S.M. & Gage, J.D. (1985c) Reproductive biology of the deep-sea holothurians *Laetmogone violacea* and *Benthogone rosea* (Elasipoda: Holothurioidea). *Marine Ecology Progress Series*, 23(3), 269–277.

Tyler, P.A. & Zibrowius, H. (1992) Submersible observations of the invertebrate fauna on the continental slope southwest if Ireland (NE Atlantic Ocean), *Oceanologica Acta*, 15(2), 211–226.

Tyler, P.A., Paterson, G.J.L., Sibuet, M., Guille, A., Murtons, B.J. & Segonzac, M. (1995). A new genus of ophiuroid (Echinodermata: Ophiuroidea) from hydrothermal mounds along the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom*, 75, 977–986.

Vadon, C. & Guille, A. (1984) Les Ophiuridae (Ophiuroidea, Echinodermata) de la campagne MD 32 du “Marion-Dufresne” autour de l’ile de La Réunion. *Bulletin Muséum National Histoire Naturelle*, Paris, 4e serie, section A, 6(3), 583–615.

Ventura C.R.R., Veríssimo, I. Nobre, C.C. & Zama, P.C. (2007) Filo Echinodermata. *In*: Lavrado, H.P. & Viana, M.S. (Eds.) *Atlas de invertebrados marinhos da região central da zona econômica exclusiva brasileira. Parte 1.* Museu Nacional, Rio de Janeiro, 25, 339–389.

Verrill, A.E. (1866) On the Polyps and Echinoderms of New England, with Descriptions of new species. *Proceedings of the Boston Society of Natural History*, 10, 323–357.

Verrill, A.E. (1867–1870) Notes on Radiata in the Museum of Yale College with descriptions of new genera and species. *Transactions of the Connecticut Academy of Arts and Sciences*, 1(2), 247–596.

Verrill, A.E. (1880) Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science*, 3(20), 390–403.

Verrill, A.E. (1884) Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science*, 28, 213–220.

Verrill, A.E. (1885a) Notice of the remarkable Marine Fauna occupying the outer banks off the Southern Coast of New England. *The American Journal of Science*, 3rd series, 169–174, 149–157.

Verrill, A.E. (1885b) Notice of recent additions to the marine invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others.part v – Annelida, Echinodermata, Hydroida, Tunicata. *Proceedings of the United States National Museum*, 8, 424–447.

Verrill, A.E. (1885c) Results of the explorations made by the steamer “Albatross”, off the northern coast of the United States, in 1883. *Report of Commissioner of Fish and Fisheries*, 503–699.

Verrill, A.E. (1894) Descriptions of new starfishes and Ophiurans, with a revision of certain species formerly described, mostly from the collections made by the United States Commission of Fish and Fisheries. *Proceedings US National Museum*, 17, 245–297.

Verrill, A.E. (1899) Revision of certain genera and species of starfishes, with descriptions of new forms. *Transactions of the Connecticut Academy of Arts and Sciences,* 10(1), 145–234.

Verrill, A.E. (1914) Monograph of the shallow-water starfishes of the North Pacific coast from the Arctic Ocean to California. *Harriman Alaska series: US National Museum*, 14, 1–408.

Verrill, A.E. (1915) Report on the starfishes of the West Indies, Florida, and Brazil, including those obtained by the Bahama expedition from the University of Iowa in 1893. *Bulletins from the Laboratories of Natural History*, 7(1), 1–232.

Walenkamp, J.H.C. (1979) Asteroidea (Echinodermata) from the Guyana Shelf. *Zoologische Verhandelingen*, 170, 1–97.

Wallenstein, F.M. & Neto, A.I. (2006) Intertidal rocky shore biotopes of the Azores: a quantitative approach. *Helgoland Marine Research*, 60, 196–206.

Wallenstein, F.M., Peres, S.D., Xavier, E.D., Neto, A.I. (2010) Phytobenthic communities of intertidal rock pools in the eastern islands of Azores and their relation to position on shore and pool morphology. *Arquipélago. Life and Marine Science*, 27, 9–20.

Wangensteen, O.S., Turon, X., Pérez-Portela, R. & Palacín, C. (2012) Natural or naturalized? Phylogeography suggests that the abundant sea urchin *Arbacia lixula* is a recent colonizer of the Mediterranean. *PLoS One*, 7(9), 1–16, doi: 10.1371/journal.pone.0045067.

Waters, J.M. & Roy, M.S. (2003) Global phylogeography of the fissiparous sea star genus *Coscinasterias*. *Marine Biology*, 142, 185–191.

Weber, W. & Dambach, M. (1974) Light-sensitivity of isolated pigment cells of the sea urchin *Centrostephanus longispinus.* Cell and Tissue Research, 148 (3), 437–440.

Wirtz, P. (2006) Ten invertebrates new for the marine fauna of Madeira. *Arquipélago*, *Life and Marine Sciences*, 23A, 75–78.

Wirtz, P. (2009) Ten new records of marine invertebrates from the Azores. *Arquipélago, Life and Marine Sciences*, 26, 45–49.

Wirtz, P. & Debelius, H. (2003) *Mediterranean and Atlantic invertebrate guide*. ConchBooks, Hackenheim, 305 pp.

Wirtz, P. & Martins, H.M. (1993) Notes on some rare and little known marine invertebrates from the Azores, with a discussion of the zoogeography of the region. *Arquipélago, Life and Marine Sciences*, 11A, 55–63.

Wirtz, P. & Vader, W. (1996) A new caprellid-starfish association: *Caprella acanthifera S.L.* (Crustacea: Amphipoda) on *Ophidiaster ophidianus* and *Hacelia attenuata* from the Azores. Arquipélago, Life and Marine Sciences, 14, 17–22.

Wisshak, M., Neumann, C., Jakobsen, J. & Freiwald, A. (2009a) Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster *Neopycnodonte zibrowii* sp. n. from the NE Atlantic. *Deep Sea Research I*, 56(3), 374–404.

Wisshak M., López Correa M., Gofas S., Salas C., Taviani M., Jakobsen J. & Freiwald A. (2009b) The ‘living-fossil community’ of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago). *Palaeogeography, Palaeoeclimatology, Palaeoecology*, 271, 77–83.

Wisshak, M., Form, A., Jakobsen, J. & Freiwald, A. (2010) Temperate carbonate cycling and water mass properties from intertidal to bathyal depths (Azores). *Biogeosciences*, 7, 2379–2396.

Wood-Mason, J. & Alcock, A. (1891) Natural history notes from H.M. Indian marine survey steamer 'Investigator', Commander R.F. Hoskyn, R.N., commanding. Series II, No. 1. On the results of deep-sea dredging during the season 1890–1891. *Annals and Magazine of Natural History*, 6th series, 48, 427–452.

WoRMS Editorial Board (2017) World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2017-01-15. doi:10.14284/170.

Wright, A. G., Pérez-Portela, R. & Griffiths, C. L. (2016) Determining the correct identity of South African *Marthasterias* (Echinodermata: Asteroidea). *African journal of marine science*, 38(3), 443–455.

Yokoyama, L.Q., Duarte, L.F.L. & Amaral, A.C.Z. (2008) Reproductive cycle of *Ophionereis reticulata* (Ophiuroidea, Echinodermata) on the southeast coast of Brazil. *Invertebrate Reproduction* & Development, 51(2), 111–118.

Yokoyama, L.Q. & Amaral, A.C.Z. (2011) Recruitment and growth variation of *Ophionereis reticulata* (Echinodermata: Ophiuroidea). *Invertebrate Reproduction & Development*, 55(2), 73–81.

Young, C.M. & Tyler, P.A. (1993) Embryos of the deep-sea echinoid *Echinus affinis* require high pressure for development. *Limnology and Oceanography*, 38(1), 178–181.

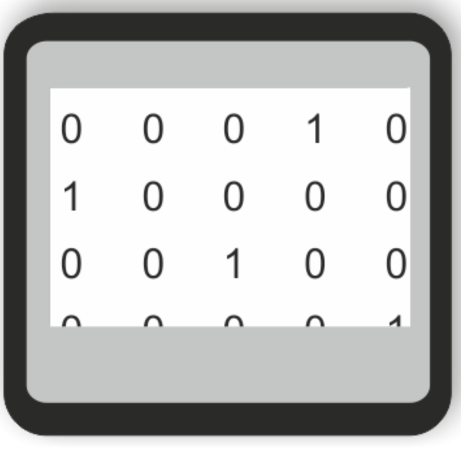
Zittel, K.A. von (1879) *Handbuch der Palaeontologie. 1. Abtheilung, Paleozoologie. I. Band: Protozoa, Coelenterata, Echinodermata und Molluscoidea*. R. Oldenbourg: Munich, viii(8)+765 pp.

Zittel, K.A. von (1913) *Text-book of paleontology: Adapted from the German by C.R. Eastman (*2nd Edition). Macmillan, London, x(10)+839 p.

Zulliger, D. E. & H. A. Lessios (2010) Phylogenetic relationships in the genus *Astropecten* Gray (Paxillosida: Astropectinidae) on a global scale: molecular evidence for morphological convergence, species-complexes and possible cryptic speciation. *Zootaxa*, 2504, 1–19.

Zulliger, D.E., Tanner, S., Ruch, M. & Ribi, G. (2009) Genetic structure of the highdispersal Atlanto-Mediterreanean sea star *Astropecten aranciacus* revealed by mitochondrial DNA sequences and microsatellite loci. *Marine Biology*, 156, 597–610.

Supplementary Material



0 0 0 1 0

1 0 0 0 0

0 0 1 0 0

Table S5.1. List of echinoderms reported for the Azores Archipelago(AZO), with information regarding their geographical distribution (End: endemic; ATL: Atlantic; NATL: North Atlantic; SATL: South Atlantic; NEAT: Northeast Atlantic; EAT: East Atlantic; MED: Mediterranean; WAT: West Atlantic; MID: Mid–Atlantic; Cosmo: cosmopolitan; ART: Arctic; PAC: Pacific Ocean; IND: Indian Ocean), bathymetrical range in the Azores, habitat (Ep: epiphyte or epibiont; In: infaunal; Hy: chemosynthetic; Sb: soft bottoms; Hb: hard substrates; M: both or mix bottoms; BPl: benthopelagic; L: littoral (<50 m); C: circalittoral (50–700 m); B: bathyal (700–2000 m); A: abyssal (2000–4000 m); H: hadal (>4000 m)), type area, status in the Azores (F: frequently documented; H: historical, referred at one time in the bibliography; R: recent addition, after the year 2000; Cf: recently confirmed; Db: doubtful record; Er: erroneous) and first record reference for the archipelago. Erroneous records based on out-dated synonymy (*), erroneously reported for the Azores (**) or misidentifications (***).

Class Crinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Order Comatulida Clark, 1908						
Family Antedonidae Norman, 1865						
Genus *Antedon* de Fréminville, 1811						
Antedon bifida moroccana (Clark, 1914)	NEAT & MED	3–60(?130)	Ep, Hd; L–C	NW Africa	F	Barrois 1888
Genus *Leptometra* Clark, 1908						
Leptometra celtica? (M'Andrew & Barrett, 1857)	EAT	?700	Sb; C	British Isles	Db	Grieg 1932
Family Pentametrocrinidae Clark, 1908						
Genus *Pentametrocrinus* Clark, 1908						
Pentametrocrinus atlanticus (Perrier, 1883a)	NATL	1,165	Sb; C–A	Iberian Peninsula	H	Koehler 1909
Family Bourgueticrinidae Loriol, 1882						
Genus *Democrinus* Perrier, 1883b						
Democrinus parfaiti Perrier, 1883b	NEAT	1,550–1,919 (?2,950)	M; A	NW Africa	H	Carpenter 1883b
Er – *Democrinus rawsonii* (Pourtalès, 1874)	WAT	–	C	Caribbean	Er*	Carpenter 1883b
Family Bathycrinidae Bather, 1899						
Genus *Bathycrinus* Thomson, 1872a						
Bathycrinus gracilis Thomson, 1872a	NEAT	5,005	Sb; A–H	off W France	H	Koehler 1909
Genus *Monachocrinus* Clark, *in* Zittel 1913						
Er – *Monachocrinus recuperatus* (Perrier, 1885a)	EAT	–	Sb;B–H	NEAT (N44°20' W17°10'46")	Er**	Clark 1980
Order Cyrtocrinida Sieverts-Doreck, *in* Moore *et al*., 1952						
Family Holopodidae Zittel, 1879						
Genus *Cyathidium* Steenstrup, 1847						
Cyathidium foresti Cherbonnier & Guille, 1972	NEAT	380–900 (?1,400)	Ep, Hb; C	AZO (N39° 23'30″ W31°19')	F	Cherbonnier & Guille 1972
Order Hyocrinida Rasmussen, 1978						
Family Hyocrinidae Carpenter, 1884						
Genus *Anachalypsicrinus* Clark, 1973						
Anachalypsicrinus nefertiti Clark, 1973	NEAT	2,200–2,810	Hb; A	British Isles	H	Roux 1980
Order Isocrinida Sieverts-Doreck, 1952						
Family Isselicrinidae Klikushkin, 1977						
Genus *Endoxocrinus* Clark, 1908						
Er – *Endoxocrinus* wyvillethomsoni (Thomson, 1872a)	NEAT	–	M; B	Iberian Peninsula	Er**	Clark 1911a

Class Ophiuroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Order Amphilepidida O'Hara *et al*. 2017						
Family Amphiuridae Ljungman, 1867						
Genus *Amphipholis* Ljungman, 1866						
Amphipholis squamata (Delle Chiaje, 1828)	Cosmo	0–1,229	Ep, M; L–B	MED	F	Ljungman 1872
Genus *Amphiura* Forbes, 1843						
Er – *Amphiura chiajei* Forbes, 1843	NEAT & MED	–	Sb; L–B	MED	Er**	Mortensen 1927a
Amphiura otteri Ljungman, 1872	NATL	1,620–1,900	Sb; C–B	Iberian Peninsula	H	Lyman 1882
Amphiura richardi Koehler, 1896b	NEAT	1,165–1,494	M; B	AZO (N38°26' W26°30'45")	H	Koehler 1896b
Amphiura sarsi Ljungman, 1872	NEAT	55–1,098	Sb; C–B	AZO	Cf	Ljungman 1872
Amphiura grandisquama Lyman, 1869	Cosmo	599–880	M; L–A	Caribbean	H	Koehler 1896a
Family Ophiactidae Matsumoto, 1915						
Genus *Ophiactis* Lütken, 1856						
Ophiactis abyssicola (Sars, 1861)	Cosmo	726–1,998	M; C–H	Scandinavia	Cf	Koehler 1896a
Ophiactis canotia Lyman, 1879	End	1,830	Sb; B	AZO (N38°30' W31°14')	H	Lyman 1879
Ophiactis plana? Lyman, 1869	ATL	?650–?914	Ep, Sb; C–B	Caribbean	Db	Koehler 1909
Ophiactis nidarosiensis? Mortensen, 1920	ATL	?1,095	?Sb; C–?B	Scandinavia	Db	Koehler 1909
Ophiactis tyleri Stöhr & Segonzac, 2005	End	842–844	Hb; B	AZO (N38°18'58"W30°40'32")	R	Stöhr & Segonzac 2005
Ophiactis virens (Sars, 1859)	NEAT & MED	≤50	Ep, Hb; L–C	MED	H	Marques 1983
Family Ophiolepididae Ljungman, 1867						
Genus *Ophiotypa* Koehler, 1897a						
Ophiotypa simplex Koehler, 1897a	Cosmo	3,665	Sb; B–H	IND	H	Cherbonnier & Sibuet 1972
Family Ophionereididae Ljungman, 1867						
Genus *Ophiochiton* Lyman, 1878						
Ophiochiton ternispinus Lyman, 1883	ATL	2,155–2,220	Sb; C–B	British Isles	H	Koehler 1906a
Genus *Ophionereis* Lütken, 1859						
Ophionereis reticulata? (Say, 1825)	WAT	?98–?560	M; L–C	Caribbean	Db	Koehler 1906b
Family Ophiopholidae O'Hara *et al*. 2018						
Genus *Ophiopholis* Müller & Troschel, 1842						
Ophiopholis aculeata? (Linnaeus, 1767)	NATL & PAC	?	Ep, M; C	?	Db	Lyman 1965
Family Ophiopsilidae Matsumoto, 1915						
Genus *Ophiopsila* Forbes, 1843						
Er – *Ophiopsila aranea* Forbes, 1843	EAT & MED	–	Ep, M; L–C	MED	Er**	Koehler 1909
Family Ophiothamnidae O'Hara *et al*. 2018						
Genus *Histampica* Clark, 1970						
Histampica duplicata (Lyman, 1875)	Cosmo	1,095–2,178	M; C–A	Caribbean	H	Koehler 1896a
Genus *Ophiothamnus* Lyman, 1869						

Class Crinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Er – *Ophiothamnus affinis* Ljungman, 1872	NATL	–	Sb; C–B	Iberian Peninsula	Er**	Nobre 1938
Family Ophiotrichidae Ljungman, 1867						
Genus *Ophiothrix* Müller & Troschel, 1840a						
Er – *Ophiothrix cotteaui* (de Loriol, 1900)	EAT	–	Ep, Sb; L–C	W Africa	Er**	Madsen 1970
Ophiothrix fragilis (Abildgaard, *in* Müller, 1789)	EAT & MED	0–150	Ep, M; L–C	–	F	Ljungman 1872
Ophiothrix luetkeni Thomson, 1873	NEAT	?54–165 (?823)	Sb; C–B	British Isles	H	Lyman 1879
Order Euryalida Lamarck, 1816						
Family Asteronychidae Verrill, 1899						
Genus *Astrodia* Verrill, 1899						
Astrodia tenuispina (Verrill, 1884)	Cosmo	2,480	Ep; C–A	Off New England	H	Sibuet 1972
Family Euryalidae Gray, 1840						
Genus *Asteroschema* Oerstedt & Lütken, *in* Lütken, 1856						
Asteroschema inornatum Koehler, 1906a	NATL	1,478–2,300	Ep; B–A	Bay of Biscay	Cf	Koehler 1909
Order Ophiacanthida O'Hara *et al.*, 2017						
Family Ophiacanthidae Ljungman, 1867						
Genus *Ophiacantha* Müller & Troschel, 1842						
Ophiacantha abyssicola Sars, 1872	NATL	880	M; L–A	Scandinavia	H	Koehler 1909
Ophiacantha aculeata Verrill, 1885a	NATL	2,954–2,968	Sb; B–A	Off Virginia	R	Martynov & Litvinova 2008
Er – *Ophiacantha anomala* Sars, 1872	ATL	–	M; C–A	Scandinavia	Er**	Gage *et al.* 1983
Ophiacantha aristata Koehler, 1895c	NEAT	1,095–1,740	Ep, Sb; B	Bay of Biscay	H	Koehler 1896a
Ophiacantha bidentata? (Bruzelius, 1805)	ART & NATL	?1,287	L–?H	Scandinavia	Db	Koehler 1898
Er – *Ophiacantha brevispina* Koehler, 1898	NEAT	–	Sb; C	Bay of Biscay	Er**	Bartsch 1987
Ophiacantha crassidens Verrill, 1885a	NATL	1,095–2,200	Sb; B–A	North Carolina	Cf	Koehler 1906a
Ophiacantha lineata Koehler, 1896b	NATL	1,165–1,378	Sb; C–A	AZO (N38°26' W26°30'45")	H	Koehler 1896b
Ophiacantha mesembria Clark, 1915	NWAT	2,870	Sb; C–A	Caribbean	H	Koehler 1898
Ophiacantha notata Koehler, 1906a	NEAT	850	B	Bay of Biscay	R	Stöhr & Segonzac 2005
Ophiacantha setosa (Bruzelius, 1805)	EAT & MED	?139–1,257	Ep, Sb; L–A	–	H	Koehler 1906b
Ophiacantha simulans Koehler, 1895c	NATL	1,919–3,018	Sb; B–A	Bay of Biscay	H	Koehler 1909
Ophiacantha smitti Ljungman, 1872	NATL	1,550	Sb; C–B	Iberian Peninsula	R	Stöhr & Segonzac 2005
Ophiacantha veterna Koehler, 1907a	NEAT	1,330–2,300	Sb; C–B	NEAT	Cf	Koehler 1921a
Genus *Ophiochondrus* Lyman, 1869						
Ophiochondrus armatus (Koehler, 1907a)	NATL	1,250	Ep; C–B	AZO (N38°35'30" W28°05'45")	H	Koehler 1907a
Genus *Ophiomitrella* Verrill, 1899						
Er – *Ophiomitrella clavigera* (Ljungman, 1865)	NATL	–	Ep, Sb; C–B	Scandinavia	Er*	Mortensen 1927a
Ophiomitrella cordifera Koehler, 1896b	NEAT	1,143	Sb; C	AZO (N38°52’45” W28°06’)	H	Koehler 1896b

Class Crinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Family Ophiobyrsidae Matsumoto, 1915						
Genus *Ophiophrixus* Clark, 1911b						
Er – *Ophiophrixus spinosus* (Storm, 1881)	NEAT	–	Sb; L–B	Scandinavia	Er**	Paterson 1985
Family Ophiodermatidae Ljungman, 1867						
Genus *Bathypectinura* Clark, 1909						
Er – *Bathypectinura heros* (Lyman, 1879)	Cosmo	–	Sb; C–A	PAC	Er**	Paterson 1985
Genus *Ophioderma* Müller & Troschel, 1840a						
Ophioderma longicauda? (Bruzelius, 1805)	NEAT & MED	?	Ep, M; L–C	–	Db	Lyman 1865
Family Ophiomyxidae Ljungman, 1867						
Genus *Ophioconis* Lütken, 1869						
Ophioconis forbesi (Heller, 1863)	NEAT & MED	98–130	M; L–C	MED	H	Koehler 1896a
Genus Ophiomyxa Müller & Troschel, 1840a						
Er – *Ophiomyxa pentagona* (Lamarck, 1816)	NEAT & MED	–	M; L–B	MED	Er**	Cherbonnier & Sibuet 1972
Ophiomyxa serpentaria Lyman, 1883	NATL	599–1,095	M; C–A	Faeroes	H	Koehler 1909
Family Ophiocomidae Ljungman, 1867						
Genus *Ophiocomella* A.H. Clark, 1939						
Er – *Ophiocomella pumila* Lütken, 1856	ATL	–	Ep, Hb; L	Bermuda	Er**	Devaney 1970
Genus *Ophiocomina* Koehler, *in* Mortensen, 1920						
Ophiocomina nigra (Abildgaard, *in* Müller, 1789)	NEAT & MED	6–30	M; L–B	?	F	Barrois 1888
Genus *Ophiotoma* Verrill, 1899						
Ophiotoma alberti (Koehler, 1896b)	NEAT	4,020	Sb; A–H	AZO (N38°09’ W23°15’45”)	H	Koehler 1896b
Ophiotoma coriacea? Lyman, 1883	NATL	?3,465	Sb; B–H	Off New England	Db	Koehler 1909
Genus Ophiotreta Verrill, 1899						
Ophiotreta valenciennesi (Lyman, 1879)	Cosmo	711–1,442	M; C–B	PAC	Cf	Koehler 1896b
Order Ophioleucida O'Hara *et al*. 2017						
Family Ophiernidae O'Hara *et al*. 2017						
Subfamily Ophioleucinae Matsumoto, 1915						
Genus *Ophiernus* Lyman, 1878						
Ophiernus vallincola Lyman, 1878	Cosmo	1,732–1,919	Sb; B–A	AZO (N37°24'; W25°13')	H	Lyman 1878
Order Ophioscolecida O'Hara *et al*., 2017						
Family Ophioscolecidae Lütken, 1869						
Genus *Ophiomyces* Lyman, 1869						
Ophiomyces frutectosus Lyman, 1869	ATL	575–1,098	M; C–B	Caribbean	H	Ljungman 1872
Family Ophiomyxidae Ljungman, 1867						
Genus *Ophiogeron* Lyman, 1878						
Er – *Ophiogeron edentulus* Lyman, 1878	PAC	–	Sb; A	PAC	Er***	Lyman 1882
Ophiogeron granulatus? (Lyman, 1883)	WAT	?1,250–?1,647	Sb; C	Caribbean	Db	Lyman 1882

Class Crinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Genus *Ophiophrura* Clark, 1911b						
Ophiophrura tripapillata (Stöhr & Segonzac, 2005)	NEAT	1,015	Hb; B	AZO (N37°50'56" W31°30'40")	R	Stöhr & Segonzac 2005
Order Ophiurida Müller & Troschel, 1840 *sensu* O'Hara *et al*., 2017						
Genus *Anthophiura* Clark, 1911b						
Anthophiura ingolfi? Fasmer, 1930	NATL	?4,020	Sb; B–A	Iceland	Db	Koehler 1896b
Family Astrophiuridae Sladen, 1879						
Genus *Ophiophycis* Koehler, 1901						
Ophiophycis mirabilis Koehler, 1901	NEAT	1,131–1,201	Ep, Hb; B–A	AZO (N38°26' W26°30'45")	Cf	Koehler 1901
Family Ophiopyrgidae Perrier, 1893						
Genus *Amphiophiura* Matsumoto, 1915						
Amphiophiura convexa (Lyman, 1878)	Cosmo	3,665–4,360	Sb; A–H	PAC	H	Koehler 1909
Genus *Ophiopleura* Duncan, 1878						
Ophiopleura inermis (Lyman, 1878)	ATL	1,740	M; C–B	Off Tristan da Cunha	H	Koehler 1921a
Genus *Ophioplinthus* Lyman, 1878						
Ophioplinthus inornata (Lyman, 1878)	Cosmo	2,995–3,200	Sb; C–A	ATL (MID)	H	Koehler 1906b
Ophioplinthus pseudotessellata Martynov & Litvinova, 2008	End	2,954–2,968	?; A	N AZO (N42°55' W30°20')	R	Martynov & Litvinova 2008
Ophioplinthus tessellata (Verrill, 1894)	NATL	1,919–2,870	Sb; C–H	New England	H	Koehler 1896a
Family Ophiosphalmidae O'Hara *et al*. 2018						
Genus *Ophiomusium* Lyman, 1869						
Er – *Ophiomusium africanum* Koehler, 1909	Cape Verde	–	Sb; C	Cape Verde	Er**	Paterson 1985
Ophiomusium lymani Thomson, 1873	Cosmo	1,384–3,300	Sb; B–A	British Isles	H	Lyman 1878
Genus *Ophiosphalma* Clark, 1941						
Ophiosphalma armigerum (Lyman, 1878)	ATL	2,870–5,005	Sb; A–H	SATL	H	Koehler 1896b
Family Ophiuridae Müller & Troschel, 1840a						
Genus *Ophiocten* Lütken, 1855						
Ophiocten affinis? (Lütken, 1858)	NATL	?	Sb; L–C	Scandinavia	Db	Simroth 1888
Ophiocten centobi Paterson *et al*., 1982	NEAT	1,680–2,837	Sb; B–A	Bay of Biscay	R	Stöhr & Segonzac 2005
Ophiocten hastatum Lyman, 1878	Cosmo	1,839–2,017	Sb; B–H	Southern Ocean	Cf	Lyman 1878
Genus *Ophioctenella* Tyler *et al*., 1995						
Ophioctenella acies Tyler *et al*., 1995	WAT	1,626–1,727	Hy; B–A	NATL (MID)	R	Stöhr & Segonzac 2005
Genus *Ophiura* Lamarck, 1801						
Ophiura albida Forbes, 1839	NEAT & MED	20–458	Sb; L–C	British Isles	H	Lyman 1869
Ophiura imprudens (Koehler, 1906a)	NEAT	560	Sb; C	AZO (MID) (N38°23' W31°10')	H	Koehler 1906a
Ophiura ljungmani (Lyman, 1878)	ATL	789–2,968	Sb; C–A	Brazil	F	Lyman 1878
Ophiura saurura (Verrill, 1894)	NATL	2,063–2,968	Sb; B–A	New England	R	Martynov & Litvinova 2008

Class Crinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Ophiura carnea carnea Lütken, 1858	NEAT & MED	14–599	M; L–A	Scandinavia	Cf	Koehler 1909
Ophiura mundata (Koehler, 1906a)	NATL	1,919–4,020	Sb; B–A	Canaries	H	Koehler 1906b
Ophiura concreta (Koehler, 1901)	EAT	2,845–2,995	Sb; A	Cape Verde	?Cf	Koehler 1906b
Ophiura irrorata? (Lyman, 1878)	Cosmo	3,005–3,050	Sb; C–H	South Africa	Db	Martynov & Litvinova 2008

Class Asteroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Order Velatida Perrier, 1884						
Family Myxasteridae Perrier, 1885						
Genus *Pythonaster* Sladen, *in* Thomson & Murray, 1885						
Pythonaster atlantidis Clark, 1948	NATL	3,200	A–H	AZO (N35°37' W30°51')	H	Clark 1948
Family Pterasteridae Perrier, 1875						
Genus *Calyptraster* Sladen, 1882						
Er – *Calyptraster coa* Sladen, 1882	WAT	–	Sb; C–B	Brazil	Er*	Walenkamp 1979
Calyptraster personatus (Perrier, 1885)	ATL	2,871– 2,995	Sb; A–H	AZO (N38°38' W25°05'46")	H	Perrier 1894
Genus *Hymenaster* Thomson, 1873						
Hymenaster anomalus Sladen, 1882	WAT	2,954–3,050	Sb; A	SATL (MID)	R	Dilman 2008
Hymenaster giboryi Perrier, 1894	NATL	1,919–4,261	Sb; A–H	NATL	H	Koehler 1909
Hymenaster pellucidus Thomson, 1873	Cosmo	2,870–3,050	Sb; C–A	Faeroes	Cf	Perrier 1896a
Hymenaster roseus Koehler, 1907a	End	1,846–2,102 (?2,370)	Sb; A	AZO	H	Koehler 1909
Hymenaster tenuispinus Sibuet, 1976	NEAT	2,120	A	Off W France	H	Sibuet 1976
Genus *Pteraster* Müller & Troschel, 1842						
Er – *Pteraster alveolatus* Perrier, 1894	NEAT	–	Sb; A	NEAT	Er**	Perrier 1894
Pteraster personatus Sladen, 1891	NATL	1,846–2,870	Sb; C–A	British Isles	H	Koehler 1909
Superorder Forcipulatacea Blake, 1987						
Order Brisingida Fisher, 1928						
Family Brisingidae Sars, 1875						
Genus *Hymenodiscus* Perrier, 1884						
Hymenodiscus coronata (Sars, 1872)	NEAT & MED	919–2,870	Sb; C–A	Scandinavia	H	Perrier 1896a
Family Freyellidae Downey, 1986						
Genus *Freyastera* Downey, 1986						
Er – *Freyastera benthophila* (Sladen, 1889)	Cosmo	–	Sb; H	PAC	Er**	Cherbonnier & Sibuet 1975
Freyastera sexradiata (Perrier, 1885c)	NATL	4,020	Sb; H	NEAT	H	Koehler 1909
Genus *Freyella* Perrier, 1885d						
Freyella elegans (Verrill, 1884)	ATL	2,063–3,050	Sb; B–A	Off New England	Cf	Cherbonnier & Sibuet 1975
Er – *Freyella recta* Koehler, 1907a	MID	–	Sb; A	MID	Er**	Grieg 1932

Class Asteroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Order Forcipulatida Perrier, 1884						
Family Asteriidae Gray, 1840						
Genus *Asterias* Linnaeus, 1758						
Asterias rubens? Linnaeus, 1758	NEAT	?0	M; L–C	–	Db	Madeira *et al*. (2017b)
Genus *Coscinasterias* Verrill, 1867						
Coscinasterias tenuispina (Lamarck, 1816)	ATL & MED	0–12	M; L–C	–	F	Barrois 1888
Genus *Sclerasterias* Perrier, 1891						
'Sclerasterias' richardi? (Perrier, *in* Milne-Edwards, 1882)	MED	135	M; C	MED	Db	Madeira *et al*. (2017b)
Genus *Leptasterias* Verrill, 1866						
Er – *Leptasterias* (*Hexasterias*) *polaris* (Müller & Troschel, 1842)	NATL & PAC	–	M; L–C	Greenland	Er***	Perrier 1896
Genus *Marthasterias* Jullien, 1878						
Marthasterias glacialis (Linnaeus, 1758)	EAT & MED	0–35	M; L	–	F	Müller & Troschel 1842
Family Pedicellasteridae Perrier, 1884						
Genus *Hydrasterias* Sladen, 1889						
Er – *Hydrasterias ophidion* (Sladen, 1889)	WAT	–	Sb; A	Nova Scotia	Er***	Clark 1949
Hydrasterias sexradiata (Perrier, *in* Milne–Edwards, 1882)	NEAT	599–3,465	Sb; C–H	Iberian Peninsula	H	Koehler 1909
Family Stichasteridae Perrier, 1885b						
Genus *Neomorphaster* Sladen, 1889						
Neomorphaster margaritaceus (Perrier, *in* Milne–Edwards, 1882)	NEAT	938–2,102	M; C–B (?H)	Bay of Biscay	H	Perrier 1885c
Family Zoroasteridae Sladen, 1889						
Genus *Zoroaster* Thomson, 1873						
Zoroaster fulgens Thomson, 1873	ATL	2,870–3,050	Sb; C–H	Faeroes	Cf	Perrier 1885c
Superorder Valvatacea Blake, 1987						
Order Notomyotida Ludwig, 1910						
Family Benthopectinidae Verrill, 1899						
Genus *Cheiraster* Studer, 1883						
Cheiraster (*Cheiraster*) *sepitus* (Verrill, 1885a)	NATL	1,165 – 3,706	Sb; B	Nova Scotia	H	Sladen 1889
Genus *Pectinaster* Perrier, 1885c						
Pectinaster filholi Perrier, 1885c	ATL	1,258	Sb; B–H	NW Africa	H	Perrier 1894
Order Paxillosida Perrier, 1884						
Family Astropectinidae Gray, 1840						
Genus Astropecten Gray, 1840						
Astropecten aranciacus? (Linnaeus, 1758)	EAT & MED	?	Sb; L–C	MED	Db	Madsen 1950
Er – *Astropecten bispinosus* (Otto, 1823)	MED	–	Sb; L	MED	Er*	Ludwig 1897
Astropecten hermatophilus Sladen, 1883	NEAT	10–165 (?823)	Sb; L–C (?B)	AZO (N38°38' W28°28'30")	Cf	Sladen 1883

Class Asteroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Er – *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827)	MED	–	Sb; L–B	MED	Er***	Simroth 188
Astropecten platyacanthus? (Philippi, 1837)	MED	?15–?20	Sb; L	MED	Db	Barrois 1888
Genus *Dytaster* Sladen, 1889						
Dytaster grandis grandis (Verrill, 1884)	NATL	2,954–5,005	Sb; B–H	NWATL	Cf	Sladen 1889
Dytaster insignis (Perrier, 1884)	ATL	2,844–3,670	Sb; A	Gulf of Mexico	H	Cherbonnier & Sibuet 1972
Dytaster intermedius Perrier, 1891	End	2,870	Sb; A	AZO (N41°40'41" W29°04'23")	H	Perrier 1896a
Dytaster mollis (Perrier, 1885c)	End	2,560–2,995	Sb; A	AZO (N38°38' W25°05'46")	H	Perrier 1894
Er – *Dytaster semispinosus* (Perrier, 1894)	NEAT	–	Sb; H	Bay of Biscay	Er**	Clark & Downey 1992
Genus *Persephonaster* Wood–Mason & Alcock, 1891						
Persephonaster patagiatus (Sladen, 1889)	NATL	1,095–1,919	Sb; B–?A	Off Cape Verde	H	Perrier 1896
Persephonaster sphenoplax (Bell, 1892)	NEAT	845–1,187	M; B	British Isles	H	Koehler 1909
Genus *Plutonaster* Sladen, 1889						
Plutonaster agassizi notatus Sladen, 1889	NEAT	1,165–2,178	Sb; B–H	AZO (N38°30' W31°14')	Cf	Sladen 1889
Genus *Psilaster* Sladen, *in* Thomson & Murray, 1885						
Psilaster andromeda andromeda? (Müller & Troschel, 1842)	NEAT	?140–?1,440	Sb; C–B	Scandinavia	Db	Perrier 1894
Family Ctenodiscidae Sladen, 1889						
Genus *Ctenodiscus* Müller & Troschel, 1842						
Er – *Ctenodiscus crispatus* (Bruzelius, 1805)	NATL & PAC	–	Sb; L–B	–	Er**	García-Diez *et al*. 2005
Family Luidiidae Sladen, 1889						
Genus *Luidia* Forbes, 1839						
Luidia ciliaris (Philippi, 1837)	NEAT & MED	?	M; L–C	MED	?Cf	Döderlein 1920
Luidia sarsii sarsii Düben & Koren, *in* Düben, 1845	NEAT & MED	?100–200	Sb; L–B	Scandinavia	H	Koehler 1909
Family Porcellanasteridae Sladen, 1883						
Genus *Hyphalaster* Sladen, 1883						
Hyphalaster inermis Sladen, 1883	Cosmo	2,995–3,200	Sb; A–H	PAC	H	Perrier 1885c
Genus *Porcellanaster* Thomson, 1877						
Porcellanaster ceruleus Thomson, 1877	Cosmo	2,995	Sb; B–H	off Delaware	H	Perrier 1885c
Genus *Styracaster* Sladen, 1883						
Styracaster armatus Sladen, 1883	Cosmo	2,995–4,020	Sb; A–H	PAC	H	Perrier 1885c
Styracaster elongatus Koehler, 1907a	Cosmo	4,020	Sb; A–H	NATL	H	Koehler 1909
Genus *Thoracaster* Sladen, 1883						
Er – *Thoracaster cylindratus* Sladen, 1883	Cosmo	–	Sb; A–H	NATL	Er**	Clark & Downey 1992
Family Pseudarchasteridae Sladen, 1889						
Genus *Paragonaster* Sladen, *in* Thomson & Murray, 1885						
Paragonaster subtilis (Perrier, 1881)	ATL	2,965–4,261	Sb; B–H	Gulf of Mexico	Cf	Perrier 1885c

Class Asteroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Genus *Pseudarchaster* Sladen, 1889						
Pseudarchaster gracilis gracilis (Sladen, 1889)	NATL	903 –1,940	Sb; C–A	AZO (N37°24' W25°13')	Cf	Sladen 1889
Pseudarchaster parelii (Düben & Koren, 1846)	NATL	1,165–1,900	Sb; C–A	Scandinavia	H	Perrier 1885c
Superorder Spinulosacea Blake, 1987						
Order Spinulosida Perrier, 1884						
Family Echinasteridae Verrill, 1867						
Genus *Henricia* Gray, 1840						
Henricia cylindrella? (Sladen, 1883)	NEAT	?1,482–?1,805	?Sb; A	British Isles	Db	Koehler 1909
Henricia oculata? (Pennant, 1777)	NEAT	?1,266–?1,557	M; L–?C	British Isles	Db	Perrier 1896a
Er – *Henricia sanguinolenta* (Müller, 1776)	NEAT	–	Hb; L	Scandinavia	Er*	Koehler 1921
Superorder Valvatacea Blake, 1987						
Order Valvatida Perrier, 1884						
Family Asterinidae Gray, 1840						
Genus *Asterina* Nardo, 1834						
Asterina gibbosa (Pennant, 1777)	NEAT & MED	0	Ep, Hb; L–C	–	H	Barrois 1888
Family Chaetasteridae Sladen, 1889						
Genus *Chaetaster* Müller & Troschel, 1840b						
Chaetaster longipes (Bruzelius, 1805)	EAT & MED	30–165(?823)	M; L–B	?MED	Cf	Sladen 1889
Family Goniasteridae Forbes, 1841						
Genus *Ceramaster* Verrill, 1899						
Ceramaster granularis granularis (Retzius, 1783)	NATL	1,384	M; L–A	NATL	H	Perrier 1896a
Ceramaster grenadensis grenadensis (Perrier, 1881)	ATL & MED	1,095–1,557	Sb; C–A	Caribbean	H	Perrier 1885c
Genus *Plinthaster* Verrill, 1899						
Plinthaster dentatus (Perrier, 1884)	ATL	1,095–1,740	Ep, Sb; C–A	Caribbean	H	Perrier 1885c
Genus *Sphaeriodiscus* Fisher, 1910						
Sphaeriodiscus bourgeti (Perrier, 1885c)	EAT	560	Sb; C	Cape Verde	H	Perrier 1885c
Family Odontasteridae Verrill, 1899						
Genus *Hoplaster* Perrier, *in* Milne–Edwards, 1882						
Hoplaster spinosus Perrier, *in* Milne–Edwards, 1882	EAT	1,829–2,595	Sb; A	British Isles	H	Sladen 1889
Family Ophidiasteridae Verrill, 1870						
Genus *Hacelia* Gray, 1840						
Hacelia attenuata Gray, 1840	NEAT & MED	1–165(?823)	M; L–C	–	Cf	Sladen 1889
Genus *Ophidiaster* Agassiz, 1836						
Ophidiaster ophidianus (Lamarck, 1816)	NEAT & MED	0–165(?823)	H; L–C	MED	F	Barrois 1888
Ophidiaster reyssi Sibuet, 1977	NEAT & MED	350	H; C	AZO (N39°33' W31°17'30")	H	Sibuet 1977

Class Echinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Subclass Cidaroidea Smith, 1984						
Order Cidaroida Claus, 1880						
Family Cidaridae Gray, 1825						
Genus *Cidaris* Leske, 1778						
Cidaris cidaris (Linnaeus, 1758)	NEAT	165–1,385	M; C–A	–	Cf	Koehler 1895a
Genus *Eucidaris* Pomel, 1883						
Eucidaris tribuloides? (Lamarck, 1816)	ATL	130	Hb; L–C	–	Db	Koehler 1895a
Genus *Stereocidaris* Pomel, 1883						
Stereocidaris ingolfiana? Mortensen, 1903	NATL	?2,050–?3,300	Sb; C–B	Denmark Strait	Db	Pérès 1992
Family Histocidaridae Lambert, 1900						
Genus *Histocidaris* Mortensen, 1903						
Histocidaris purpurata? (Thomson, 1872b)	NATL	?800	Sb; C–B	British Isles	Db	Pérès 1992
Subclass Euechinoidea Bronn, 1860						
Infraclass Acroechinoidea Smith, 1981						
Order Diadematoida Duncan, 1889						
Family Diadematidae Gray, 1855a						
Genus *Diadema* Gray, 1825						
Diadema africanum? Rodríguez *et al*., 2013	EAT	8	Hb; L	Canaries Islands	Dd	Minderlein & Wirtz 2014
Genus *Centrostephanus* Peters, 1855						
Centrostephanus longispinus (Philippi, 1845)	ATL & MED	6–468	M; L–C	MED	F	Barrois 1888
Order Pedinoida Mortensen, 1939						
Family Pedinidae Pomel, 1883						
Genus *Caenopedina* Agassiz, 1869						
Caenopedina cubensis Agassiz, 1869	NATL	1,187	Sb; C–B	Caribbean	H	Koehler 1909
Infraclass Carinacea Kroh & Smith, 2010						
Superorder Calycina Gregory, 1900						
Order Salenioida Delage & Hérouard, 1903						
Family Saleniidae Agassiz, 1838						
Genus *Salenocidaris* Agassiz, 1869						
Salenocidaris hastigera (Agassiz, 1879)	Cosmo	793–2,440	C–A	PAC	Cf	Koehler 1895a
Er – *Salenocidaris profundi profundi* (Duncan, 1877)	NEAT	–		Iberian Peninsula	Er*	Mortensen 1927a
Salenocidaris varispina Agassiz, 1869	Cosmo	(?718)1,165–1,830	Sb; C–A	Caribbean	Cf	Agassiz 1881
Superorder Echinacea Claus, 1876						
Order Arbacioida Gregory, 1900						
Family Arbaciidae Gray, 1855						
Genus *Arbacia* Gray, 1835						
Arbacia lixula (Linnaeus, 1758)	ATL & MED	0–55	Hb; L	?	F	Drouët 1861
Genus *Arbaciella* Mortensen, 1910						
Er – *Arbaciella elegans* Mortensen, 1910	EAT	–	L	W Africa	Er***	Marques 1983

Class Echinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Order Camarodonta Jackson, 1912						
Infraorder Echinidea Kroh & Smith, 2010						
Family Echinidae Gray, 1825						
Genus *Echinus* Linnaeus, 1758						
Echinus melo Lamarck, 1816	NEAT & MED	200–475	M; L–B	–	Cf	Koehler 1909
Genus *Gracilechinus* Fell & Pawson, 1966						
Gracilechinus acutus? (Lamarck, 1816)	NEAT & MED	?380–?500	Sb; L–B	–	Db	Koehler 1898
Gracilechinus affinis (Mortensen, 1903)	NATL	1,482–2,252	Sb; B–A	Iceland	H	Koehler 1909
Er – *Gracilechinus elegans* (Düben & Koren, 1844)	NEAT & MED	–	Sb; B	Scandinavia	Er**	Mortensen 1927a
Gracilechinus alexandri (Danielssen & Koren, 1883)	NATL	1,165–1,940(?2,560)	Sb; B	Scandinavia	Cf	Koehler 1895b
Family Parechinidae Mortensen, 1903						
Genus *Paracentrotus* Mortensen, 1903						
Paracentrotus lividus (Lamarck, 1816)	NEAT & MED	0–40(?207)	Hb; L	–	F	Drouët 1861
Genus *Psammechinus* Agassiz & Desor, 1846						
Er – *Psammechinus microtuberculatus* (Blainville, 1825)	MED	–	M; L–C	MED	Er**	Barrois 1888
Psammechinus miliaris? (Müller, *in* Knorr, 1771)	NEAT	?10–?20	M; L–C	–	Db	Barrois 1888
Superfamily Odontophora Kroh & Smith, 2010						
Family Echinometridae Gray, 1855						
Genus *Echinometra* Gray, 1825						
Er – *Echinometra lucunter lucunter* (Linnaeus, 1758)	ATL	–	Hb; L	–	Er**	Agassiz 1872
Family Toxopneustidae Troschel, 1872						
Genus Sphaerechinus Desor, 1856						
Sphaerechinus granularis (Lamarck, 1816)	NEAT & MED	0–60	M; L–C	?	F	Drouët 1861
Infraorder Temnopleuridea Kroh & Smith, 2010						
Family Trigonocidaridae Mortensen, 1903						
Genus *Trigonocidaris* Agassiz, 1869						
Trigonocidaris albida Agassiz, 1869	Cosmo	349–550	M; C–B	Caribbean	H	Koehler 1895a
Genus Genocidaris Agassiz, 1869						
Genocidaris maculata Agassiz, 1869	ATL & MED	(?0)20–200(?823)	Sb; L–C	Caribbean	Cf	Agassiz 1881
Order Echinothurioida Claus, 1880						
Family Echinothuriidae Thomson, 1872b						
Genus *Araeosoma* Mortensen, 1903b						
Araeosoma fenestratum (Thomson, 1872b)	NATL	?900	Sb; C–B	Iberian Peninsula	R	Mironov 2006
Genus *Calveriosoma* Mortensen, 1934						
Calveriosoma hystrix (Thomson, 1872b)	NEAT	800–1,528	Sb; C–A	British Isles	H	Koehler 1895a
Genus *Hygrosoma* Mortensen, 1903						
Er – *Hygrosoma luculentum* (Agassiz, 1879)	PAC & IND	–	C–B	PAC	Er***	Koehler 1895a
Hygrosoma petersii (Agassiz, 1880)	ATL	1,165–2,870(?3,237)	Sb; C–A	Caribbean	?Cf	Koehler 1895a
Genus *Sperosoma* Koehler, 1897b						

Class Echinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Sperosoma grimaldii Koehler, 1897b	NEAT	1,213–2,107	Sb; C–A	AZO	Cf	Koehler 1897b
Genus *Tromikosoma* Mortensen, 1903						
Tromikosoma koehleri Mortensen, 1903	NATL	2,954–2,968	A	Davis Strait	R	Mironov 2008
Tromikosoma uranus? (Thomson, 1877)	NEAT	?1,830	?Sb; B–A	Off Iberian Peninsula	Db	Agassiz 1881
Family Phormosomatidae Mortensen, 1934						
Genus *Phormosoma* Thomson, 1872						
Phormosoma placenta placenta Thomson, 1872	NATL	1,257	Sb; C–A	British Isles	H	Mortensen 1927b
Infraclass Irregularia Latreille, 1825						
Superorder Atelostomata Zittel, 1879						
Order Holasteroida Durham & Melville, 1957						
Suborder Meridosternata Lovén, 1883						
Infraorder Urechinina Clark, 1946						
Family Calymnidae Mortensen, 1907						
Genus *Calymne* Thomson, 1877						
Er – *Calymne relicta* Thomson, 1877	NATL	–	Sb; A–H	Bermuda	Er**	Agassiz 1881
Order Spatangoida Agassiz, 1840						
Family Hemiasteridae Clark, 1917						
Genus *Holanthus* Lambert & Thiéry, 1924						
Er – *Holanthus expergitus expergitus* (Lovén, 1874)	NATL & MED	–	In; C–A	Iberian Peninsula	Er**	Agassiz 1881
Suborder Brissidina Stockley *et al.*, 2005						
Family Brissidae Gray, 1855						
Genus *Anabrissus* Mortensen, 1950						
Er – *Anabrissus damesi* (Agassiz, 1881)	WAT	–	Sb; L–C (?B)	Brazil	Er***	Agassiz 1881
Genus *Brissopsis* Agassiz, 1840						
Brissopsis lyrifera lyrifera (Forbes, 1841)	NEAT & MED	130	Sb; L–B	British Isles	H	Koehler 1895a
Genus *Brissus* Gray, 1825						
Brissus unicolor (Leske, 1778)	ATL & MED	?7–45	Sb; L–?C	–	F	Barrois 1888
Family Palaeotropidae Lambert, 1896						
Genus *Palaeotropus* Lovén, 1874						
Palaeotropus josephinae Lovén, 1871	EAT	500–1600	M; C–B	AZO	H	Lovén 1874
Superfamily Spatangoidea Gray, 1825						
Family Spatangidae Gray, 1825						
Genus *Spatangus* Gray, 1825						
Er – *Spatangus purpureus* Müller, 1776	NEAT & EAT	–	In; L–B	?	Er**	Agassiz 1881
Er – *Spatangus raschi* Lovén, 1869	NEAT	–	Sb; C–B	Scandinavia	Er**	Agassiz 1872
Family Loveniidae Lambert, 1905						
Genus *Araeolampas* Serafy, 1974						
Araeolampas atlantica Serafy, 1974	NATL	2,585	In; A	Off Virginia	H	Serafy 1974
Subfamily Echinocardiinae Cooke, 1942						

Class Echinoidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area	Status	First record
Genus *Echinocardium* Gray, 1825						
Echinocardium cordatum (Pennant, 1777)	Cosmo	15–20	In; L–C	–	Cf	Marques 188
Echinocardium flavescens (Müller, 1776)	NEAT & MED	?15–?30	In; L–C	–	H	Tortonese 1965
Family Maretiidae Lambert, 1905						
Genus *Homolampas* Agassiz, 1874						
Er – *Homolampas fragilis* (Agassiz, 1869)	WAT	–	In; C–A	Caribbean	Er***	Clark 1949
Suborder Paleopneustina Markov & Solovjev, 2001						
Family Paleopneustidae Agassiz, 1904						
Genus *Peripatagus* Koehler, 1895b						
Peripatagus cinctus Koehler, 1895b	Cosmo	880–1,494	M; C–B	AZO (N38°47’40” W28°17’5”)	H	Koehler 1895b
Family Schizasteridae Lambert, 1905						
Genus *Aceste* Thomson, 1877						
Aceste bellidifera Thomson, 1877	ATL	1,360	In; B–H	Canaries Islands	H	Koehler 1909
Superorder Neognathostomata Smith, 1981						
Order Clypeasteroida Agassiz, 1872						
Suborder Scutellina Haeckel, 1896						
Infraorder Laganiformes Desor, 1847						
Family Echinocyamidae Lambert & Thiéry, 1914						
Genus *Echinocyamus* van Phelsum, 1774						
Echinocyamus grandiporus Mortensen, 1907	NATL	320–1,385	Sb; C–A	–	Cf	Koehler 1898
Echinocyamus pusillus (Müller, 1776)	NEAT & MED	0–207(?1,250)	Sb; L–?B	–	F	Drouët 1861
Echinocyamus scaber macrostomus Mortensen, 1907	NATL	1,560–2,178	Sb; B–A	–	H	Mortensen 1907

Class Holothuroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area (AZO)	Status	First record
Order Apodida Brandt, 1835						
Family Chiridotidae Östergren, 1898						
Genus *Chiridota* Eschscholtz, 1829						
Chiridota abyssicola Marenzeller, 1892	End	2,870 m	Sb; A	AZO (N41°40’41” W26°44’09”)	H	Marenzeller 1892
Family Synaptidae Burmeister, 1837						
Genus *Leptosynapta* Verrill, 1867						
Leptosynapta inhaerens (Müller, 1776)	NEAT & MED	0	In; L–C	Scandinavia	R	Wirtz 2009
Genus *Synaptula* Oersted, 1849						
Er – *Synaptula hydriformis* (Lesueur, 1824)	WAT	–	Ep; L	Caribbean	Er***	Hérouard 1923
Order Dendrochirotida Grube, 1840						
Family Cucumariidae Ludwig, 1894						
Genus *Abyssocucumis* Heding, 1942						
Abyssocucumis abyssorum (Théel, 1886a)	Cosmo	2,870	Sb; B–H	IND	H	Marenzeller 1892

Class Holothuroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area (AZO)	Status	First record
Genus *Pawsonia* Rowe, 1970						
Pawsonia saxicola? (Brady & Robertson, 1871)	NEAT & MED	?130	M; L	British Isles	Db	Marenzeller 1892
Family Phyllophoridae Östergren, 1907						
Genus *Thyone* Jaeger, 1833						
Thyone inermis? Heller, 1868	NEAT & MED	?130–?1,385	In; L	MED	Db	Marenzeller 1892
Order Elasipodida Théel, 1882						
Family Elpidiidae Théel, 1882						
Genus *Amperima* Pawson, 1965						
Amperima furcata (Hérouard, 1899)	Cosmo	1,846–2,968	Sb, BPl; B–H	AZO (MID) (N39°11’ W30°44’40”)	Cf	Hérouard 1899
Genus *Ellipinion* Hérouard, 1923						
Ellipinion delagei (Hérouard, 1896)	NATL	1,165–1,494	Sb, BPl; B–A	AZO (N37°42’40” W25°05’15”)	H	Hérouard 1896
Genus *Peniagone* Théel, 1882						
Peniagone azorica Marenzeller, 1892	NATL	1,385–4,020	Sb, BPl; B–A	AZO (N41°40’41” W26°44’09”)	H	Marenzeller 1892
Peniagone diaphana (Théel, 1882)	Cosmo	5,005	Sb, BPl; B–H	PAC	H	Hérouard 1899
Peniagone longipapillata Gebruk, 2008	NEAT	2,954–3,050	BPl; A	MID	R	Gebruk 2008
Peniagone marecoi Gebruk, 2008	MID	2,063–3,050	B–A	AZO (MID)(N42°46’ W29°16’)	R	Gebruk 2008
Genus *Penilpidia* Gebruk, 1988						
Penilpidia midatlantica Gebruk, 2008	MID	2,063–2,107	?BPl; A	AZO (MID)(N42°46’ W29°16’)	R	Gebruk 2008
Genus *Psychroplanes* Gebruk, 1988						
Er – *Psychroplanes obsoleta* (Hérouard, 1899)	Cosmo	–	Sb; H	NATL	Er**	Perrier 1902
Family Laetmogonidae Ekman, 1926						
Genus *Benthogone* Koehler, 1895c						
Benthogone rosea Koehler, 1896c	Cosmo	1,900	Sb; C–A	Bay of Biscay	H	Hérouard 1923
Genus *Laetmogone* Théel, 1879						
Laetmogone violacea Théel, 1879	Cosmo	1,442–?1,550	Sb; C–B	PAC	H	Perrier 1902
Er – *Laetmogone wyvillethomsoni* Théel, 1879	Southern Ocean	–	Sb; C–H	PAC	Er***	Hérouard 1902
Family Psychropotidae Théel, 1882						
Genus *Benthodytes* Théel, 1882						
Benthodytes gosarsi Gebruk, 2008	NEAT	2,954–2,968	Sb, BPl; A	AZO (MID)(N42°55’ W30°20’)	R	Gebruk 2008
Benthodytes janthina Marenzeller, 1892	End	2,870	Sb; A	AZO (N41°40’41” W26°44’09”)	H	Marenzeller 1892
Benthodytes lingua Perrier, 1896	ATL	2,102–3,050	Sb; BPl; B–H	NW Africa	Cf	Hérouard 1902
Benthodytes sanguinolenta Théel, 1882	Cosmo	2,954–2,968	Sb; BPl; B–H	PAC	R	Gebruk 2008
Benthodytes typica Théel, 1882	Cosmo	2,063–3,300	Sb; BPl; B–H	NW Africa	Cf	Hérouard 1902
Benthodytes valdiviae Hansen, 1975	EAT	3,005–3,050	A	NW Africa	R	Gebruk 2008
Genus *Psychropotes* Théel, 1882						

Class Holothuroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area (AZO)	Status	First record
Psychropotes depressa (Théel, 1882)	Cosmo	2,063–3,050	Sb, BPl; B–A	NW Africa	Cf	Perrier 1902
Psychropotes longicauda Théel, 1882	Cosmo	2,954–4,020	Sb, BPl; A–H	PAC	Cf	Hérouard 1896
Psychropotes semperiana Théel, 1882	Cosmo	5,005	Sb, BPl; A–H	SATL	H	Hérouard 1902
Order Holothuriida Miller *et al*., 2017						
Family Holothuriidae Burmeister, 1837						
Genus *Holothuria* Linnaeus, 1767						
Holothuria mexicana? Ludwig, 1875	WAT	?98	M; L	Gulf of Mexico	Db	Hérouard 1902
Er – *Holothuria dakarensis* Panning, 1939	ATL	–	M; L	W Africa	Er***	Rowe 1969
Holothuria mammata Grube, 1840	NEAT & MED	<30	M; L–C	MED	F	Nobre 1924
Er – *Holothuria tubulosa* Gmelin, 1791	MED	–	Sb; L–C	MED	Er***	Nobre 1924
Holothuria forskali Delle Chiaje, 1823	NEAT & MED	0–12	M; L–C	–	F	Marques 1983
Holothuria sanctori Delle Chiaje, 1823	NEAT & MED	0–30	M; L	MED	F	Selenka 1867
Er – *Holothuria arguinensis* Koehler & Vaney, 1906	NEAT & MED	–	M; L	NW Africa	Er**	Rowe 1969
Holothuria lentiginosa lentiginosa Marenzeller, 1892	NEAT & MED	(?130)208–275(?316)	M; C	AZO (N38°31’19” W28°34’31”)	Cf	Marenzeller
Family Mesothuriidae Smirnov, 2012						
Genus *Mesothuria* Ludwig, 1894						
Mesothuria maroccana Perrier, 1898	NATL	(?1,600)1,740–2,968	M; C–A	NW Africa	Cf	Hérouard 1923
Mesothuria milleri Gebruk & Solís-Marín, *in* Gebruk *et al*., 2012	NEAT	1,258–2,155 (?3,018)	Sb; C–H	British Isles	R	Gebruk *et al*. 2012
Er – *Mesothuria intestinalis* (Ascanius, 1805)	NATL & MED	–	Sb; L–A	Scandinavia	Er*	Mortensen 1927a
Mesothuria murrayi (Théel, 1886a)	Cosmo	?1,660–1,940	Sb; C–H	PAC	H	Gebruk *et al*. 2012
Mesothuria rugosa Hérouard, 1912	NATL	1,600	Sb; B–A	Cape Verde	H	Hérouard 1902
Er – *Mesothuria verrilli* (Théel, 1886b)	WAT		Sb; B–A	Caribbean	Er***	Marenzeller 1893
Genus *Zygothuria* Perrier, 1898						
Zygothuria lactea (Théel, 1886a)	Cosmo	1165–2,102	Sb; B–H	PAC	H	Théel 1886a
Order Persiculida Miller *et al*., 2017						
Genus *Benthothuria* Perrier, 1898						
Benthothuria funebris Perrier, 1898	EAT	2,954–2,968	Sb,?BPl; B–A	NW Africa	R	Gebruk 2008
Family Molpadiodemidae Miller *et al*., 2017						
Genus *Molpadiodemas* Heding, 1935						
Er – *Molpadiodemas atlanticus* (Perrier, 1898)	Cosmo	–	Sb; A–H	NATL	Er***	Deichmann 1930
Er – *Molpadiodemas villosus* (Théel, 1886a)	Cosmo	–	Sb; B–H	PAC	Er***	Hérouard 1902
Family Pseudostichopodidae Miller *et al*., 2017						
Genus *Pseudostichopus* Théel, 1886						
Er – *Pseudostichopus occultatus* Marenzeller, 1893	MED	–	Sb; C–B	MED	Er***	Hérouard 1902
Pseudostichopus peripatus (Sluiter, 1901)	Cosmo	(?2,871)4,020–4,400	Sb; C–H	PAC	H	Hérouard 1902
Order Synallactida Miller *et al*., 2017						

Class Holothuroidea	Geographical Range	Bathymetry (AZO, m)	Habitat	Type area (AZO)	Status	First record
Family Deimatidae Théel, 1882						
Genus *Deima* Théel, 1879						
Deima validum validum Théel, 1879	Cosmo	2,954–2,968	Sb; B–H	PAC	R	Gebruk 2008
Genus *Oneirophanta* Théel, 1879						
Oneirophanta mutabilis mutabilis Théel, 1879	Cosmo	2,954–3,050	Sb; A–H	IND	R	Gebruk 2008
Family Stichopodidae Haeckel, 1896						
Genus Parastichopus Clark, 1922						
Parastichopus regalis (Cuvier, 1817)	ATL & MED	40–275	Sb; L–B	MED	R	Wirtz & Debelius 2003
Family Synallactidae Ludwig, 1894						
Genus *Paelopatides* Théel, 1886						
Paelopatides atlantica Hérouard, 1902	End	4,020	H	AZO (N38°08’ W23°15’45”)	H	Hérouard 1902

Chapter 6. Non-destructive tissue sampling and the use of PCR-RFLP s in two edible sea cucumbers, *Holothuria mammata* Grube, 1840 and *H. sanctori* Delle Chiaje, 1823 (Echinodermata: Holothuroidea)

Madeira, P., Stefanni, S. & Ávila, S.P. (2018). Non-destructive tissue sampling and the use of PCR-RFLP's in two edible sea cucumbers from the Northeastern Atlantic, *Holothuria mammata* Grube, 1840 and *H*. *sanctori* Delle Chiaje, 1823 (Echinodermata: Holothuroidea). *The European Journal of Zoology* (formerly known as *Italian Journal of Zoology*), 10.1080/24750263.2018.1438529. *Submitted* 3 September 2017. *Accepted 1 February 2018.*

Abstract

Historically, the harvest and consumption of sea cucumbers have been largely restricted to Asian countries. Recently, however, the western world has witnessed a rapid growth of holothurian-related industries, and *Holothuria mammata* Grube, 1840 and *H*. *sanctori* Delle Chiaje, 1823 are now being commercially harvested in European and North African countries. The identification of holothurian species tends to be difficult and time-consuming, and in many cases needs experienced taxonomists. The present work suggests a simple non-destructive DNA sampling, using tube feet or oral tentacles from these two species. A simple and fast method of diagnose is also described, based on PCR-RFLPs using restriction nuclease Sau3AI on 16S rRNA fragments. The use of RFLPs to rapidly and inexpensively identify species with no need for taxonomical or genetic expertise could prove a valuable asset for conservation and fishery purposes targeting commercially harvested animals such as the holothurians in the Northeast Atlantic and the Mediterranean Sea.

Key words: Non-destructive DNA sampling; PCR-RFLP; *Holothuria mammata*; *Holothuria sanctori*; Northeast Atlantic.

6.1. Introduction

The sea cucumbers, class Holothuroidea, one of the five extant classes of the exclusively marine phylum Echinodermata (Pawson 2007), are a conspicuous presence throughout all oceans and seas, at all latitudes and depths, occurring in virtually any marine habitat, from corals to rocky, sandy, muddy and mangrove habitats (Purcell *et al*. 2012). Roughly 1,400 extant species are known worldwide (Pawson 2007) but only 66 are commercially harvested, comprising predominantly species belonging to the order Aspidochirotida from tropical shallow-waters (Purcell 2010). The processed products (cooked or dried), also known as 'beche-de-mer', 'trepang' or 'haishen', are chiefly exported to Asian markets (Purcell *et al*. 2012).

Possibly due to the over-exploitation of the typical valuable holothurians and in response to the growing demand for sea cucumber products (Purcell 2010), several Atlanto-Mediterranean holothurians are now being increasingly harvested, such as *Holothuria mammata* Grube, 1840 and *H. sanctori* Delle Chiaje, 1823 (see González-Wangüemert *et al*. 2016). This could pose a potential threat to many important ecosystems (*e.g.,* seagrass beds) as many of the targeted species are viewed as key species, contributing to the recycling of bottom detritus as continuous deposit-feeders and, thus, playing an important role in the soft-sediment biochemical cycles (Mezali *et al*. 2003).

The identification of even well-known holothurian species tends to be difficult and time-consuming, and in many cases needs experienced taxonomists, particularly if dealing with preserved specimens (*e.g.,* in ethanol, dried or frozen), which tend to suffer from varying degrees of shrinkage and deformation, and loss of internal organs through evisceration (Tortonese 1965; Borrero-Pérez *et al*. 2009). Furthermore, in sea-cucumber industries, many critical morphological characters tend to be destroyed or discarded (Wen *et al*. 2010). DNA based genetic analyses have emerged as a popular and inexpensive tool within the echinoderm research community, used for a variety of objectives including monitoring populations in conservation and fishery studies (*e.g.,* Uthicke *et al*. 2010; Wen *et al*. 2010). Problems associated with the identification of holothurian species in 'beche-de-mer' transformed products, and the high incidence of fraud and illegal trading (*e.g.,* marketing less-valuable species under the identification of high-value species), have led to multiple efforts in the development of genetic tools for the rapid identification and assessment (Uthicke *et al*. 2010). PCR amplification followed by restriction fragment length polymorphism (RFLP) techniques, particularly based on a fragment of the slow-evolving 16S region, have been presented as viable methods for identification of commercial species and authentication of highly valuable species by Asian markets (Wen *et al*. 2010).

Conservation and management of marine resources are increasingly demanding the development of tissue-sampling techniques that are as non-intrusive as possible (Beebee & Rowe 2008). For holothurians, the most widely targeted tissues are the muscles, gonads and gut (*e.g.,* Uthicke *et al*. 2004; Borrero-Pérez *et al*. 2010; So *et al*. 2011), though other structures such as tentacles (Kerr *et al*. 2005) or the body wall (Uthicke *et al*. 2004; Borrero-Pérez *et al*. 2010) sporadically appear in the literature. Sampling any of these tissues does not necessarily result in the death of the specimen, due to the holothurian's natural capacity for regeneration (García-Arrarás & Greenberg 2001). However, a non-destructive sampling method should favour: (1) a selection of tissues that do not imply the dissection of the specimens; (2) easy identification by untrained personnel; and, (3) if dealing with live specimens, the rapid regeneration of the specimens. The use of any internal structures could also prove to be an issue, as many shallow-water Northeast Atlantic species naturally eviscerate (Tortonese 1965). Furthermore, internal parts are generally discarded in sea-cucumber fisheries (Purcell 2010). The tentacle tissue or the tube feet appear to be the best alternative, for they comply with any of the needs listed above – more so if dealing with collection specimens or commercialised animals, allowing for a fast assessment of several individuals (and easy storage) without specimen destruction (including of taxonomical characters).

An easy, fast, non-intrusive method of DNA sampling and identification of two edible northeastern Atlantic holothurian species is described, using RFLPs on 16s PCR products derived from tube feet and tentacle tissue.

6.2. Study area and ecological considerations

The Azores is an archipelago composed of nine volcanic oceanic islands and several islets, spreading around 600 km in the Northeast Atlantic (Fig. 6.1). Among the shallow-water echinoderms reported from the archipelago (Pereira 1997; Wirtz 2009), four species are currently considered edible: *Parastichopus regalis* (Cuvier, 1817), *Holothuria forskali* Delle Chiaje, 1823, *H. mammata* and *H. sanctori* (Ramón *et al.* 2010; Sicuro & Levine 2012; González-Wangüemert *et al.* 2016). The last two species are very common inhabitants of Azorean low intertidal and shallow subtidal areas, achieving occasionally spectacular densities in calm areas, such as protected bays, marine lagoons, ports and marinas. These two species are also found throughout the Mediterranean and Northeast Atlantic, from the Bay of Biscay to North Africa, including the archipelagos of Madeira and Canaries (Tortonese 1965). Additionally, *H. sanctori* extends its distribution southward and was reported in Cabo Verde, Ascension Island and Santa Helena Island (Tortonese 1965).

Holothuria mammata and *H. sanctori* are perfect candidates for a study of this nature in the Azores considering their easy access and abundance in the archipelago, as well as their geographical range and commercial potential. Individuals of these two species were collected during low tide or by snorkelling in four islands of the Azores, between 2010 and 2012, covering the eastern group (Caloura, São Miguel Island; N37°42’25”, W25°30’32”), the central group (São Roque, Pico Island; N38°31’39”, W28°19’08”) and the western group (Santa Cruz, Flores; N39°27’17”, W31°07’29”) (see Fig. 6.1). The identification was based on gross morphological characters and later confirmed by the observation of the ossicles under the binocular microscope, following Tortonese (1965).

6.3. Materials and methods

Tissue sampling and DNA extraction

For comparison purposes, several tissues were initially sampled in each individual: body wall, longitudinal muscle, intestine, tube feet and tentacle. Each sampled tissue was fixed in ethanol. DNA extraction was obtained on 15 mg of tissue using E.Z.N.A.® Mollusc DNA Kit (Omega, USA), with minor adaptations to the instructions in the supplier’s manual (vortex steps were replaced by manual agitation, and DNA elution buffer was replaced by purified water). DNA concentration was measured using a NanoVue Spectrophotometer (GE Healthcare Bio-Sciences).

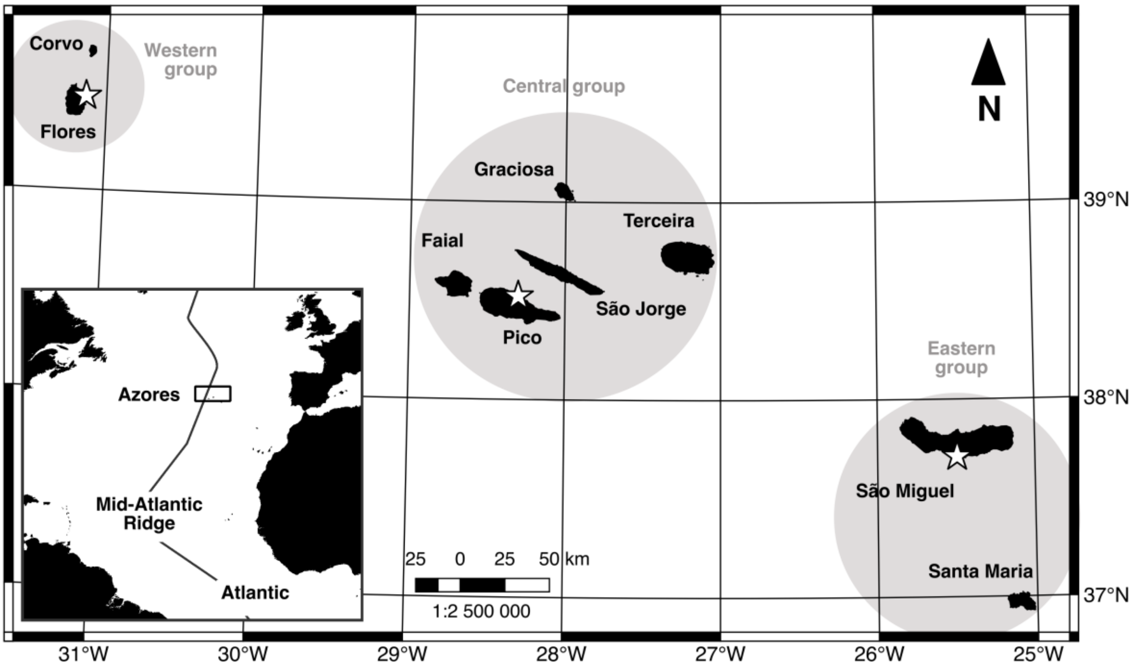


Figure 6.1. Sampling sites (stars) in the Azores for *Holothuria mammata* and *H. sanctori*: eastern group (Caloura, São Miguel Island; N37°42’25” W25°30’32”), central group (São Roque, Pico Island; N38°31’39” W28°19’08”) and western group (Santa Cruz, Flores; N39°27’17” W31°07’29”).

PCR

A pair of invertebrate universal primers (16Sar: 5’-CGCCTGTTTATCAAAAACAT-3’ and 16Sbr: 5’-CTCCGGTTTGAACTCAGATCA-3’) was used for PCR amplification. The conserved 16S region discriminates between species and this molecular marker is extensively used in invertebrate phylogenetic studies, including holothurian species targeted in this study (Borrero-Pérez *et al*. 2009, 2010). The thermal cycling profile started at 95°C, with an initial denaturation time of 5 minutes, followed by 35 cycles of 60 seconds denaturation at 95°C, 60 seconds annealing at 50°C and 60 seconds extension at 72°C, and a final extension of 10 minutes at 72°C. PCR products were screened by 1% agarose gel electrophoresis at 90V for 60 minutes and visualise d under UV exposure. The length of fragments was determined by comparison with commercial 1- kb DNA ladder (Invitrogen, UK).

RFLP analysis

The restriction nuclease Sau3AI (Promega) was tested on amplified PCR products without previous purification, from 10 sampled individuals (see Fig. 6.1). Following Stefanni *et al*. (2009), reaction mixtures were slightly modified from the protocol proposed by the manufacturer: 2 µL of PCR product, 2 µL of buffer (RE), 0.2

µL of BSA, 1 µL of enzyme solution and, finally, purified water to a final volume of 20 µL. All mixtures were incubated at 37°C for 4 hours. Digest products were separated by electrophoresis in a 2.0% agarose gel at 90V for 120 minutes. The sizes of the resulting DNA fragments were estimated by comparison with a commercial 1-kb DNA ladder (Invitrogen, UK). After the electrophoresis, the gel was visualized under UV light.

6.4. Results and discussion

The final concentrations of DNA extraction product were similar in the two species, but varied according to the sampled tissues (Table 6.1). Though it was possible to extract DNA from any of the sampled tissues, the muscle or body wall produced less clean extracts. In the particular case of the body wall, the presence of inhibitors in the extract at higher concentrations caused the frequent failure to successfully produce any PCR products. The choice of using either tissue will depend ultimately on the target species and on the available material. For example, holothurian species such as the ones used here introvert and retract the tentacles when inactive or stressed. Though it is easy to force the appearance of the tentacles by gently squeezing the oral area, the same is not possible when dealing, for example, with preserved animals (*e.g.,* dry or frozen). And of course, when dealing with highly processed 'beche-de-mer', products, in which none of the referenced structures will have survived, the traditionally used longitudinal muscle will have to be the chosen tissue.

The direct digestion of the 16S PCR products with Sau3AI resulted in species-specific restriction patterns, as shown in Fig. 6.2. The digestion of Sau3AI, the 16S PCR product for *H. mammata* (lane 9), yielded one fragment, close to 552 bp in length (lanes 10–13), and for *H. sanctori* (lane 1) yielded two fragments, approximately 565 bp and 488 bp in length, respectively (lanes 2 and 7). The RFLP digestion produced

Table 6.1. Final concentrations of genomic DNA extraction eluted in 150 µL and A260/A280 ratios for each sampled tissue

Sampled Tissue	[DNA (µg/ml)] – (A260/A280)
Body Wall	3.6 (1.479) – 12.2 (2.030)
Muscle	4.6 (2.116) – 11.0 (2.037)
Tube Feet	30.0 (1.842) – 35.0 (2.013)
Intestine	35.5 (2.029) – 89.0 (2.000)
Tentacle	77.0 (1.949) – 98.0 (1.960)

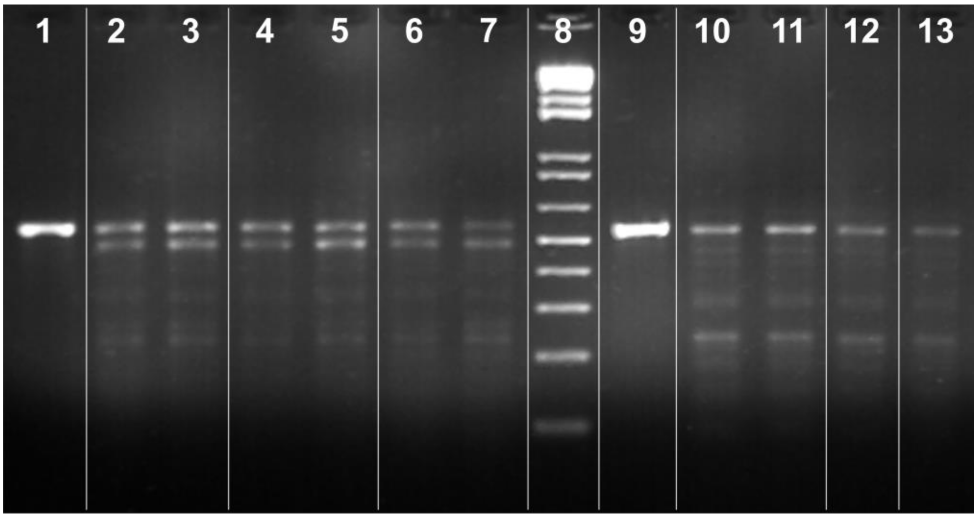


Figure 6.2. PCR products of 16S rRNA gene and respective RFLP profiles generated by restriction nucleases Sau3AI; marker (8). *Holothuria sanctori* (lanes 1 –7): 16S rRNA PCR product (1) and RFLP profiles by island group, western group (2, 3), central group (4,5) and eastern group (6,7). *Holothuria mammata* (lanes 9 to13): 16S rRNA PCR product (9) and RFLP profiles by island group, western group (10, 11), central group (12) and eastern group (13).

fragments about 234 bp long for both species, but only *H. mammata* revealed a reasonable clear banding. These results showed that the PCR-RFLP is a suitable technique to identify the sea-cucumber species included in this work.

PCR-RFLP is one of the most widely used DNA-based methods in species identification, for its simplicity, rapidity, reproducibility, limited equipment requirements and cost-effective results (Rasmussen & Morrissey 2011); thus, routine and field- oriented methodologies of genetic screening and discrimination (‘diagnostic kits’) are now available for a wide range of commercial marine species (*e.g.,* Aranishi 2005; Stefanni *et al*. 2009; Wen *et al*. 2010; Guerao *et al*. 2011) and product authentication in food- related industries (*e.g.,* Martinez *et al*. 2005; Rasmussen & Morrissey 2009; Sawicki & Klein 2010). Simultaneously, coupling such protocols with non-destructive DNA sampling techniques combines the advantages mentioned above with a more environmentally sensitive collection method. Though this study was restricted to two common species in the Azorean shallow waters, considering the simplicity of the methodology herein described, efforts should be made to contemplate applying it to other European commercial species.

ACKNOWLEDGEMENTS

P. Madeira was supported by FCT (the Portuguese Foundation for Science and Technology) under grant SFRH/BD/61146/2009. S.P. Ávila was funded by FCT (IF 00465/2015) and by FEDER funds through the Operational Programme for Competitiveness Factors–COMPETE, and by National Funds (FCT): UID/BIA/50027/2013 and POCI-01-0145-FEDER-006821. We gratefully acknowledge the support from the funding agency Direcção Regional da Ciência e Tecnologia (DRCT, Governo Regional dos Açores). We also want to thank Diana Catarino and colleagues from DOP for their support. We thank the associate laboratory LARSyS #9, with financial support from OE and COMPETE, through FCT and DRCT/ GovAzores.

This work was supported by the Fundação para a Ciência e a Tecnologia [IF 00465/2015,SFRH/ BD/61146/2009,UID/BIA/50027/2013]; FEDER – Operational Programme for Competitiveness Factors–COMPETE [POCI-01-0145-FEDER- 006821].

6.5. References

Aranishi, F. (2005) Rapid PCR-RFLP method for discrimination of imported and domestic mackerel. *Marine Biotechnology*, 7(6), 571–575.

Beebee, T. & Rowe, G. (2007) *An Introduction to Molecular Ecology*. 2nd edn. Oxford University Press, x+535.

Borrero-Pérez, G.H., Gómez-Zurita, J., González-Wangüemert, M., Marcos, C. & Pérez-Ruzafa, A. (2010) Molecular systematics of the genus *Holothuria* in the Mediterranean and Northeastern Atlantic and a molecular clock for the diversification of the Holothuriidae (Echinodermata: Holothuroidea). *Molecular Phylogenetics and Evolution*, 57, 899–906.

Borrero-Pérez, G.H., Pérez-Ruzafa, Á., Marcos, C. & González-Wangüemert, M. (2009) The taxonomic status of some Atlanto-Mediterranean species in the subgenus *Holothuria* (Echinodermata: Holothuroidea: Holothuriidae) based on molecular evidence. *Zoological Journal of the Linnean Society*, 157(1), 51–69.

García-Arrarás, J.E. & Greenberg, M.J. (2001) Visceral regeneration in holothurians. *Microscopy Research and Technique*, 55, 438–451.

González-Wangüemert, M., Valente, S., Henriques, F., Domínguez-Godino, J.A. & Serrão, E.A. (2016) Setting preliminary biometric baselines for new target sea cucumbers species of the NE Atlantic and Mediterranean fisheries. *Fisheries Research*, 179, 57–66.

Guerao, G., Andree, K., Froglia, C., Simeó, C.G. & Rotllant, G. (2011) Identification of European species of *Maja* (Decapoda: Brachyura: Majidae): RFLP analyses of COI mtDNA and morphological considerations. *Scientia Marina*, 75(1), 129–134.

Kerr, A.M., Janies, D.A., Clouse, R.M., Samyn, Y. & Kuszak, J. & Kim, J. (2005) Molecular phylogeny of coral-reef sea cucumbers (Holothuriidae: Aspidochirotida) based on 16S mitochondrial ribosomal DNA sequence. *Marine Biotechnology*, 7(1), 53–60.

Madeira, P., Stefanni, S. & Ávila, S.P. (2018). Non-destructive tissue sampling and the use of PCR-RFLP's in two edible sea cucumbers from the Northeastern Atlantic, *Holothuria mammata* Grube, 1840 and *H. sanctori* Delle Chiaje, 1823 (Echinodermata: Holothuroidea *The European Zoological Journal*, 85: 89–94. DOI: 10.1080/24750263.2018.1438529

Martinez, I., James, D. & Loréal, H. (2005) Application of Modern Analytical Techniques to Ensure Seafood Safety and Authenticity. *FAO Fisheries Technical Paper*, 455, 73 pp.

Mezali, K., Chekaba, B., Zupo, V. & Asslah, B. (2003) Comportement alimentaire de cinq especes d'holothuries aspidochirotes (Holothuroidea: Echinodermata) de la presqu'ile de Sidi-Fredj (Algerie). *Bulletin de la Société zoologique de France*, 128, 49–62.

Pawson, D.L. (2007) Phylum Echinodermata. *Zootaxa,* 1668, 749–764.

Pereira, M.O.R. (1997) Checklist of the littoral echinoderms of the Azores. *Açoreana*, 8(3), 331–337.

Purcell, S.W. (2010) Managing sea cucumber fisheries with an ecosystem approach. *FAO Fisheries and Aquaculture Technical Paper*, 520, 157 pp.

Purcell, S.W., Samyn Y. & Conand, C. (2012) Commercially important sea cucumbers of the world. *FAO Species Catalogue for Fishery Purposes*, 6, 150 pp.

Ramón, M., Lleonart, J. & Massutí, E. (2010) Royal cucumber (*Stichopus regalis*) in the northwestern Mediterranean: Distribution pattern and fishery. *Fisheries Research*, 105, 21–27.

Rasmussen, R.S. & Morrissey, M.T. (2009) Application of DNA-based methods to identify fish and seafood substitution on the commercial market. *Comprehensive Reviews in Food Science and Food Safety*, 8(2), 118–154.

Rasmussen, R.S. & Morrissey, M.T. (2011) Advances in DNA-Based Techniques for the Detection of Seafood Species Substitution on the Commercial Market. *JALA: Journal of the Association for Laboratory Automation*, 16(4), 308–321.

Sawicki, W. & Klein, D. (2010) Sea Fish and Shellfish Authentication Issues. *In*: Daczkowska-Kozon, E. & Sun Pan, B. (Eds.) *Environmental Effects on Seafood Availability, Safety and Quality.* Taylor & Francis Group, USA, pp 275–294.

Sicuro, B. & Levine, J. (2012) Sea cucumber: a new candidate species for aquaculture in Mediterranean Sea. *Reviews in Fisheries Science*, 19(3), 299–304.

So, J.J., Uthicke, S., Hamel, J.-F. & Mercier, A (2011) Genetic population structure in a commercial marine invertebrate with long–lived lecithotrophic larvae: *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Marine Biology*, 158, 859–870.

Stefanni, S., Bettencourt, R., Knutsen, H. & Menezes, G. (2009) Rapid PCR-RFLP method for discrimination of the two Atlantic cryptic deep-sea species of scabbardfish. *Molecular ecology resources*, 9, 528–530.

Tortonese, E. (1965) *Fauna D'Italia – Echinodermata*. Edizioni Calderini, Bologna, 422 pp.

Uthicke, S., Byrne, M. & Conand, C. (2010) Genetic barcoding of commercial Bêche-de-mer species (Echinodermata: Holothuroidea). *Molecular ecology resources*, 10(4), 634–646.

Uthicke, S., Welch, D., Benzie, J.A.H. (2004) Slow growth and lack of recovery in overfished holothurians on the Great Barrier Reef: Evidence from DNA fingerprints and repeated large-scale surveys. *Conservation Biology*, 18(5), 1395–1404.

Wen, J., Hu, C., Zhang, L., Luo, P., Zhao, Z., Fan, S. & Su, T. (2010) The application of PCR–RFLP and FINS for species identification used in seacucumbers (Aspidochirotida: Stichopodidae) products from the market. *Food Control*, 21, 403–407.

Wirtz, P. (2009) Ten new records of marine invertebrates from the Azores. *Arquipelago*, 26, 45–49.

Chapter 7. Biodiversity and biogeographic patterns of Echinodermata in the North and Central Atlantic Ocean and the Mediterranean Sea

Madeira, P., Kroh, A., Martins, A.M.F., Johnson, M.E. & Ávila, S.P. (*submitted*). Biodiversity and biogeographic patterns of Echinodermata in the North and Central Atlantic Ocean and the Mediterranean Sea. *Zoological Journal of the Linnean Society*

Abstract

The geographical distribution of shallow-water (≤50 m and ≤200 m) echinoderms from the North and Central Atlantic Ocean and the Mediterranean Sea was compiled from literature. A total of 341 genera and 891 species of shallow-water echinoderms are presently recorded in the study area. The tropical West Atlantic is by far the most diverse region (483 species, 210 of which are endemic), supporting the 'Centres of Marine Fauna Redistribution' hypothesis, a biogeographic-unit concept that progresses from an initial stage of species accumulation to an intermediate stage of speciation, ending in a source area for species (the dispersal stage). The Mediterranean Sea does not emerge as a biodiversity hotspot, with biodiversity rates similar to the neighbouring regions of Iberia and NW Africa, but presents a significant endemism rate. Among the insular systems, Canary Islands show the highest echinoderm biodiversity with 85 species, followed by Cabo Verde with 76. In general, insular systems exhibit low levels of endemism; moreover, endemism decreases with latitude. Our results agree with previous studies wherein NE Atlantic insular systems (both islands and seamounts) are classified as recipient areas with a strong mix of faunas from different geographical origins. In general, species from insular faunas presented broader depth ranges when compared with those from continental coasts, regardless of the average latitude. A positive correlation between geographical range and latitude, and between bathymetric range and latitude was detected, confirming the Rapoport's latitudinal gradient. Thorson's rule, which dictates non-pelagic development to predominate at higher latitudes was not supported by our analysis. Endemic species, as well as planktonic species are especially numerous among mobile sediment-associated habitats, whereas broadly distributed species show no preference for either soft or hard bottoms. Most areas reflect a natural decrease of shared species with increasing geographical distance, particularly in oceanic systems where insular faunas proved to be most similar to those of the nearest continental shores, regardless of the prevailing sea-surface currents. In conclusion, the present study: 1) provides a baseline for future studies on Atlantic and Mediterranean echinoderms, enabling research on their response to increasing human pressure and climate change; and 2) demonstrates that shallow-water echinoderm faunas in the Atlantic tend to be closely related to those in nearby areas, but simultaneously showing marked latitudinal gradients in terms of species richness, species geographical range, endemism, bathymetrical zonation, modes of larval development, and asexual reproduction.

Key words: biodiversity and biogeographic patterns, Parsimony Analysis of Endemicity, faunal flows, shallow-water echinoderms, North and Central Atlantic, Mediterranean Sea.

7.1. Introduction

The phylum Echinodermata is a diverse group of strictly marine deuterostome invertebrates, including the brittle stars (Ophiuroidea: 2,064 species), sea stars (Asteroidea: 1,900 species), sea cucumbers (Holothuroidea: 1,400 species), sea urchins (Echinoidea: 1,012 species), sea lilies and feather stars (Crinoidea: 623 species) (Pawson 2007a; Appeltans *et al*. 2012; Mah & Blake 2012; Stöhr *et al*. 2012; Kroh & Mooi 2018). Echinoderms are among the most abundant and ecologically successful groups of fully marine animals, occurring at almost all latitudes and in virtually any fully marine habitat, from coastal areas down to the abyssal plains (Gillespie & McClintock 2007). Echinoderms are also of particular ecological significance, being useful indicators of environmental degradation, either by playing key functions in structuring marine communities and ecosystems, or due to their destructive capabilities as those observed during outbreaks of echinoid or sea-star populations (Uthicke *et al*. 2009). In many countries, echinoderms are also considered as an economical asset, since several species are currently being traded for human consumption (Lawrence 2001; Purcell *et al*. 2012), souvenir memorabilia, and decorative trinkets (Micael *et al*. 2009). Some echinoderms also are under investigation for bioactive compounds in search of antibiotic, antifungal and anticancer agents (Petzelt 2005; Kornprobst 2014; Aminin *et al*. 2015). For these reasons, extensive data is available on their biology, ecology, behaviour, and geographic and bathymetric ranges, making echinoderms a perfect choice as a target group for biogeographic studies. Moreover, due to their calcitic skeleton, echinoderms are commonly documented in marine palaeontological studies (Clarkson, 1998; Madeira *et al*., 2011), offering an in-depth temporal perspective for evolutionary and phylogenetic studies.

The main aims of the present study are: 1) to determine echinoderm geographical patterns of biodiversity in the North and Central Atlantic Ocean, and in the Mediterranean Sea; 2) to use the extensive presence/absence dataset to understand the extent to which latitudinal diversity patterns are a feature of the marine environment, correlating bathymetric zonation and modes of larval development with latitudinal range; and 3) to identify biotic similarities between the areas and to analyse the probable directions of faunal flows.

7.2. Materials and methods

Geographical distribution

Echinoderm occurrences were compiled through an exhaustive search of the primary literature published up to September 2018. Species lists from each of the echinoderm classes were taken from the World Register for Marine Species (WoRMS Editorial Board 2017) and were used as an initial basis for the construction of the database (Supplementary material, Table S7.1). Two datasets were compiled: 1) from the intertidal down to 50 m; and 2) from the intertidal down to 200 m. Uncertain occurrences, non-native species and species for which there is no clear record of their bathymetrical range were not included (for details please see Supplementary material, Table S7.2).

The following references were considered for bathymetric and geographical distribution on each class: **General** — Verrill (1885a), Koehler (1909), Mortensen (1927a), Moyse & Tyler (1995), Saldanha (1995), Pomory (2003), Wirtz & Debelius (2003); **Asteroidea** — Verrill (1885b, 1895), Sladen (1889), Perrier (1894), Döderlein (1920), Fisher (1930, 1941), Cadenat (1938), Clark (1949), Madsen (1950), Grainger (1966), Halpern (1972), Downey (1973), Nataf & Cherbonnier (1973, 1975), Miller (1984), Madsen (1987), Clark & Downey (1992), Ahearn (1995), Clark & Mah (2001), Waters & Roy (2003), O'Loughlin & Waters (2004), Zulliger & Lessios (2010), Dilman (2008, 2014), Mah *et al.* (2014), Mah (2015); **Crinoidea** — Clark (1914, 1931, 1977), Clark & Clark (1967), Messing & Dearborn (1990), Améziane *et al.* (1999), Messing (2013); **Echinoidea** — Agassiz (1881), Mortensen (1903, 1927b, 1928, 1935, 1936, 1940, 1943a,b, 1948, 1951a,b), Clark (1907a, 1925), Grieg (1932), Chesher (1966a, 1968b, 1969, 1970), Higgins (1975), Serafy (1971, 1979), Serafy & Fell (1985), Pawson & Miller (1983), Gagnon & Gilkinson (1994), Zaixso & Lizarralde (2000), Mironov (2006a, 2008, 2014), Schultz (2006), Lessios *et al.* (2011), Wangensteen *et al.* (2012), Coppard *et al.* (2013), Rodriguez *et al.* (2013), Martínez-Melo *et al.* (2014); **Holothuroidea** — Hérouard (1902, 1923), Östergren (1902), Perrier (1902), Heding (1928, 1931, 1935a, 1942), Deichmann (1930, 1936), Cherbonnier (1963a, 1964, 1965a, 1984), Pawson (1977), Miller & Turner (1986), Tuwo & Conand (1992), Pawson *et al.* (2001, 2010), Thandar (2001), O'Loughlin & Ahearn (2005), Borrero-Pérez *et al.* (2009), Mercier *et al.* (2010), Gebruk *et al.* (2012, 2014), Martins (2013); **Ophiuroidea**

— Ljungman (1872), Lyman (1878, 1882, 1883), Studer (1882), Koehler (1898, 1906b, 1914a), Brooks & Grave (1899), Clark (1915, 1918, 1953, 1976), Mortensen (1933a), Ziesenhenne (1955), Thomas (1962), Madsen (1970), Zibrowius (1978), Guille (1981), Paterson *et al.* (1982), Hendler & Miller (1984), Paterson (1985), Bartsch (1987), Alvà & Vadon (1989), Hendler (1995, 2011), Sumida *et al.* (2000), Martynov & Litvinova (2008), Manso (2010), Martynov (2010), Herrero-Pérezrul *et al.* (2014), Manso *et al.* (2014), Stöhr & Alme (2014), Brogger & O'Hara (2015).

For the construction of the distributional matrix, data were organised into 28 regions (Fig. 7.1), largely adapted from Ávila *et al*. (2012). Though the main focus was on the North Atlantic area, seven southern regions also were included in order to further substantiate some of the observed patterns. These additional areas are mostly from South Atlantic oceanic islands and archipelagos, and the continental shores of Angola and southern Brazil, adjacent respectively to tropical Africa and Central America. For interpretation purposes, regions were grouped into two main groups: continental and oceanic shores. The latter category included a number of volcanic oceanic islands (sensu Whittaker & Fernández-Palacios 2007) and the Lusitanian seamounts (Gorringe, Ampère, Josephine, and Seine). The Icelandic plateau encloses a large volcanic island (100,300 km2 total area) representing 30% of its area, whereas the remaining submerged topography is characterised by 50–200 km distance across a shallow insular shelf (Thordarson & Larsen 2007) with depths mostly between 100 and 300 m (Pálmason 1974). Despite being a true oceanic island by definition, the sheer size of its coastal and shelf waters set Iceland apart from any other oceanic region included in the present work, and as such, it was grouped together with the continental systems.

The adopted distributional areas (Fig. 7.1) were largely adapted from Ávila *et al.* (2012) as follows (with additional references): **MED** — Mediterranean Sea, Marmara Sea, Black Sea and Sea of Azov (Forbes 1843; Tortonese 1965; Cherbonnier & Guille 1968; Cherbonnier 1969a; Salvini-Plawen 1972; Froglia 1975; Alvà 1991; Alvà & Jangoux 1992; Bohn 2004; Koukouras *et al.* 2007; Mastrototaro & Mifsud 2008; Mifsud *et al.* 2009; Mastrototaro *et al.* 2010; Cihangir & Papadopoulou 2012; Prato & Pastore 2012; Mecho *et al.* 2014); **ART** — Arctic, above N75° (Piepenburg *et al.* 1996; Anisimova & Cochrane 2003; Rogacheva 2007); **SCA** — Scandinavian coasts, *i.e.*

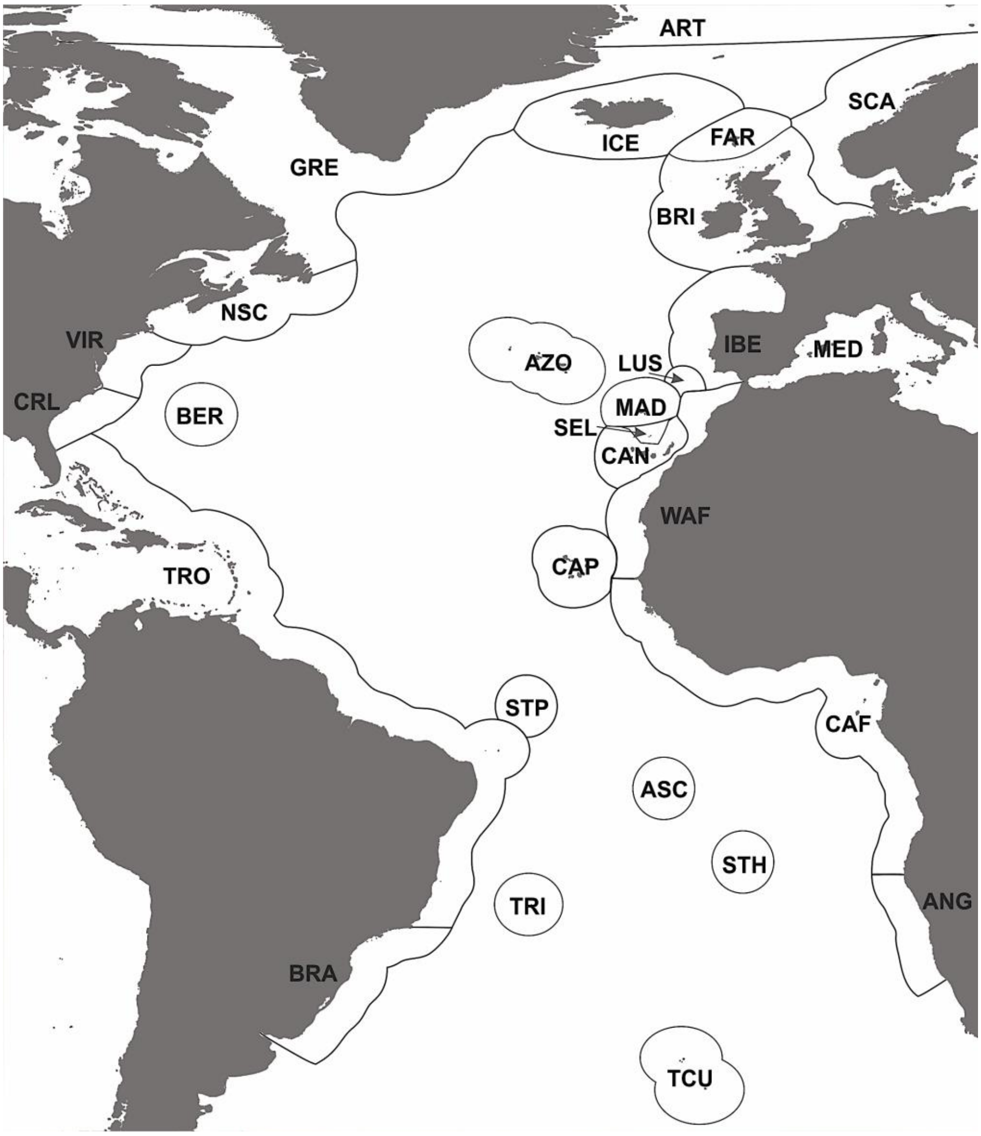


Figure 7.1. Atlantic and Mediterranean areas used to construct the table with the geographical distribution of the shallow (≤50 m and ≤200 m) echinoderm species. For further information, please see text.

Norway Sea, Skagerrak and Kattegat and Baltic Sea (Kramers 1971; Høisæter 1990); **ICE** — Iceland (Copley *et al.* 1996; Dilman 2006); **GRE** — Greenland, western shores of Baffin Island, Baffin Bay, Davis Strait and Labrador Sea (Heding 1935b, 1936); **BRI** — British Isles and North coast of France (Herapath 1865; Farran 1913; Crump & Emson 1983; Gage *et al.* 1983, 1985; Harvey *et al.* 1988; Picton 1993; Broszeit *et al* 2010; Godet *et al.* 2010; Muths *et al.* 2006, 2010); **IBE** — Atlantic Iberian and West France coasts to the Gulf of Cadiz (Koehler 1896, 1906, 1921; Nobre 1938; Cherbonnier 1969b, 1970; Marques 1980; Marques *et al.* 1982; Besteiro & Urgorri 1988; Jesus & Fonseca 1999; Rueda *et al.* 2011); **WAF** — West African shores, from Straits of

Gibraltar (Morocco) south to Dakar, Senegal (Mortensen 1925; Hérouard 1929; Cherbonnier 1972; Anadón 1977; Massin 1993); **CAF** — west coasts of Central Africa from Dakar south to Congo (≈S6°) (Greef 1882; Koehler 1914b; Cherbonnier 1949; Buchanan 1958; Cherbonnier 1957a, 1958a, b, c, d, 1963b, 1965b, 1966, 1973, 1988; Le Loeuff & Intès 1968; Le Loeuff 1993; Thandar & Mjobo 2014); **NSC** — New Scotia biogeographical province, *i.e*. Atlantic shores of USA, between Newfoundland (N50°) and Cape Cod (N42°) (Pawson 1976a; Haedrich & Maunder 1985; Eckelbarger & Riser 2013; Kenchington *et al.* 2014; Massin *et al.* 2014; Murillo *et al.* 2015); **VIR** — Virginian biogeographical province *sensu* Engle & Summers (2000), *i.e*. Atlantic shores of USA, between Cape Cod (N42°) and Cape Hatteras, North Carolina (N35°) (Loosanoff 1964); **CRL** — Carolinian biogeographical province, *i.e*. Atlantic shores of USA, between Cape Hatteras, North Carolina (N35°) and Cape Canaveral (N28°30’) (Gray *et al.* 1968; Schwartz & Porter 1977; Wenner *et al.* 1984; Lawrence *et al.* 2013); **TRO** — Tropical biogeographical province (from now on generically designated as ‘Caribbean’), *i.e*. Atlantic shores of USA, south of Cape Canaveral (N28°30’), including western and eastern shores of Florida, Gulf of Mexico, Bahamas, Caribbean Sea, south to Cabo Frio (Brazil) (S23°); (Rathbun 1879; Verrill 1899; Clark 1900, 1933, 1934, 1939, 1941; Bernasconi 1955; Cherbonnier 1959a; Chesher 1966b, 1968a, 1972; Pawson 1967, 1968, 1976b, 2007b; Tommasi 1972; Devaney 1974; Walenkamp 1976, 1979; Meyer *et al.* 1978; Hendler 1979, 1988, 2005; Hotchkiss 1982; Campbell & Turner 1984; Messing 1985; Hendler & Turner 1987; Caso 1990; Schoppe 1996; Hendler & Pawson 2000; Albuquerque *et al.* 2001; Turner & Graham 2003; Laguarda-Figueras *et al.* 2004, 2005a; Manso 2004; Abreu-Pérez *et al.* 2005; Valle-García *et al.* 2005; Borrero-Pérez *et al.* 2008; Hernández-Herrejón *et al.* 2008; Pawson *et al.* 2009; Solis-Marin & Laguarda-Figueras 2010; Benavides-Serrato *et al.* 2011, 2012; Lima *et al.* 2011; Pomory *et al.* 2011; Arriaga-Ochoa *et al.* 2012; Prata & Christoffersen 2012; Gondim *et al.* 2013a,b; Hernández-Díaz *et al.* 2013; Pawson & Pawson 2013; Rodríguez-Barreras & Messing 2013; Prata *et al.* 2014; Rodríguez-Barreras 2014; Solís-Marín *et al.* 2014, 2015; Paim *et al.* 2015; Martins *et al.* 2016); **BRA** — Biogeographical province of Brazil, the Paulista and Patagonic Provinces *sensu* Palacio 1980, *i.e.* from Cabo Frio (S23°) south to River Plate (S35°) (Ancona Lopez 1965; Tommasi 1966, 1969a,b, 1970a,b, 1971, 1974, 2004; Tommasi & Lima-Verde 1970; Tommasi & Oliveira 1976; Carrera-Rodríguez & Tommasi

1977; Freire & Grohmann 1989; Mooi 1990a,b; Borges *et al.* 2002; Netto *et al.* 2005; Borges 2006; Borges & Amaral 2006; Martínez 2009; Barboza *et al.* 2010; Borges & Campos 2011; Tâmega *et al.* 2013; Gondim *et al.* 2014, 2015); **ANG** – Angola (from ≈S6° south to ≈S17°) (Cherbonnier 1959b; Thandar *et al.* 2010, 2013; Glück *et al.* 2012); **FAR** — Faroe Islands (Klitgaard 1995; Sneli 1999; Tyler *et al.* 2005); **AZO** — Azores (Madeira *et al. Submitted*); **LUS** — Lusitanian seamounts (a chain of seamounts located between Portugal and Madeira), including Gorringe, Josephine, Ampère, Seine seamounts (Pérès 1964); **MAD** — Madeira, Porto Santo and Desertas Islands (Augier 1985; Jesus & Abreu 1998; Bianchi *et al.* 1998; Alves *et al.* 2001; Wirtz 2001, 2006); **SEL** — Selvagens Islands (Pérez-Ruzafa *et al.* 2002); **CAN** — Canary Islands (Moreno-Batet & Bacallado 1980; Bacallado *et al.* 1985; Pérez-Ruzafa *et al.* 1992a,b, 2003; Bianchi *et al.* 2000; Garrido *et al.* 2004; Tuya *et al*. 2007; Hernández *et al.* 2013; Riera *et al.* 2013; Gonzales-Irusta *et al.* 2015); **CAP** — Cabo Verde archipelago (Pérez-Ruzafa *et al.* 1999; Entrambasaguas 2008); **BER** — Bermuda Island (including Challenger Bank) (Clark 1922, 1942); **STP** — Saint Paul and Saint Peter rocks (Edwards & Ubboc 1983; Barboza *et al.* 2015); **ASC** — Ascension Island (Pawson 1978; Brown *et al.* 2016); **STH** — Saint Helena Island (Gislén 1933; Mortensen 1933b; Colman 1946); **TRI** — Trindade & Martin Vaz islands (Krau 1952; Bernasconi 1955; Brito 1971; Guille & Albuquerque 1990; Albuquerque & Guille 1991; Ventura *et al.* 2006, 2007); **TCU** — Tristan da Cunha, Nightingale, Inaccessible and Gough islands (Mortensen 1941).

Historical cruise reports using the 'Paris Meridian' system (*e.g.,* Koehler 1906) were converted to the Greenwich meridian system, by adding or subtracting 2° 20′ 14″ to a station's east and west coordinates, respectively. Latitudinal values were presented in a decimal degree notation and pertain to the geographic midpoint in each selected area. For interpretation purposes, the negative latitudinal values of South Atlantic areas were ignored. Sea surface temperatures (SSTs) were obtained from the World Ocean Atlas 2013 version 2 (Locarnini *et al*., 2013), and correspond to the annual mean temperature at the geographic mid-point for each area.

Bathymetrical zonation

The applied bathymetric zonation considers shallow species (those living between the intertidal and 50 m depth) and deeper shelf species (those usually living from 50 m down to 200 m depth). The choice of the threshold at 50 m depth is related with the following reasons: (1) algal species which many shallow-water echinoderms rely on as food or habitat are rare below 50 m depth; (2) direct sampling by scuba-diving is more frequent in waters less than 50 m depth; (3) in deeper waters data collection is usually obtained via indirect methodologies (*e.g.,* grabs, trawls, dredges). The maximum depth limit of 200 m is based on the average continental shelf maximum depth (Gage & Tyler 1991).

Modes of larval development and asexual reproduction

The developmental mode as a measure of potential for larval dispersion is often considered a major determinant of geographical range (Emlet 1995; Scheltema 1986). Echinoderms show a rather diverse spectrum of larval development patterns within and between classes (for a review, see McEdward & Miner 2001). Therefore, there is always the danger that the application of a system based on few categories to answer complex questions on dispersion may reduce the possibility to assess the true dispersal potential (but see Jablonski & Lutz 1983). Nonetheless, we have chosen a classification that categorizes larval duration and habitat as follows: planktotrophic (with a free-swimming feeding stage), lecithotrophic (with a free-swimming non-feeding stage) and aplanktonic development sensu Pechenik (1999). The latter category gathers all the modes of larval development in which juveniles are released directly into the adult habitat, whether their development is demersal, viviparous, or brooded by adults. The adopted classification system focuses on timing and location of pre-juvenile development rather than morphological differences. Data on reproduction and modes of larval development was based on the following references: Mortensen (1913, 1921); Fell (1945); Schoener (1972); Domanski (1984); Guillou & Diop (1988); Balser *et al.* 1993; McClintock *et al.* (1993); Vernon *et al.* (1993); O'Loughlin (1994); Pearse (1994); Emlet (1995); Hamel & Mercier (1995); Kasyanov *et al.* (1998); Young & George (2000); McEdward & Miner (2001); Carvalho & Ventura (2002); Eléaume *et al.* (2003); Young (2003); Cisternas *et al.* (2004); Stöhr (2005); Haesaerts *et al.* (2006); Reitzel & Heyland (2007); Metaxas *et al.* (2008); Schipper *et al.* (2008); Baillon *et al.* (2011); Contins & Ventura (2011); Navarro *et al.* (2012); Young *et* *al.* (2012); Micael *et al.* (2014); Domínguez-Godino *et al.* (2015); Lopes & Ventura (2016).

Most echinoderms are gonochoric broadcast spawners, *i.e*., one (male) or both sexes shed their gametes into the water column (Harvey 1956). The proportion of released eggs that become zygotes is dependent on the probability of sperm encountering and fertilizing eggs (Levitan & Young 1995). Such reproductive success is dependent on the density of spawning individuals in the population (mating limitation or Allee effect; Allee 1931), an effect that limits population growth in low density areas, such as newly settled, resource-poor, or high mortality habitats (Tilquin & Kokko 2016). Some echinoderms may reproduce asexually by fragmentation (fission, paratomy, autotomy, or budding), amictic parthenogenesis, and polyembryony (Mladenov 1996). Some hermaphrodite echinoderms are also capable of reproducing through self-fertilization (‘selfing’), which is a form of sexual reproduction since it involves merging of two gametes from the same individual (autogamy). As it does not require the presence of a mate, it thus can be viewed as a form of asexual reproductive strategy in an otherwise typical gonochoristic group. Therefore, it is grouped herein together with fragmentation, as another extreme form of direct recruitment (and inbreeding). Data on asexual reproduction in echinoderms was largely based on Mladenov (1996), but also on the following references: Strathmann *et al.* (1984); Hendler & Littman (1986); Mlandenov & Emson 1988; Mckenzie 1991; Hendler 1995; Baker *et al.* 2001; O’Loughlin & Waters 2004; Stöhr & Segonzac 2005; Barbosa *et al.* 2012; Dolmatov 2014. Knowledge on cloning during the larval stage is still largely restricted to laboratory experiments and was not included in the present analysis.

Inclusion of asexual reproduction as an analytical category allows assessment of Baker’s law (Baker 1955, 1967; Pannell *et al*. 2015), which predicts that long-distance dispersal is biased towards colonists capable of establishing a population from a single individual after a rare chance colonization event.

Habitat

Rafting by juvenile and adult stages also has been suggested as alternative mechanism of long-distance dispersal (Thiel & Haye 2006). Dispersion potential by rafting is influenced by life habit and preferred substrate, with rafting being much more likely in epibenthic species in comparison with species living within the sediment (Scheltema 1986). Species were classified according to the type of substrate which they inhabit, *i.e.*, soft, hard or both substrates. Additionally, data on burrowing and association with other organisms (colonial coral, sponges, algal and sea grass communities) also was compiled from the literature. The following additional references were also used: Danielssen & Koren (1881); Rathbun (1886); Clark (1907b, 1921); Rochette *et al.* (1994); Tzetlin *et al.* (1997); Bluhm *et al.* (1998); Rogers (1999); Denisenko *et al.* (2003); Laguarda-Figueras *et al.* (2001); Buhl-Mortensen & Mortensen (2005); Manso *et al.* (2008); Lima & Fernandes (2009); Fredriksen *et al.* (2010); Gukov (2011); Stevenson & Rocha (2012).

Parsimony Analysis of Endemicity (PAE)

A Parsimony analysis of endemicity (PAE) was applied to the area vs. taxa matrices (≤50 and ≤200 m). LUS was excluded from the ≤50 m analysis, as most of its area is well below this depth. TCU was also excluded from both analyses as this southern archipelago falls outside the latitudinal limits of the present analysis. Unique taxa (restricted endemics, autapomorphies) were removed prior to the PAE analysis (Rosen & Smith, 1988). One outgroup with an all-0 score was added to allow topologies to be rooted (Watrous & Wheeler 1981; Morrone 1994). Tree reconstruction was based on the heuristic search algorithm in PAUP* (version 4.0a; Swofford 2002) including 100,000 random stepwise-addition sequence replicates with tree-bisection-reconnection (TBR) and MULTREES on, and Acctran optimization in effect, but restricting the number of optimal trees per replicate to one. Strict consensus trees were generated and bootstrap resampling was applied to assess support for individual nodes using 100,000 bootstrap replicates with 100 random additions per replicate (again with TBR and MULTREES enabled).

Biotic similarities between areas: Probable Directions of Faunal Flows

The analysis of the historical relationships between the selected areas was complemented by using the following formulas (X_A and X_B) for each pair of areas (A and B) (Almada *et al.* 2001):

X_A = species present in areas A and B/ species present in area A

X_B = species present in areas A and B/ species present in area B

When faunal exchange happened in historical times, from a source area to the target area, we expect the target area to show a subset of the species present in the source area. So, different values of the two indices (XA and XB) are expected, and the source area will show the smaller value (Almada *et al*., 2001). TCU was also excluded from the analysis as this southern archipelago falls well outside the latitudinal limits of the present analysis.

7.3. Results

A total of 1,444 species of echinoderms are presently recorded from the intertidal down to the abyssal depths in the Mediterranean Sea and the North and Central Atlantic Ocean (as far south as Uruguay (*c*. 35°S) in the West, and to Angola (*c*. 17° S) in the East). Of these, 891 are shelf species that occur at depths between the intertidal and 200 m, accounting for 13% of the 6,999 world's total (Table 7.1). From a total of 341 genera, 200 genera were represented by single species in the analysed regions. In total, 779 species and 91 genera are restricted to the analysed area. The Ophiuroidea was the most diverse class with 318 species (36%), followed by the Holothuroidea with 219 species (25%), Asteroidea with 186 species (21%), and 126 Echinoidea species (14%) (Table 7.1). The least diversified class was the Crinoidea, with 42 species, corresponding roughly to 5% of all analysed species. The most diverse genus was *Amphiura* Forbes, 1843 (Ophiuroidea) with 39 species, followed by *Astropecten* Gray, 1840 (Asteroidea) and *Holothuria* Linnaeus, 1767 (Holothuroidea) with 29 and 27 species, respectively.

Geographical distribution

Tropical waters were by far the most diverse areas (TRO: 483 species; CAF: 167; CRL: 166) (Table 4.2 MED (142) presented intermediate levels of biodiversity between the two adjacent Atlantic regions, IBE (153) and WAF (126). ART (66) was the least diverse continental region, followed by ANG (68). Among the oceanic archipelagos, CAN (85) had the highest biodiversity, followed by CAP (76). Among insular systems, the least diverse areas were SEL (18) and STP (11) (Table 7.2).

Table 7.1. Number of echinoderm species per class globally and in the studied area, including the number of endemic species in each bathymetrical range, and the number of species with depth ranges broader than 200 m and 500 m. Global echinoderm diversity adapted from Pawson (2007), Appeltans *et al*. (2012), Mah & Blake (2012), Stöhr *et al.* (2012) and Kroh & Mooi 2018. Depth ranges were calculated as the difference between the maximum reported depth of occurrence of a given species and its minimum reported depth.

	Global	Total (studied area) (≤50 m)	Total (studied area) (≤200 m)	Endemic (≤50 m)	Endemic (≤200 m)	Eurybathic (>200 m)	Eurybathic (>500 m)
Crinoidea	623	24	42	11	23	30	19
Asteroidea	1,900	133	186	32	51	106	71
Ophiuroidea	2,064	210	318	74	128	167	106
Echinoidea	1,012	97	126	22	36	76	43
Holothuroidea	1,400	191	219	85	103	52	34
Total	6,999	655	891	224	341	431	273

The ART waters differed from the general pattern by presenting the highest proportion of asteroids (31 spp.; 47%) and the lowest proportion of echinoids (3 spp.; 5%) (Fig. 7.2). The relative representation of echinoderm classes in all other areas mirrored somewhat the general pattern, *i.e*., the Ophiuroidea was generally the most diverse group and the Crinoidea the least. Among zones with continental waters (excluding ART), holothurians had a lower representation in the West Atlantic shores (18%) when compared with the East Atlantic (31%) and the Mediterranean Sea (35%). The class Holothuroidea was exceptionally diverse in CAF (53 species) and MED (50 species), surpassing the globally most specious group, the ophiuroids (50 and 34 species, respectively). Oceanic areas presented higher proportions of asteroids (29%) and echinoids (19%), but fewer holothurians (14%) and crinoids (3%) than continental waters (20%, 14%, 25%, and 5% respectively) (Fig. 7.2). Oceanic areas also presented a lower proportion of irregular echinoids (46%) in comparison with continental areas (60%).

Comparing both sides of the continental Atlantic coasts (excluding ART), the western shores proved to be more diverse, with a total of 605 species, in contrast to 359 species in the east. The only echinoderm class to have a higher diversity in the East Atlantic was the Holothuroidea, with 112 species, surpassing only by 5 species the

Table 7.2. Number of echinoderm species per area in each bathymetrical range (≤50 m and ≤200 m), including endemic species (in brackets, the number of species known only from the type material).

Area	Total species (≤50 m)	Total species ≤200m	Endemic species (≤50 m)	Endemic species (≤200 m)
MED	126	142	22	26(4)
ART	54	66	2	4
SCA	101	129	0	0
ICE	64	89	0	0
GRE	61	85	4	5(4)
BRI	103	141	2	3
IBE	112	153	0	2(1)
WAF	98	126	4	4(2)
CAF	149	167	42	50(27)
NSC	62	93	3	7(4)
VIR	57	85	0	1(1)
CRL	131	166	0	0
TRO	339	483	125	210(43)
ANG	61	68	4	4(4)
BRA	120	143	9	13(5)
FAR	67	98	0	0
AZO	42	64	0	0
LUS	18	28	0	0
MAD	59	69	0	0
SEL	18	18	0	0
CAN	73	85	0	0
CAP	64	76	0	1(1)
BER	55	64	1	2(1)
STP	11	11	0	0
ASC	22	25	0	0
STH	27	31	3	3(2)
TRI	38	39	1	1(1)
TCU	10	19	2	5(4)
Total	655	891	224	341(104)

West Atlantic (Fig. 7.2). A total of 135 amphi-Atlantic species, *i.e*. known to both sides of the Atlantic Ocean, were found in continental areas (Fig. 7.3). In the oceanic areas, 69 and 99 species have respectively an exclusive western or eastern geographical distribution. An additional 32 species presented an exclusive oceanic distribution and 106 were Amphi-Atlantic (Fig. 7.3).

Overall, species exhibited more restricted geographical distributions towards the lower latitude continental shores. For example, the proportion of species with a distribution limited to three areas or less (*i.e*. to one area plus two adjacent) when compared with those present in more than 3 areas ranges from 6:1 in TRO and 1:3 in

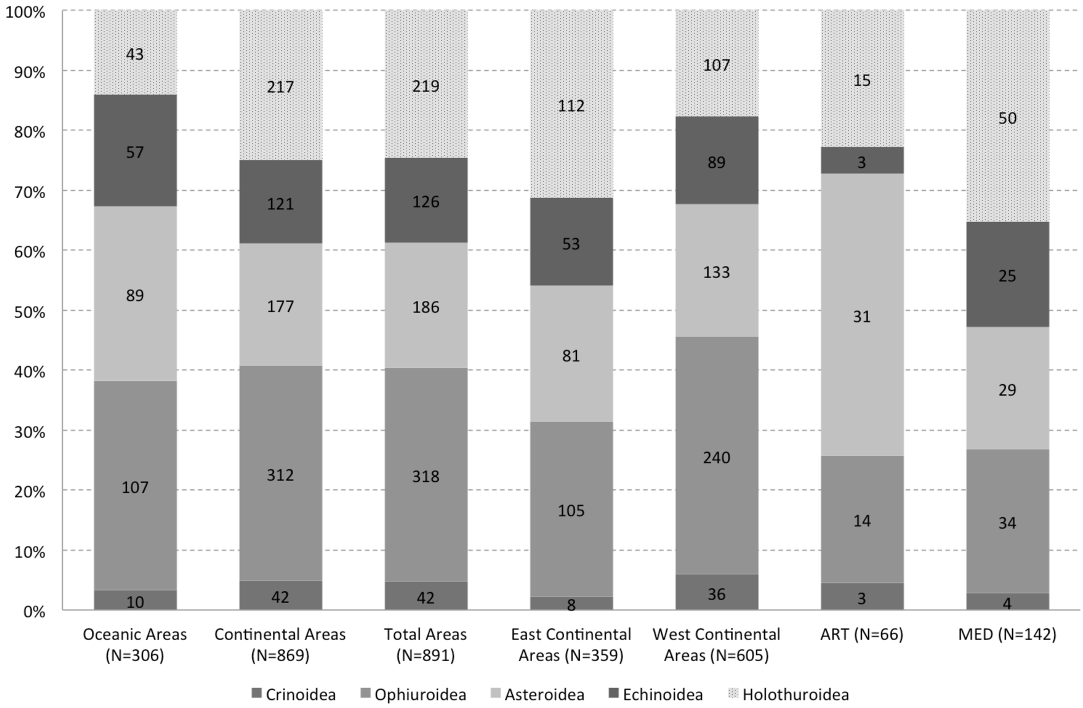


Figure 7.2. Number of echinoderm species per class in each group of studied areas in the Atlantic Ocean and the Mediterranean Sea.

the ART. The relation between species' geographical range and latitude was slightly stronger when the southern areas (BRA & ANG) were excluded (Fig. 7.4). The observed pattern persisted even after the removal of the endemics, with TRO still presenting higher values (2:1) than ART (1:4).

Oceanic shores revealed a similar latitudinal pattern, though faunas in these systems were characterised on average by species with relatively larger geographical ranges, when compared to continental areas. For example, in the tropical STP this proportion was about 2:1 decreasing to 1:36 in the boreal arctic FAR. Again, the observed pattern was stronger, after the removal of southern islands and archipelagos (ASC, STH, TRI, and TCU). This is best illustrated by TCU, which presented a significant component of its fauna (12 out of 19 species) characterised by species with geographical ranges well beyond the limits of the area analysed by this work.

Endemic species

Among the echinoderms, 341 species were restricted to one of the studied areas, representing 38% of the total species and mostly occurring at depths ≤50 m (224 species; Table 7.2). Tropical latitudes had most endemics, with TRO waters having

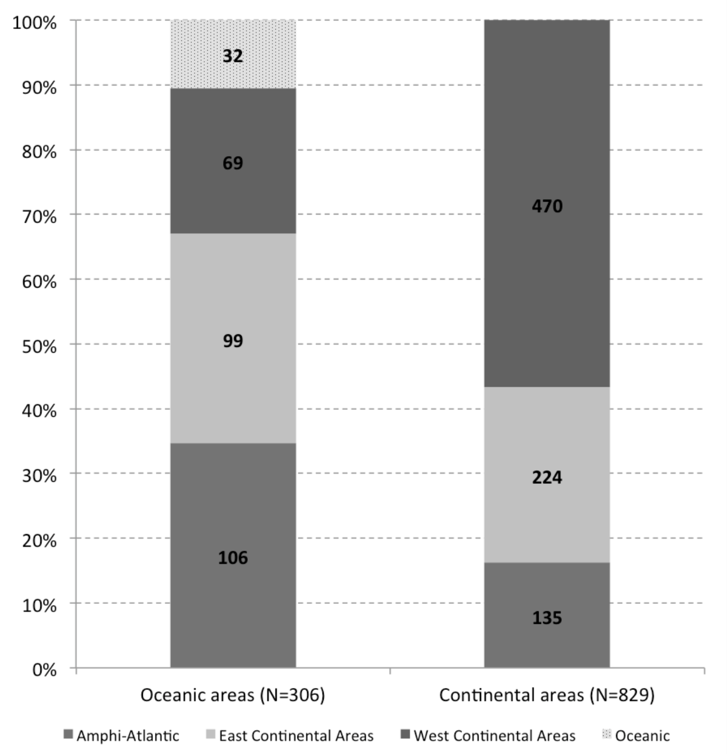


Figure 7.3. Number of echinoderm species according to their distributional range in oceanic and continental shores of the Atlantic Ocean. ART excluded from this analysis.

210 species, followed by the CAF with 50 species, representing respectively 44% and 30% of the total fauna in each area. MED and BRA waters included 26 (18%) and 13 (9%) endemic species, respectively (Table 7.2). Continental waters harboured relatively few endemics reaching a maximum of 7 species in NSC (*c*. 8%). Arctic waters had just 4 endemic species (6%). Among the islands, endemism was generally absent, with the exception of TCU (5 endemic species; 26%) followed by STH (3; 10%), BER (2; 3%) and CAP with just one (1%) (Table 7.2).

Ophiuroidea was the class with most endemic species (128; 40% of all ophiuroid species), followed by the Holothuroidea (103; 47% of all holothuroid species) (Table 7.2). The best-represented classes among the areas of highest endemism were the ophiuroids in TRO (103 endemic species), and the holothurians in CAF (37) and MED (12). The asteroids exhibited intermediate levels of endemism with 51 species (27% of all asteroids). Crinoidea included the least absolute number of endemic species (23), yet the highest proportion of endemics per class (55%). Finally, Echinoidea had 36 endemic species (29%), 27 of which were irregular echinoids (Table 7.2).

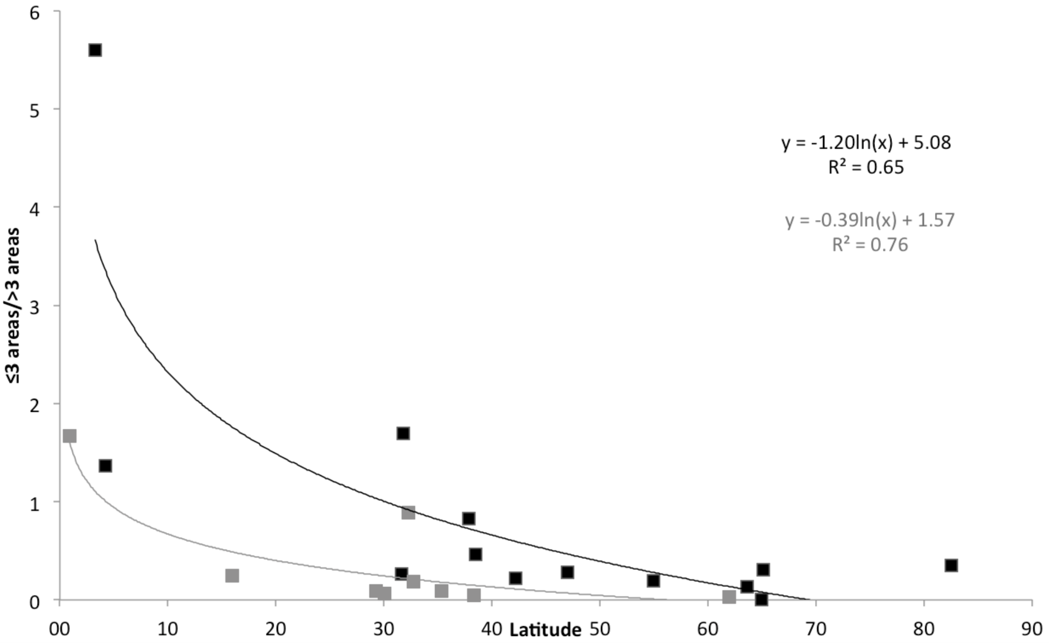


Figure 7.4. Relation between the ratio of narrow and wide range equinoderm species and average latitude. The vertical axe depicts the relation between the number of echinoderm species with narrow geographical distribution (restricted to ≤3 areas) and the number of species with wide geographical distribution (occurring in >3 areas), in continental (black squares) and oceanic (grey squares) areas, as a function of their average latitudes in the North Atlantic Ocean and the Mediterranean Sea (black and grey correlation values restricted to continental and oceanic areas, respectively; for explanation see text). Southern Atlantic areas (BRA, ANG, TCU, ASC, STH and TRI) were excluded from this analysis.

Bathymetric zonation

Although most echinoderms in the study area (655 species; 74%), were reported from shallow shelf waters (≤50 m depth), almost half of the species could be considered as eurybathic, as their vertical ranges surpass 200 m (431 species) and almost a third surpasses 500 m (Table 7.2). This is particularly evident in the crinoids, 30 species (71%) of which exhibit bathymetrical ranges above 200 m. On the other side of the spectrum, holothurians were the only group to have less than a quarter of species (24%) with depth ranges exceeding 200 m. Towards lower latitudes, we observed narrower bathymetric ranges than at high latitudes (Fig. 7.5). In ART waters, only four out of 66 species show narrow bathymetric ranges (≤200 m). In contrast, the proportion between species with narrow and wide bathymetric ranges in TRO is almost equal to one (233 to 250 species) and in CAF is almost double (109 to 58). This pattern is also visible among the islands. The tropical CAP, STH, and ASC islands have almost the same proportion of species, a situation that contrasts with the boreal-arctic

FAR where the number of species with depth ranges narrower than 200 m is 4 out of 98. Only the small islands of SEL (2:1), STP (1:3), and the LUS seamounts (1:13) did not follow this pattern. The latitudinal gradient was stronger when only continental shores were considered (Fig. 7.5A), as oceanic echinoderm faunas are characterised by species with wider bathymetric ranges. Indeed, 195 species (64%) from these faunas presented depth ranges wider than 200 m. This contrasted with the values found on the continental shores, where the proportion between wide and narrow-bathymetric ranges was almost equal (427:442).

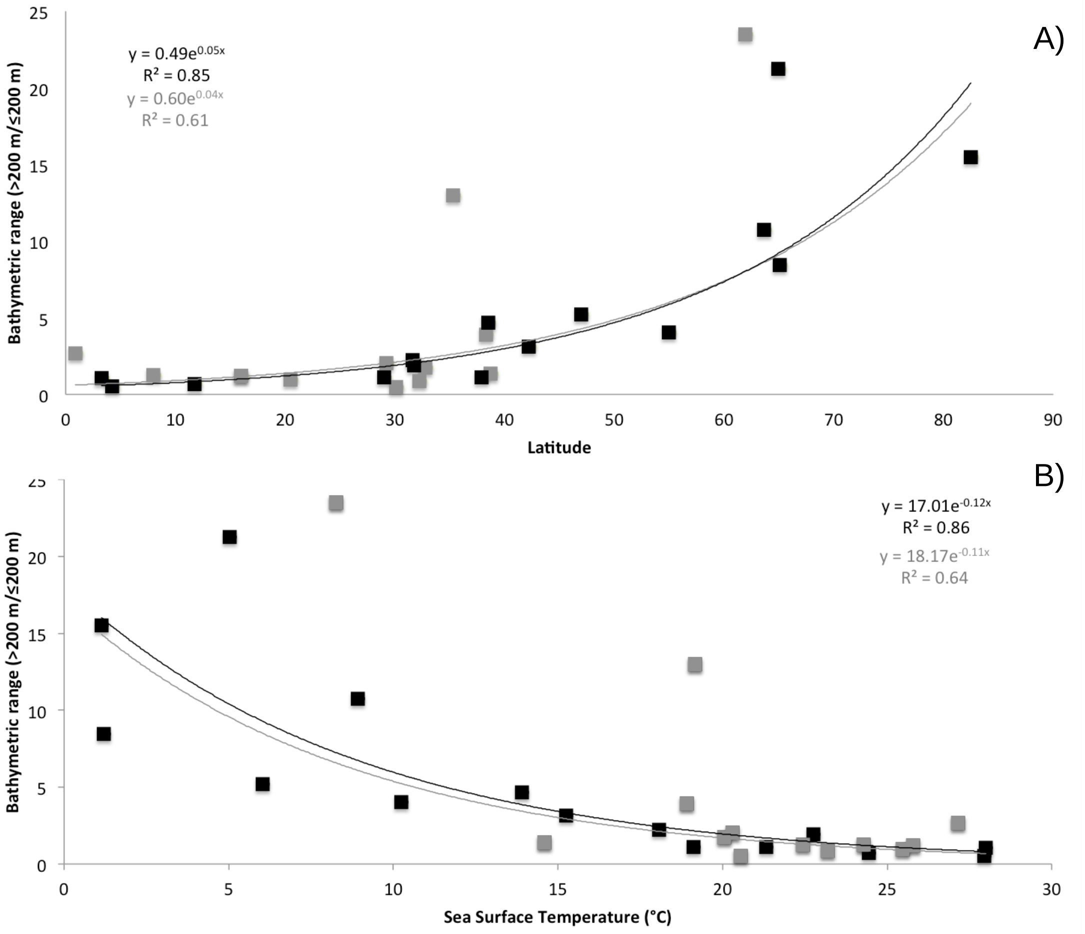


Figure 7.5. Relation between the ratio of >200 m and ≤200 m deep and latitude (A) and sea surfasse temperature (B).The vertical axe depicts the proportion between echinoderm species with wide (>200 m) and narrow (≤200 m) bathymetrical ranges according to latitude (A) and sea surface temperatures (B) for continental (black squares) and oceanic areas (grey squares) (grey correlation values pertain all areas; black correlation values restricted to continental areas).

Table 7.3. Larval development modes and asexual reproduction in echinoderm classes.

	Crinoidea	Ophiuroidea	Asteroidea	Echinoidea	Holothuroidea	Total
Aplanktonic	2	22	14	2	7	47
Lecithotrophic	7	28	21	4	11	71
Planktotrophic	0	24	20	62	13	119
Asexual	0	15	9	0	7	31

Modes of larval development and asexual reproduction

Information on larval development was available for only 237 echinoderm species (27% of the total species). The most common larval development was planktotrophic, representing half of the species (119), followed by lecithotrophic (71), and aplanktonic (47) (Table 7.3). Crinoidea was the only class with no species producing planktotrophic larvae. In this echinoderm group, information was available for 9 species only, in which the lecithotrophic (non-feeding planktonic) development was dominant (7 species). Ophiuroidea and Asteroidea show similar composition of developmental modes, with lecithotrophic larvae being most common (28 [38%] and 21 species [38%], respectively). Among the echinoids and holothurians, planktotrophic development was the preferred mode of development, but at considerable different proportions, with respectively 91% (62 species) and 42% (13 species) (Table 7.3).

No clear pattern was found between different depth zones and the modes of larval development, with planktotrophic species dominating all faunas from 0 to 200 m. Likewise there was no correlation between larval development and substrate type among the analysed species.

Aplanktonic development was most common only among species associated with shallow-water hard substrata (0-2 m), which, however, may be an effect of the small sample size (n=16) for these habitats (Table 7.4). Wide spatial distribution was correlated with planktotrophic development in the study area (Fig. 7.6). From a total of 31 endemic species with known mode of larval development, 10 present aplanktonic development and the remaining were planktonic (9 lecithotrophic and 12 planktotrophic). On the other side of the spectrum, from a total of 9 species known to 11 or more areas, 7 presented a planktotrophic mode of development and the remaining were aplanktonic (Fig. 7.6).

In all studied areas (Table 7.5), planktonic development (*i.e.* lecithotrophic + planktotrophic) was the most frequent mode of larval development, except for TCU

Table 7.4. Development modes in echinoderm species according with substrate and minimum known depth.

	Sediment (N=101)		Hard (N=24)		Both (N=108)	
	≤2 m (N=39)	>2 m (N=62)	≤2 m (N=16)	>2 m (N=8)	≤2 m (N=79)	>2 m (N=29)
Aplanktonic (N=44)	9	10	7	1	9	8
Lecithotrophic (N=74)	8	21	4	2	25	10
Planktotrophic (N=123)	22	31	5	5	45	11

with 4 species with aplanktonic development, followed by the remaining 2 species with planktotrophic development (N=6 species). For planktonic species, the proportion of lecithotrophic mode of development in relation to planktotrophs increased towards higher latitude areas (Fig. 7.7).

Aplanktonic development also increased with latitude, but this pattern only became significant if restricted to northern continental areas (*i.e*. excluding BRA & ANG) (Fig. 7.8). For example, ART (N=37) harbours 51% and 30% of the species with lecithotrophic and aplanktonic developments, respectively, whereas in TRO (N=121), these proportions decrease to 30% and 16%, respectively (Table 7.5). In oceanic areas, planktotrophic development was more common than in continental ones, representing 79 (54%) out of 146 species.

Asexual development was only found in ophiuroids (15 spp.), asteroids (9 species) and holothurioids (7 spp.) (Table 7.3). Most of these species were reported from the first few meters (63%) decreasing to just 4 species at depths >50 m. Asexual reproduction did not appear to be particularly related with substrate type (Table 7.4) or geographical range, with 67% of species occurring in three or less areas, including 4 endemic species. On the other hand, the fissiparous sea star *Coscinasterias tenuispina* (Lamarck, 1816) is one of the two species known to occur in more than 13 areas.

Among species known to occur outside the study area, the cosmopolitan *Amphipholis squamata* (Delle Chiaje, 1828) was the only species to be recorded in more than 17 areas, and is also known to reproduce through self-fertilization. The incidence of asexual reproduction was higher in tropical areas, with higher number of species in TRO (17) and BER (11). Moreover, and in spite of its rare occurrence (31 from a total of 891 species), the incidence of asexual reproducing species in small

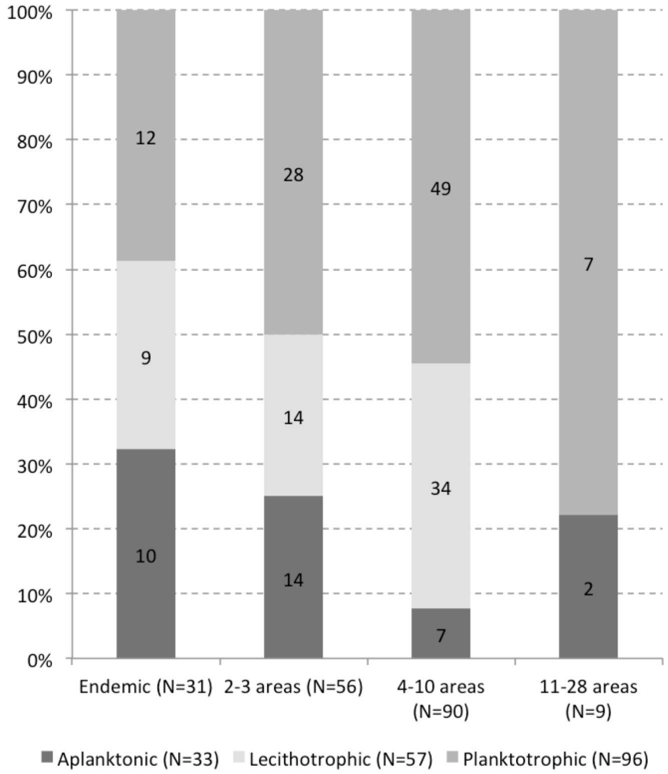


Figure 7.6. Relation between echinoderm species' geographical ranges (endemic (*i.e.*, restricted to 1 area), 2–3 areas, 4–10 areas and 11–28 areas) and modes of development (aplanktonic, lecithotrophic and planktotrophic species).

islands is particularly high, summing up 19 species. For example, in STP, 4 out of 10 species are known to reproduce asexually (Table 7.5).

In both continental and insular areas, there is an increase in the ratio of aplanktonic/asexual reproduction towards lower latitudes (Fig. 7.9A), and at mid-latitudes both modes tend to approach similar numbers. The relation between aplanktonic development and asexual reproduction is particularly strong when plotted against sea surface temperatures and if southern areas are excluded (ANG, BRA, ASC, STH, TRI, and TCU) (Fig. 7.9B).

Habitat

Information related to species habitat was available for 824 echinoderms (Fig. 7.10). In addition to substrate type, 107 species were classified as infaunal, 275 associated with sessile animals (*e.g.,* sponges, corals), 121 with sea grass beds, and 135 with macro-algae. Sediment-associated species dominated all depths. Proportions of substrate type favoured by echinoids (regular + irregular) was similar as in holothurioids. Within echinoids, however, proportions were very different, with irregular echinoids almost exclusively associated with soft substrate, while the regular echinoids showed no particular preference for either hard or soft substrata (Fig. 7.10). Widespread species are less selective in terms of preferred substrate type than less widespread and endemic ones (Fig. 7.11).

Table 7.5. Modes of larval development and asexual reproduction in echinoderm species per area, latitude and mean annual sea-surface temperatures.

			Development Mode			
	Latitude	SST (°C)	Aplanktonic	Lecithotrophic	Planktotrophic	Asexual
MED	37,8693	19,1	8	13	40	8
ART	82,5000	1,1	11	19	7	4
SCA	63,6173	8,9	13	28	37	6
ICE	64,9417	5,0	12	25	25	6
GRE	65,0900	1,2	12	24	10	4
BRI	54,9762	10,3	12	32	40	7
IBE	42,2193	15,2	7	23	45	5
WAF	31,6131	18,1	7	15	33	6
CAF	4,2296	27,9	4	10	28	4
NSC	46,9941	6,0	13	26	14	3
VIR	38,5000	13,9	5	15	21	2
CRL	31,7500	22,8	8	19	39	9
TRO	3,2500	28,0	19	36	66	17
ANG	(-)11,7608	24,4	2	3	12	3
BRA	(-)29,0000	21,3	9	11	25	6
FAR	61,9220	8,3	11	25	27	2
AZO	38,3188	18,9	4	10	22	3
LUS	35,3062	19,2	2	0	10	1
MAD	32,7522	20,1	4	4	28	6
SEL	30,0817	20,6	1	3	9	2
CAN	29,2327	20,3	6	10	32	6
CAP	15,9591	24,3	2	8	23	8
BER	32,256178	23,2	6	5	24	11
STP	0,9000	27,2	1	0	5	4
ASC	(-)7,9873	22,4	1	0	11	3
STH	(-)15,9570	25,8	3	2	7	5
TRI	(-)20,5000	25,5	3	4	15	2
TCU	(-)38,7105	14,6	4	0	2	4
Total			47	71	119	31

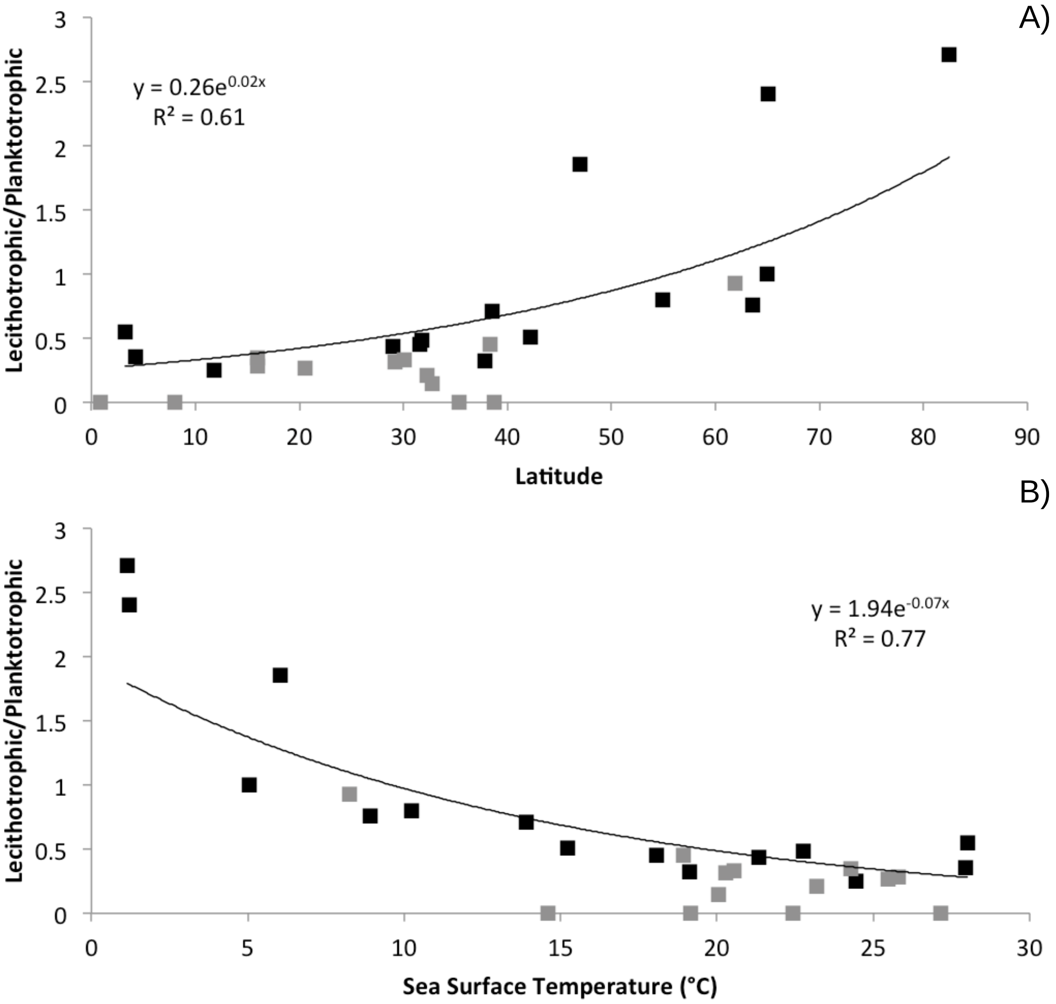


Figure 7.7. Relation between echinoderm modes of larval development and (A) latitude; and (B) sea-surface temperature. The vertical axe depicts the proportion between echinoderm species with lecithotrophic and planktotrophic larval development in continental (black squares) and oceanic (grey squares) areas, as a function of their average latitudes (A) and sea-surface temperatures (B) in the Atlantic Ocean and the Mediterranean Sea.

Biotic similarities between areas: Parsimony Analysis of Endemicity

The For PAE analysis, endemic species and species restricted to a single region in the study were excluded, leading to a distribution matrix of 412 species occurring in depths ≤50 m, and 517 species occurring in depths ≤200 m.

Analysis of the shallow shelf echinoderms (≤50 m) resulted in eleven most parsimonious cladograms, the strict consensus of which (L = 966, CI = 0.427, RI = 0.616) displays three main area groups (Fig. 7.12): (1) the Eastern Atlantic and the Mediterranean group, with a bootstrap value of 85%, which includes Southern European coasts, NE Atlantic archipelagos, and West African coasts; (2) the boreal-arctic North Atlantic group, with a bootstrap value of 96%, which includes northern American and European shores, plus ICE, GRE, and ART; and (3) the tropical West Atlantic group, with a bootstrap value of 54%, which includes the eastern coasts of the Americas from Carolinas to southern Brazil, including the West and Central Atlantic islands.

The PAE analysis on the shelf echinoderms (≤200 m) produced three most parsimonious dendrograms, the strict consensus of which (L = 1293, CI = 0.400, RI = 0.577) included the same main groups as the ≤50 m PAE tree (Fig. 7.12), though with

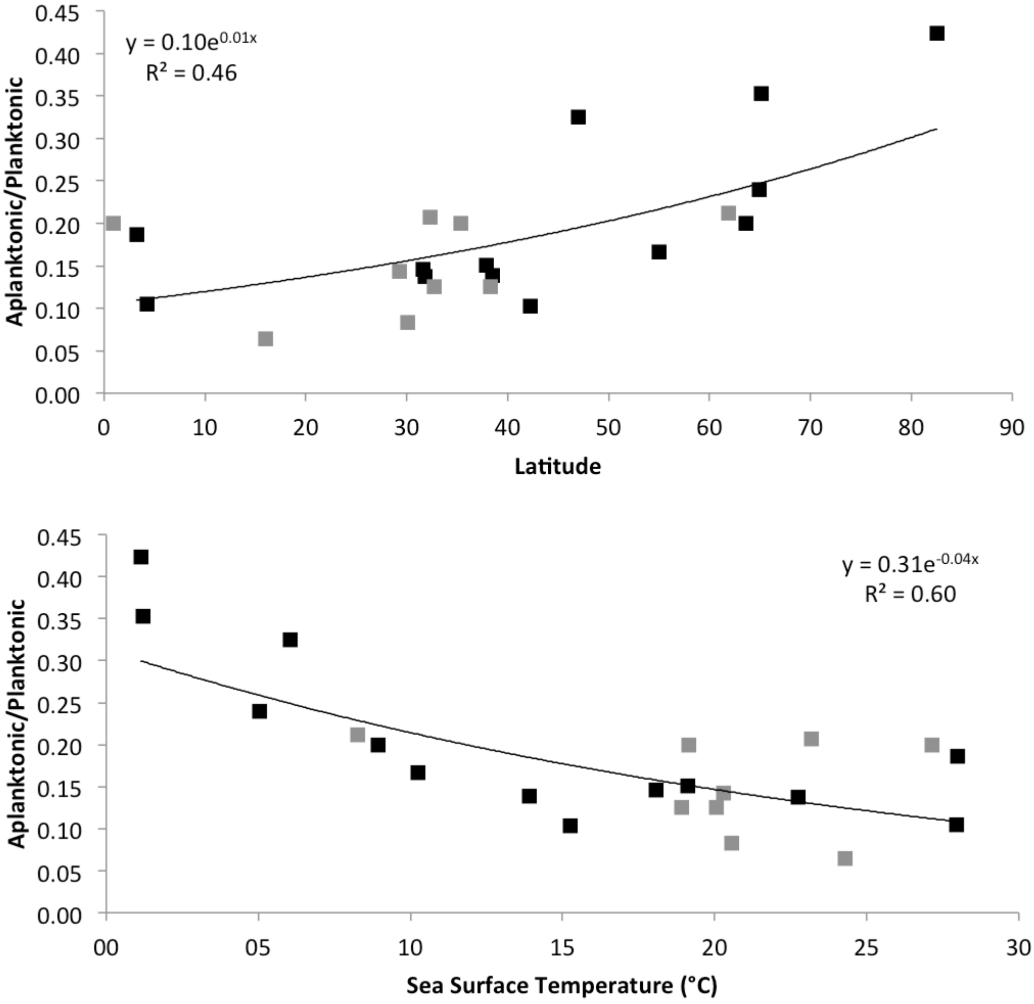


Figure 7.8. Relation between echinoderm modes of larval development and (A) latitude; and (B) sea-surface temperature. The vertical axe depicts the proportion between echinoderm species with aplanktonic and planktonic larval development in continental (black squares) and oceanic (grey squares) areas, as a function of their average latitudes (A) and sea-surface temperatures (B) in the North Atlantic Ocean and the Mediterranean Sea. Southern Atlantic areas (BRA, ANG, TCU, ASC, STH, and TRI) excluded from this analysis.

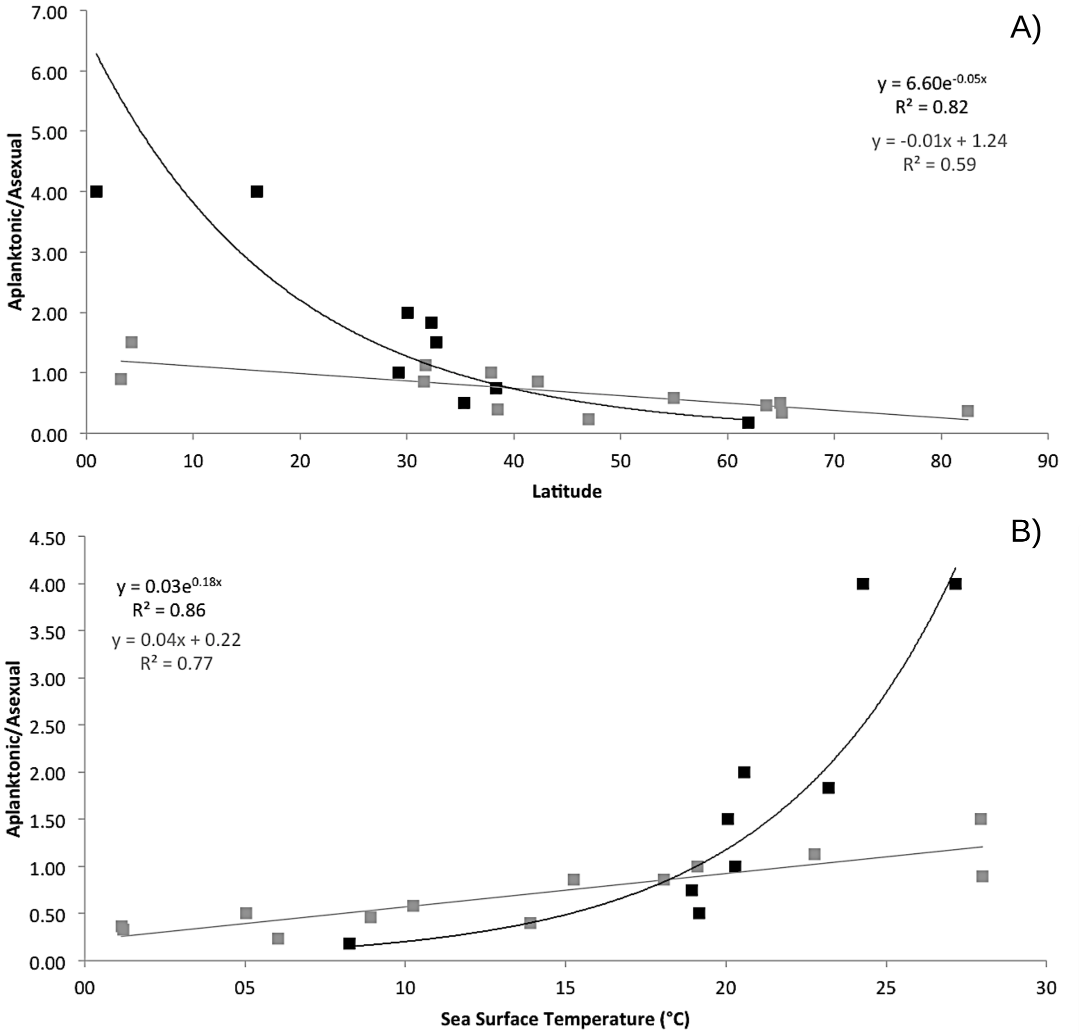


Figure 7.9. Relation between echinoderm modes of larval development and (A) latitude; and (B) sea-surface temperature. The vertical axe depicts the proportion between echinoderm species with aplanktonic larval development and asexual reproduction in continental (black squares) and oceanic (grey squares) areas, as a function of their average latitudes (A) and sea-surface temperatures (B) in the North Atlantic Ocean and the Mediterranean Sea. Southern Atlantic areas (BRA, ANG, TCU, ASC, STH, and TRI) excluded from this analysis.

slightly different bootstrap values (71%, 96%, 63%, respectively).

The main difference from the ≤50 m tree is the inclusion of the Lusitanian seamounts in the East Atlantic Mediterranean group, and a slightly different rooting of AZO, NSC and BER/TRI in, respectively, the East Atlantic Mediterranean, the boreal-arctic North Atlantic group, and the tropical West Atlantic group. As a rule, PAE clustered areas according to their geographical proximity, reflecting higher numbers of shared species in nearby areas.

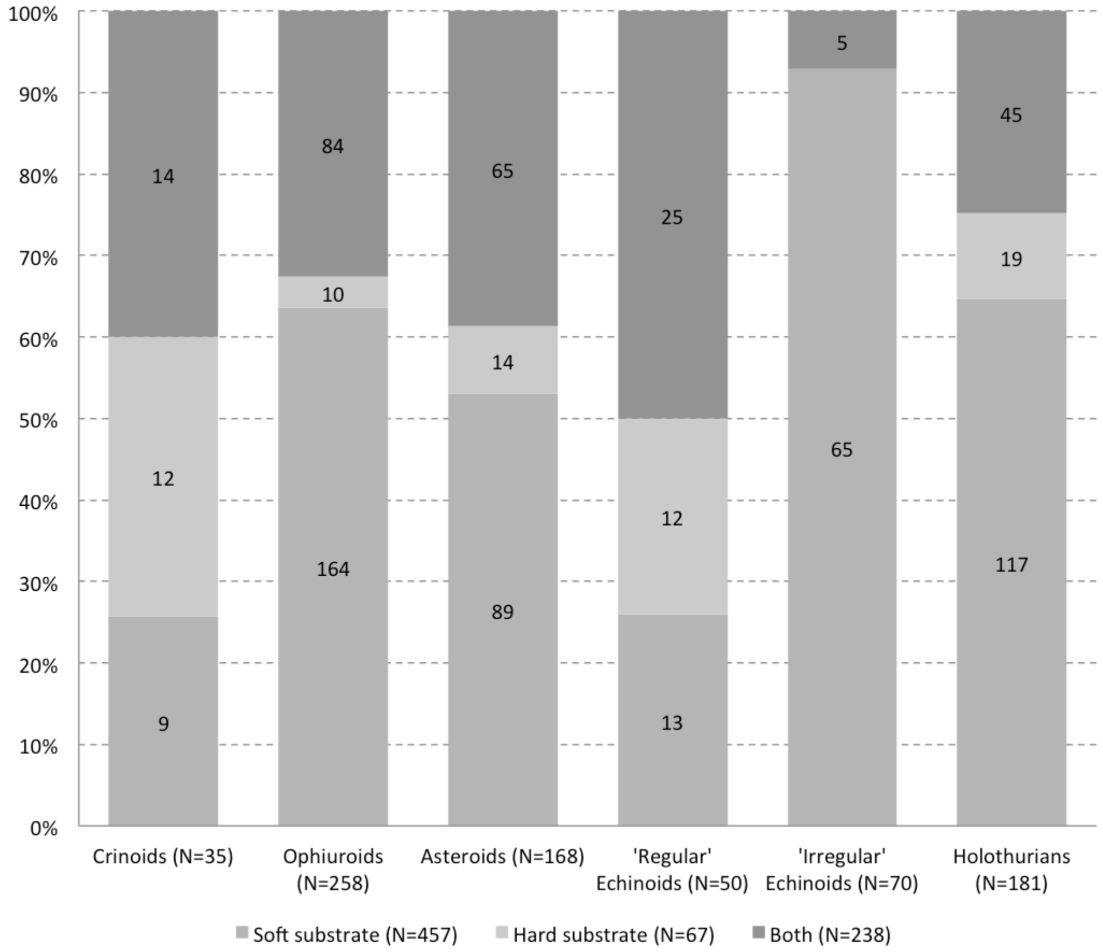


Figure 7.10. Relation between echinoderm groups and type of substrate.

Biotic similarities between Areas: Probable Directions of Faunal Flows

The analysis of the probable directions of faunal flows carried out on the shallow shelf echinoderms dataset (≤50 m, data not shown) yielded no major differences when compared with the results obtained for the total shelf fauna (≤200 m). The latter analysis is summarized in Fig. 7.13 (for shared species, see Supplementary material, Table S7.3), and support the patterns found by PAE analysis. TRO appears as one of the most important source areas in the Atlantic, being the point of origin for many CRL (0.93), BRA (0.79), BER (0.94), TRI (0.95), BER (0.94), TRI (0.95), STP (0.91), and ASC (0.80) echinoderm species. Though to a lesser extent, it also appears to supply VIR and STH coasts. TRO influence is also visible in the NE Atlantic oceanic systems, such as the archipelagos of the Azores (0.42) and Cabo Verde (0.41), as well as the Lusitanian seamounts (0.39). Overall, the West Atlantic echinoderm species have wider longitudinal ranges when compared with the East Atlantic species. There is, however,

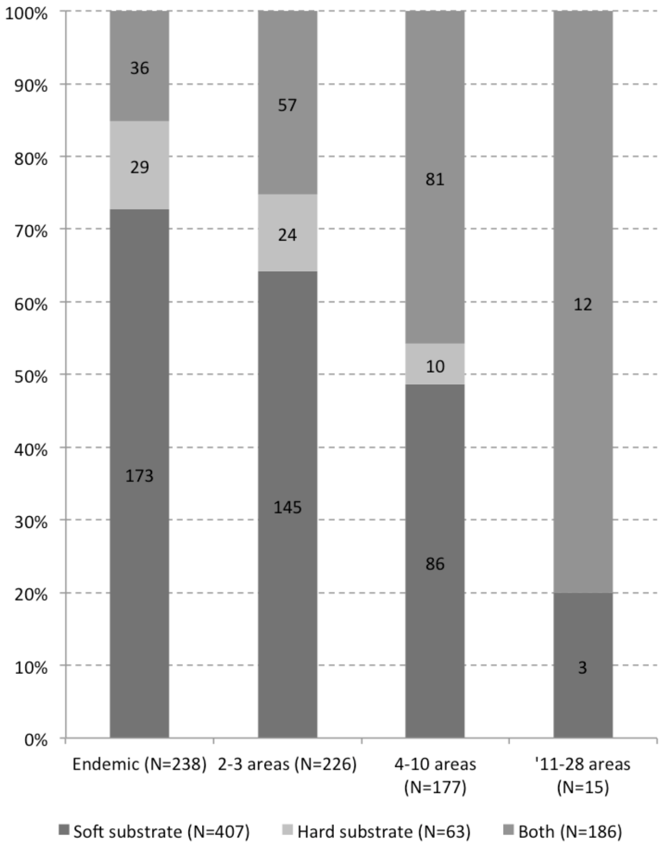


Figure 7.11. Relation between echinoderm geographical range and type of substrate for species with geographical distribution restricted to the studied area in the Atlantic and Mediterranean.

no evidence of a significant trans-Atlantic faunal flow between mid and lower latitude shores (in either direction), in spite of the central oceanic archipelagos being influenced at various levels by the West tropical American shores. TRO eastward flow reaches the West African shores in much reduced manner, with a small west component in the coasts of WAF (0.29), CAF (0.23), and ANG (0.22).

MED, IBE, and WAF coasts emerge as main source areas for the NE Atlantic, supplying the NE archipelagos and seamounts (with the exception of Cabo Verde). IBE fauna is also in close proximity with BRI (XA= 0.72/XB= 0.67), WAF coasts (0.73/0.60), and MED (0.65/0.60), with faunal exchanges favouring the Iberian Peninsula as the source element. CAN appears to play an important role as source area for the remaining NE oceanic systems. The most northwest archipelago of this group of oceanic systems, AZO, appears somewhat detached from the closest shores, though also strongly influenced by the continental coast of IBE (0.81/0.34) and WAF (0.70/0.36) AZO connection with the southern archipelagos of CAN (0.69/0.52) and

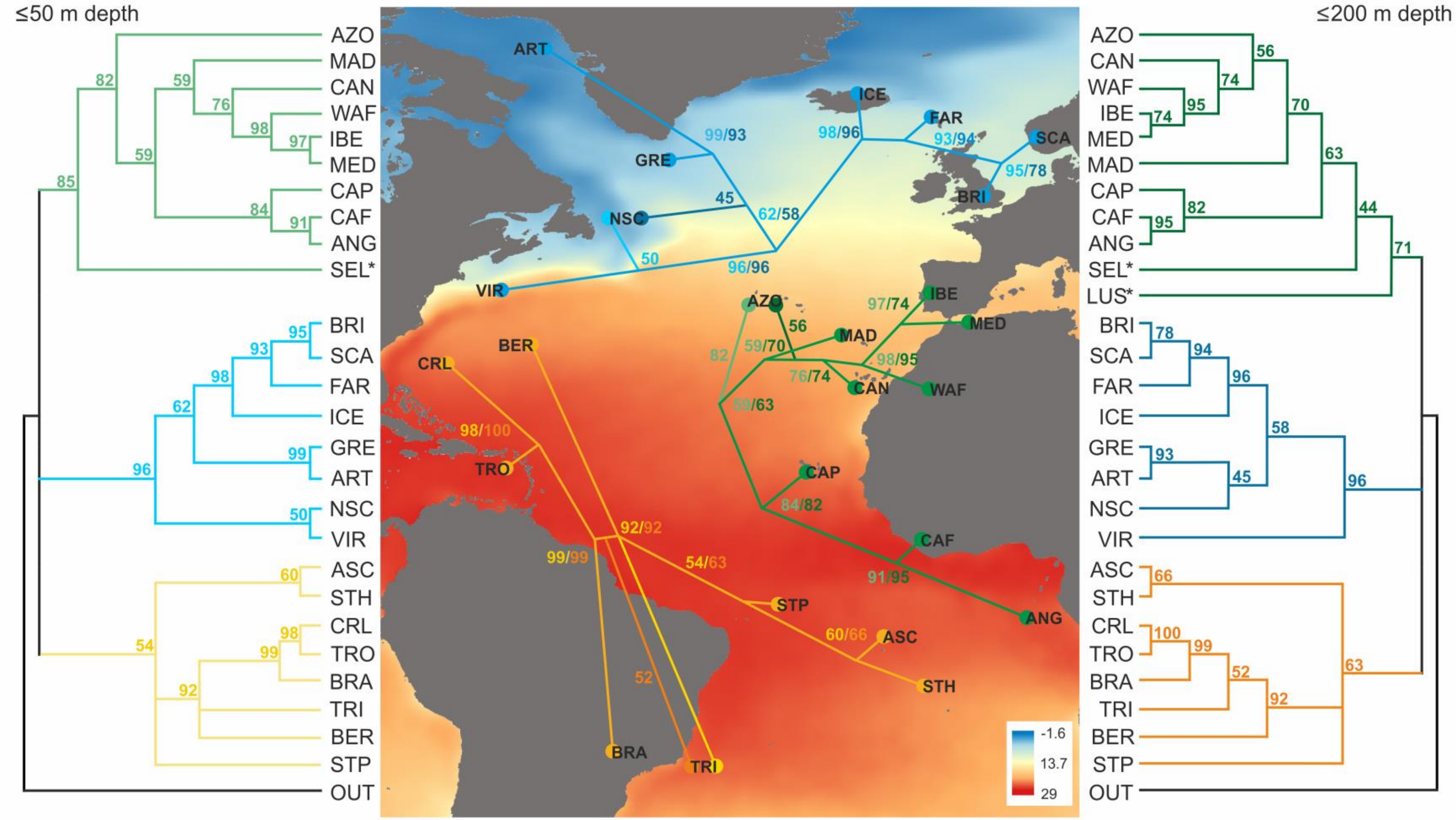


Figure 7.12. Strict consensus tree of the PAE analysis with bootstrap values (based on 100,000 replicates) for shallow (≤50 m; left side) and deep shelf echinoderms (≤200 m; right side). Lighter and darker colours are used to highlight differences between ≤50 m and 200 m PAE analysis. (*) LUS and SEL not shown in the central map.

MAD (0.53/0.49) is characterised by a small but significant two-way faunal flow, with northwest direction slightly stronger. On the other hand, CAP appears separated from the northern archipelagos, as its mains source area is CAF (0.72). The influence of the latter continental shores also reaches the central South Atlantic islands of ASC (0.44), STH (0.42), STP (0.45), and TRI (0.28), but much diminished when compared with their West Atlantic component. LUS seamounts were not included in Fig. 7.13, as they appear to receive faunal influences from most of the nearby areas. These seamounts appear to be mainly influenced by the continental shores of IBE (0.79), WAF (0.75), and MED (0.71), and the CAN (0.71) showing almost equal proportions. Though to a lesser extent, they are also influenced by Madeira (0.57) and the Azores (0.54).

In the Northern arctic-boreal Atlantic shores, the main direction of faunal flow is northwards. For example, ART appears to function as a sink from contiguous southern sources, such as SCA (0.88/0.45), GRE (0.89/0.69) and, to a lesser extent, NSC (0.67/0.47). Nonetheless, the general north flow is not as clear in the West Atlantic, as NSC appears to function as a source to both GRE (at north; 0.71/0.65) and VIR (at south; 0.62/0.57).

7.4. Discussion

Geographical distribution

The present study demonstrates that the geographical range of shallow-water echinoderms in the North Atlantic increases towards high latitude areas, agreeing with Rapoport's Latitudinal Rule, which predicts a positive correlation between geographical range of the organisms and latitude at which they occur (Stevens 1989). In contrast, shallow-water echinoderm's richness generally decreased towards high latitude areas, and this latitudinal gradient was also observed within individual echinoderm classes here, which is consistent with previous echinoderm studies (*e.g.,* Price *et al*. 1999; Stöhr *et al*. 2012). The observed differences between the relative contribution of asteroids and ophiuroids to the overall echinoderm diversity from low to high latitude areas was again consistent with previous studies (Stöhr *et al*. 2012; Mah & Blake 2012). For example, Piepenburg *et al*. (1996) found in the arctic Svalbard waters more than twice the number of asteroid taxa than ophiuroids (the second richest class), though the latter dominated the shelf fauna in terms of abundance.

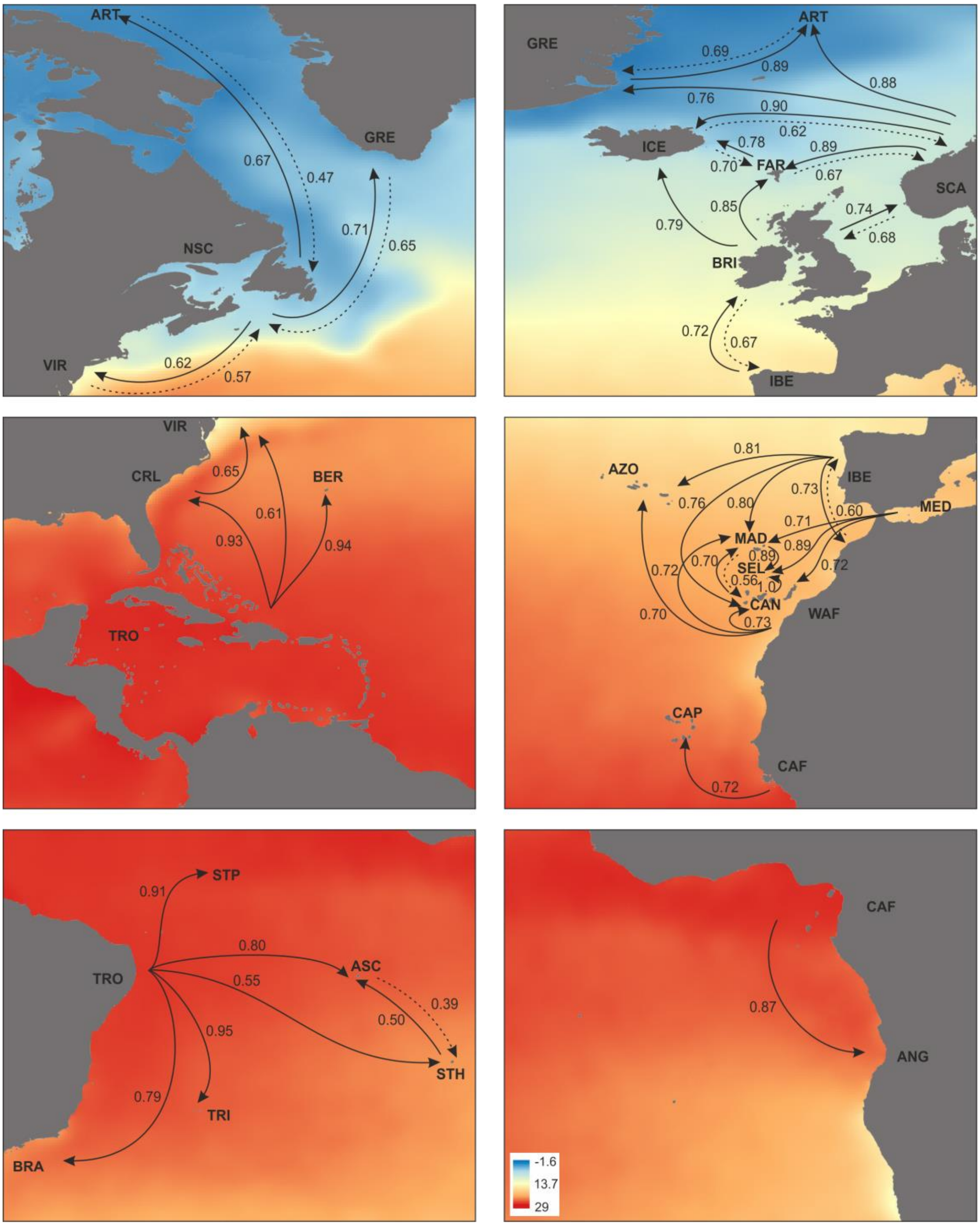


Figure 7.13. Probable directions of faunal flows of shallow-water echinoderms (≤200 m) in the Atlantic Ocean and the Mediterranean Sea.

The positive correlation between Asteroidea abundance and latitude or depth (Mah & Blake 2012) may account for the slightly lower proportion of Asteroidea species included in this study, as the analysis was restricted to the shallow-water realm and did not take into account southernmost regions such as Argentina, South Africa and Antarctic.

In the Atlantic, the least diverse continental shores were from Arctic waters, a situation that is consistent with previous studies (*e.g.,* Smirnov 1994; Stöhr *et al*. 2012). The impoverish echinoderm fauna in the Arctic (and lowest level of endemism) is probably a consequence of the impact of the Last Glacial period, with the bulk of its fauna composed of postglacial invaders, particularly boreal species from the North Atlantic (Mironov & Dilman 2010).

The tropical western Atlantic comprises a large area of coastal waters (increased by the presence of numerous islands), which is characterised by high ecosystem diversity, including coral reefs, mangroves, and sea-grass beds, but also sandy beaches and rocky shores (Miloslavich *et al*. 2010). The associated faunal diversity (as exemplified by our results) places these tropical waters as the most diverse among the analysed areas. The observed pattern of high diversity and endemism in the western tropical waters agrees with the Mironov's (2006b) concept of 'Centres of Marine Fauna Redistribution', a biogeographic-unit concept that progresses from an initial stage of species accumulation to an intermediate stage of speciation, ending in a source area (dispersal stage). According to this author, the central western Atlantic entered the accumulation stage during the Neogene, as characterised by its warm climate and a complex system of seas and islands between the two American continents (Mironov 2006b; Mironov & Krylova 2006). Despite suffering high extinction rates during the Pliocene and especially the Pleistocene glaciations, these losses were highly compensated, mainly by speciation, according to Vermeij & Rosenberg (1993). Our results show that this area is currently characterised by high echinoderm diversity and by high rates of endemism, with no parallel in any of the analysed areas.

Echinoderm diversity in the Mediterranean Sea is not particularly high when compared to adjacent areas (Table 2). This contrasts with studies on other animal groups, which categorised the Mediterranean area as a hotspot of marine biodiversity (*e.g.,* Macpherson 2002; Ávila *et al*. 2012). On the other hand, the Mediterranean presented a much higher degree of endemism than Atlantic areas of comparable latitudes (Table 2). Generally, temperate regions have lower rates of endemism and are characterized by the overlap of tropical/temperate and temperate/polar echinoderm faunas (Stöhr *et al*. 2012; Mah & Blake 2012). The complex geological history and the present-day oceanographic landscape may help to understand this apparent contrast. During the Late Palaeogene, the early ‘Mediterranean’ (as part of the Western Tethys Region) was characterised by high species diversity (Harzhauser *et al*. 2007) serving as a ‘centre of marine redistribution’, much like the tropical western Atlantic is at present (Mironov 2006b). Its importance as a centre of diversity declined gradually during the Palaeogene and Neogene (Mironov 2006b Harzhauser *et al*. 2007) and by the end of the Miocene, the marine gateway between the Mediterranean and the Atlantic had closed, leading to the Messinian Salinity Crisis (MSC; 5.96–5.33 Ma), a relatively short-lived desiccation event that resulted in a widespread extinction (Hsü *et al*. 1973; Krijgsman *et al*. 1999; Duggen *et al*. 2003). The isolation of the Mediterranean basin terminated with the reopening of the connection at the end of the MSC, inducing a recolonization by species from the Atlantic (Harzhauser *et al*. 2002, 2007). During the Pliocene and especially during the Pleistocene, glacial cycles heavily affected the eastern Atlantic shores, but the Mediterranean acted as a refugium, especially along the south-eastern shores (Thiede 1978). Presently, the surface current patterns in the area suggest that Atlantic invaders still enter the Mediterranean basin through the shallow Strait of Gibraltar. To compensate for the hydric deficiency in the Mediterranean, surface waters from the Atlantic (characterised by cooler temperatures and normal oceanic levels of salinity) pass the strait eastward (Bas 2009). The excess inflow is balanced in part by an outflow of cooler, higher saline Mediterranean waters into the Atlantic along the shallow bottom of the Strait of Gibraltar (*c*. 300 m) (Thiede 1978). The highly stratified nature of the water circulation in the Strait of Gibraltar may on one hand facilitate migration and gene-flow from the Atlantic into the Mediterranean, whereas on the other hand may provide enough isolation to prevent Mediterranean shallow-water species from dispersing outside this basin.

The second most diverse area was located in the tropical east Atlantic, along the coasts of Central Africa. This large area seems to somewhat mirror the faunal patterns previously described for the Mediterranean and tropical West Atlantic, though largely lacking enclosed seas and the multitude of islands present in the latter. Vermeij & Rosenberg (1993) estimated that the extinction rates in this area were much less severe than in the west Atlantic, and recognized its tropical coasts as a major refugium for taxa that disappeared from south-western Europe and the western Atlantic during the Pliocene and early Pleistocene. However, the observed diversity differences (and the levels of endemism) between tropical areas of the Atlantic could also be an effect of sampling bias. For instance, the Caribbean has been extensively studied and sampling effort in this area surpasses that of other regions. For example, in recent years, researchers have joined in a concerted effort to revise the echinoderm fauna of the entire Latin America (Alvarado & Solís-Marín 2013). In contrast, most of the knowledge about West African fauna is a product of punctual expeditions and the resulting reports (*e.g.,* Koehler 1914b; Cherbonnier 1958a; Chesher 1966a; Madsen 1970). Thus, large components of the tropical east Atlantic echinoderm fauna are in desperate need of revision (or verification) and there are ample stretches of West African coast with virtually no data. Price *et al*. (1999) analysed the shallow and deep-water asteroid faunas in the Atlantic and found that a disparity in sampling efforts was an important factor influencing the interpretation of geographic patterns, particularly between shallow and deep-water faunas. In our analysis, this was particularly evident among the oceanic systems (with the exception of the Canary Islands), as most of what we know today is largely derived from international expeditions that sporadically visited the islands. For instance, the available data on the echinoderm fauna from Selvagens is based on a single publication by Peréz-Ruzafa *et al*. (2002), with no reported species from deeper shelf waters (*i.e*., between 50 and 200 m).

Endemic species

Stöhr *et al*. (2012) concluded that evaluating global diversity of ophiuroids was problematic, as many species have not been reported again since their original description and their current taxonomic status is unknown. Unfortunately, this dilemma is not restricted to brittle stars but also to other echinoderm classes, with at least 30% of the endemic species included here known only from the type material. For example, almost 20% of TRO are known only from their original descriptions. In CAF, this number rises to 54% of the 50 endemic species (mostly holothurians). Among the oceanic islands this scenario is even more conspicuous. For example, in the south Atlantic, TCU has 4 out of 5 endemic species that have not been sampled again since first found. In STH, 2 out of the 3 endemic species are known only from the types and the third species has last been collected more than 80 years ago. *Ophiarachnella semicincta* (Studer, 1882) is the only known endemic species of CAP (to depths ≤ 200 m), and it is not seen since it was described. Regardless, our results show that the number of endemic species decreases with latitude, with tropical West Atlantic presenting over 53 times more endemics than the low diverse arctic latitudes.

Bathymetrical Zonation

Viewed overall, bathymetric ranges of the echinoderms in the study area show an increase towards high latitudes in continental areas. Stevens (1996) found a similar pattern in Pacific fishes and attributed it to the effect of Rapoport's Bathymetric Rule. Nevertheless, almost half of the species included in this study could be characterized as eurybathic, as differences between the minimum and maximum recorded depths surpass the average shelf depth (200 m; cf. Table 2). A wide bathymetric range may confer a special aptitude to tolerate a large range of environmental conditions and thus to occupy large latitudinal ranges (Price *et al*. 1999). For example, Franz *et al*. (1981) observed the West Atlantic tropical sea-stars *Luidia clathrata* (Say, 1825) and *Astropecten articulatus* (Say, 1825) at increasingly deeper shelf waters north of Cape Hatteras which, according to these authors, was correlated with the average 10°C winter isotherm position and reflected the species tracking of warmer winter isotherms into deeper waters. Stevens (1996) observed that the shift in depth ranges with latitude in Pacific marine fishes was best explained by the 'seasonal variability hypothesis', as depth thermal gradients decline towards the poles. Stevens (1996) argued that, as seasonal variation determines the organism's minimum tolerance range, a non-migratory species living at high latitude should be able to tolerate a wider range of climatic conditions than a species from low latitude. It is beyond the scope of this paper to explore the rich bibliography related with latitudinal gradients in species richness (*e.g.,* Pianka 1966, 1989; Rohde 1992; Roy *et al*. 1998, 2000; Macpherson 2002) and the power of the proposed models to explain bathymetrical ranges. At first instance, the observed patterns cannot be explained by any single one of these models and it is most likely they form a complex interaction between several factors such as temperature, energy availability, habitat diversity, competition, and predation, that operate at different spatial and temporal scales.

In general, species from insular faunas presented broader depth ranges when compared with those from continental coasts, regardless of the average latitude. Oceanic systems, where accommodation space is scarce (with bathymetrical profiles dropping to abyssal depths within a few miles from the coast) may favour arrival of species that are less specific in their bathymetric requirements. This could be particularly important in young islands, in which the available littoral area defined by the island shelf is comparably smaller (Quartau *et al*. 2014), and during glacial episodes by further reducing the available space as sea-level drops (Ávila 2013; Ávila *et al*. 2018, 2019).

Modes of larval development and asexual reproduction

The evolutionary picture that emerges from many echinoderm studies is one of repetitive, unidirectional evolution away from planktotrophy (the ancestral state) independently in the different echinoderm groups (Jablonski & Lutz 1983; Wray 1996; McEdward & Miner 2001; Raff & Byrne 2006). According, to Uthicke *et al*. (2009), the derived lecithotrophic development dominates all echinoderm classes but echinoids, representing 68% of all species with known development. Our analysis revealed a different trend in the Atlantic shallow-water echinoderms in which planktotrophic larval development is the commonest type. This may be a direct consequence of the slightly over-representation of echinoids, one of the best-studied invertebrate groups, with regard to their reproduction and development (Gillespie & McClintock 2007). If the class Echinoidea is excluded, lecithotrophic development becomes indeed the most frequent (40%, from a total of 169 species), though followed closely by planktotrophic development (34%).

Most data on larval development in echinoderms are limited to extrapolations based on egg size and fertility (*e.g.,* Schoener 1972; Hendler 1975; Tyler & Gage 1980), with few laboratory studies (*e.g.,* Mortensen 1921; Emlet 1995). Direct observation of pelagic larval life in the wild is often impossible, thus estimates such as length of larval development reared in the laboratory are of upmost importance, although they only indicate possible, and not actual, pelagic periods in nature (Strathmann 1978). Planktonic larval duration is highly plastic and strongly influenced by abiotic factors such as temperature (O'Connor *et al*. 2007). Furthermore, ecological shifts in habitat (*i.e*. from planktonic to aplanktonic) are not necessarily dependent on correlated changes in morphogenesis (McEdward & Janies 1997). For example, the tropical clypeasteroid echinoids *Cassidulus caribaearum* Lamarck, 1801 and *C. mitis* Krau, 1954 are known to produce lecithotrophic larvae that, despite being equipped to a planktonic life, remain among the mother's spines until post-metamorphosis stage is reached, in a brooded-like behaviour (Gladfelter 1978; Contins & Ventura 2011). For other species, brooding behaviour appears to be entirely facultative, and cases of poecilogony have been documented. The brooding circumpolar sea star *Pteraster militaris* (O.F. Müller, 1776) releases part of their clutch as free-swimming larvae (McClary & Mladenov 1990). The tropical irregular echinoids *Clypeaster rosaceus* (Linnaeus 1758) and *Brisaster latifrons* (A. Agassiz 1898) are known to produce planktonic larvae with facultative feeding larvae (McEdward & Janies, 1997). Moreover the potential for pelagic dispersal may not be always restricted to larval stages. Most examples of pelagic juvenile stages are restricted to deep-sea elasipodid holothurians (Gebruk *et al.* 1997) but fully transformed juveniles of the temperate *Luidia sarsii* Düben & Koren *in* Düben, 1844 are also known to occur in the water column (Grieg 1932). This sea star produces a relatively large planktotrophic larva that develops a post-larval rudiment whilst in the plankton, apparently without need of a substratum stimulus (Domanski 1984).

Theoretically, species with planktotrophic larvae have longer pelagic stages and, as a consequence, have greater potential for dispersion in a single generation. Broad geographic ranges buffer species against extinction caused by local disturbance events (Emlet 1995). Therefore, lineages with long larval development are assumed to contain geologically long-lived species with low extinction and speciation rates (Jablonski & Lutz 1983). Following the same reasoning, non-planktotrophic lineages are expected to include species with smaller geographic ranges and short geologically lives characterized by higher extinction rates (Jeffery & Emlet 2003). The dual relation between dispersal strategies and geographic range is readily apparent on oceanic islands, where aplanktonic spawners are more frequently endemic (through lack of genetic exchange), and pelagic spawners proportionately more diverse (through higher dispersal) than at continental shelves (Floeter & Gasparini 2000). The fact that species with non-planktotrophic development are found on oceanic islands probably testifies to the intensity of selection favouring this type of development (Jablonski & Lutz 1983). Furthermore, the oceanic setting in these islands may favour the presence of species with aplanktonic development, through avoidance of loss of larvae, that otherwise might be carried away from the islands by prevailing currents into the open ocean (Mileikovsky 1971). In other words, evolution of island faunas is expected to favour suppression of larval planktonic stage. Our analysis, however, reveals that in the Atlantic, echinoderm faunas in oceanic islands are dominated by species with planktonic larval stages, including in older islands such as Bermuda (47 million years (Ma); Vogt & Jung 2007). Conversely, our results show predominance of the planktotrophic mode of larval development in species with wide geographical ranges (Fig. 7.6), in accordance with similar observations made by Emlet (1995) for shallow-water echinoids.

Thorson's rule, which dictates non-pelagic development to predominate at higher latitudes (Thorson 1950) was not supported by our analysis. Nonetheless, our analysis revealed a relative loss of planktonic development with increasing latitudes and decreasing temperatures (Fig. 7.8). Marshall *et al*. (2012) also found an association between lower temperatures with lessening of planktonic development incidence, but this correlation was stronger at low productivity levels, *i.e*., planktonic larvae are more common when food levels and temperature are high. Development modes reflect trade-offs in terms of parental investment, fecundity, and offspring mortality, dispersal, and development time, all of which ultimately influence potential reproductive success (Gillespie & McClintock 2007). Thus, and similar to the observed latitudinal gradients of species richness, the observed pattern is likely a result of a complex interaction between biotic and abiotic factors, acting on various scales of space and time (see above discussion under Bathymetrical zonation).

Rafting has been offered as alternative explanation for larval dispersal in echinoderm species that lack planktonic larval stages (Highsmith 1985). In the first instance, aplanktonic life stages appear to have no advantage over planktonic larval stages, as the latter could equally settle on drifting objects. Buoyant material (whether flotsam or larvae) has a tendency to concentrate by surface drift into long 'windrows' or 'slicks' along lines formed by Langmuir cells (Jokiel 1989; Fraser *et al*. 2011). Thus, colonization of a raft may occur directly by larval recruitment or, before the raft is formed, by larval recruitment or by growth onto an anchored, buoyant substratum (*e.g.,* kelp, sea grasses, pumice) that subsequently breaks off and drifts away (Jackson 1986). However, in a long-distance rafting scenario (*i.e*., multi-generation rafting), internal fertilisation and direct development appear to confer an advantage of direct recruitment in a low gamete concentration environment (Thiel & Gutow 2005a).

The potential for rafting may not be homogeneous between echinoderm classes. For example, the ophiuroids and echinoids when compared with the asteroids or holothurians are believed to be poor rafters due to overall lack or inefficiency of attaching structures (O'Hara 1998). Nonetheless, examples of the presence of sea stars and brittle-star species in drifting objects or detached algae are available almost in an equal measure (Highsmith 1985; Edgar 1987; Holmquist 1994; Tzetlin *et al*. 1997). Drifting objects (*e.g.,* macrophytes and sea grasses) could provide shelter and food for small organisms for a considerable period of time, but would be less likely to do so for large animals (Highsmith 1985). Most sea urchins lack the ability to cling to floating objects and do not find suitable habitats on these. Shallow-water sea urchins inhabiting hard substrates, which often are exposed to high wave energy and strong currents, in contrast, possess all the necessary prerequisites for dispersal by rafting, and indeed have been found among drifting objects. For example, the amphi-Atlantic *Arbacia lixula* (Linnaeus, 1758) has been found attached to ships' hulls (Mortensen 1935) and floating debris through the Mediterranean waters (Aliani & Molcard 2003). *Arbacia* species possess large numbers of oral tube feet and are able to cling strongly to the substrate. Conversely, the pencil urchin *Eucidaris tribuloides* (Lamarck, 1816) lacks specialized tube feet for attachment and thus appears to be ill-suited for rafting. Nevertheless, Pfaller *et al*. (2008) reported one animal of this species under the scute of a hawksbill turtle *Eretmochelys imbricata* (Linnaeus, 1766). Nonetheless, empirical data on long-distance dispersal by rafting in shallow-water echinoderms is scarce, despite being pointed out as an alternative vector for dispersal underlying wide geographical ranges (Highsmith 1985), presence on remote oceanic islands (O'Hara 1998), or lack of genetic drift between isolated populations (Sponer & Roy 2002).

The evolution of different reproductive strategies appears to favour aplanktonic development in two specific cases: long-distance dispersal through rafting; and long-term establishment of population in remote island-like areas. Yet, most echinoderms reported for tropical to temperate areas reproduce through planktonic larvae, where aplanktonic development was deemed disadvantageous (Highsmith 1985). Some echinoderms, however, are equipped with an additional mode of direct recruitment, asexual reproduction or even self-fertilisation. These ‘deviant’ types of reproduction were documented in a total of 95 echinoderm species (Imaoka 1991; Mckenzie 1991; Hendler 1995; Mladenov 1996; Baker *et al*. 2001; Stöhr 2003 2011; O’Loughlin & Waters 2004; Komatsu *et al*. 2004; O’Loughlin & Rowe 2006; Benavides-Serrato *et al*. 2007; Okanishi & Fujita 2011; Barbosa *et al*. 2012; Okanishi *et al*. 2013; Dolmatov 2014). The best-documented type of asexual reproduction in echinoderms is fragmentation through fission, possibly because of its easily identified trademarks in ophiuroid and asteroid species (*e.g.,* multiple madreporites, non-pentamerous symmetry and different sized arms; Mladenov *et al*. 1986). In contrast, the number of species reproducing through selfing is likely to be underestimated. Hermaphroditism (simultaneous or protandous) is known in all echinoderm classes other than Echinoidea (Ghiselin 1969; Obuchi *et al*. 2010), despite reported cases of abnormal hermaphrodite individuals among otherwise gonochoristic echinoid species (Tyler *et al*. 1984). Unfortunately, and unlike fission, confirmation of autogamy or any other forms of asexual reproduction such as parthenogenesis, generally requires the use of genetic tools, in order to establish paternity and thus, documented cases in echinoderms are scarce (*e.g., Amphipholis squamata*; Poulin *et al*. 1999). Additionally, cloning by fragmentation in planktotrophic larval stages is believed to confer adaptational advantages by prolonging larval life span and increase of the total number of dispersive propagules (clonal amplification of genotypes), without additional reproductive costs to the primary adult (Mladenov 1996; Balser 2004). There have been a few instances of documented larval cloning in species occurring in the tropical West Atlantic (*e.g., Ophiopholis aculeata* (Linnaeus, 1767), *Luidia senegalensis* (Lamarck, 1816); Balser 2004). However, our understanding of the processes regulating larval cloning in the natural environment or its incidence is still largely limited, and presently it is not clear whether this mode of reproduction has any realised consequences in dispersal capability or in the ‘survival’ capability of the cloned genotypes (Knott *et al*. 2003). For these reasons, the following discussion on asexual reproduction in echinoderms will focus mainly on fission by adult or juvenile stages.

Our results show not only a latitudinal gradient between aplanktonic development and asexual reproduction in the North Atlantic (Fig. 7.9), but as well a significant presence of species capable of asexual reproduction in oceanic systems. Clark & Downey (1992) observed that sea stars capable of fission were likely to have wider distribution ranges, often including remote islands, when compared with non-fissiparous taxa. The fissiparous *Coscinasterias tenuispina* appears to be a perfect case to illustrate these authors' assumptions. This sea star is widely distributed in the Mediterranean Sea and on both sides of the Atlantic, including all NE Atlantic islands, as well as Saint Helena and Bermuda (Peréz-Ruzafa *et al.* 2002). Although studies on the incidence of fission in this species are scarce, 'pseudopopulations' supported solely by fission were located both near north and south distributional limits of this species (Cisneros *et al.* 2016). Strangely enough, there are no data on the type of larva in this species, but they are expected to produce a planktotrophic larvae similar to *C. calamaria* (Gray, 1840) (Barker 1978) or *C. acutispina* (Stimpson, 1862) (Shibata *et al.* 2011). Therefore, *C. tenuispina* appears to be equipped with both long-lived larva and rafting capabilities for long-distance dispersal and, on arrival, clonal recruits have an additional mechanism for the rapid establishment of populations. However, when compared with non-fissiparous shallow-water echinoderms, the advantages of fission in the establishment of wide geographical ranges become less clear. Like *C. tenuispina*, the Amphi-Atlantic *Arbacia lixula* develops through a long-lived planktotrophic larva (George *et al*., 1990), and both adult and juvenile morphologies present traits that may confer some attributes for rafting life (see above and Kroh *et al*. 2011). Also, similar to *C. tenuispina*, this strictly shallow-water species reveals an overall weak phylogeographic structure over large distances, and the modern geographical distribution in both species is believed to be a result of a recent range expansion by long-distance dispersal, possibly in Pleistocene times (Waters & Roy 2003; Lessios *et al*. 2012; Wangensteen *et al*. 2012; Cisneros *et al*. 2016). However, unlike *C. tenuispina*, the West Atlantic populations of *A. lixula* presented higher genetic differentiation (forming a private clade nested within the large *A. lixula* clade in the mitochondrial COI-trees and a sister-group to a clade with all other *A. lixula* sequences in the nuclear binding-tree). Notwithstanding, Baker's law predicts that asexual reproduction is favoured on the arrival in a remote island-like scenario, but by no means implies the same on a post-colonization evolutionary scenario. The relation between geographical range and asexual reproduction, all fall outside Baker's law, as it centres on processes underlying the colonization stage but not range expansion as a whole.

In a review of Baker's law, Pannell *et al*. (2015) selected four scenarios where asexual reproduction might be favoured: (1) colonization of islands by a single long-distance dispersal event; (2) repeated colonization in metapopulations, as a balance to local extirpations; (3) colonization in the context of species invasions; and (4) repeated colonization in range expansions. However, the sheer rarity of fissiparous species in echinoderms could suggest that the costs associated with this type of asexual reproduction are counteracting its occurrence among echinoderm lineages, regardless of phylogenetic preconditions. Despite providing an additional mechanism for rapid colonization, low offspring/parent ratios and long generation times (growth between fission events) are clearly powerful counter-pressures (Lawrence & Herrera 2002). Asexual reproduction also provides protection against outbreeding depression and potentially deleterious effects of genetic drift in local adaptation. In the long run, however, it can also lead to inbreeding depression, through an extreme form of founder effect (in islands-like or marginal areas) or/and genetic bottlenecks (in a metapopulation scenario) (Tilquin & Kokko 2016). As deleterious mutations accumulate through time, small isolated asexual populations may suffer from mutational meltdowns (and thus extirpations) (Tilquin & Kokkos 2016). Subsequent to establishment, selection during the long persistence phase (post-colonization evolution phase) is less likely to be characterized by mate limitation (Allee's effect), so that mechanisms for outcrossing may then be favoured (Pannell *et al*. 2015). Whether the ability to reproduce through fission is a primitive character, as suggested by Waters & Roy (2003), or co-evolved independently among taxonomic groups, the mechanisms that trigger fission in echinoderms are still unclear.

Latitudinal gradients in asexual reproduction such as those revealed by our analysis have been placed under the broad term 'Geographic parthenogenesis', applied to an array of patterns in which sexual and their asexual counterparts differ in their geographic distribution (Tilquin & Kokko 2016). These have been better studied in the terrestrial realm in which asexual forms appear to be favoured for example in higher latitudes (and high altitudes) (Peck *et al*. 1998), *i.e.*, where the abiotic selection pressures appear to outnumber the biotic ones (but see Tilquin & Kokko 2016). In these areas, local selection should tip the balance in favour of inbreeding by, for example, freezing the best-adapted genotypes in the local population (Pannell *et al*. 2016). Transposing this scenario to the oceanic realm, it would be expected a higher incidence of asexual reproduction in the polar and deep-waters. However, the echinoderms in the North Atlantic show precisely the contrary tendency. Yet, asexual reproduction in echinoderms has been generally associated with adverse conditions that result in decrease of productivity (lower gamete or off-spring production) (Lawrence & Herrera 2002), caused by low availability of food, high temperature, desiccation, storms or lowering of the ambient oxygen (Emson & Wilkie 1980; Mladenov 1996).

Habitat

In their study on the dispersal potential of marine macro-invertebrates from different habitats in the west coast of the United States, Grantham *et al*. (2003) obtained somewhat different results to ours, where non-planktonic development dominated the intertidal sandy environment, and the planktonic development predominated in rocky and sandy subtidal environments. Grantham and co-workers accounted for the summed strategies in each community rather than focused on particularly elements of that community. Conversely, we have focused our measure for dispersal under each element's potential for integrating each community over different geographical and vertical ranges. Grantham and co-workers concluded that high local disturbance and patchiness favours non-planktonic or reduced planktonic development, as was observed in intertidal sandy communities. However, our results also suggest that dispersal strategies in each element (whether restricted or not to a type of environment or community) result from a sum of selective pressures through its geographical and vertical distribution. In that sense, species inhabiting patchy or locally unpredictable but widespread habitats are thus more likely to have planktotrophic larvae, regardless of 'adaptive strategy' in the classic ecological sense (Jablonski & Lutz 1983). Soft sediment substrata spatially predominate at all latitudes and depths in the benthic marine environment (Todd 1998) therefore it is expected to find species with planktotrophic type of development dominating the echinoderm fauna living in such substrata.

In fact, our analysis reveals that most species associated with mobile sediments have a planktonic development. Among the 11 species recorded strictly in soft bottoms with no planktonic larval stage, 5 species proved to be endemic. For the most part, the geographical distribution of species such as the circumpolar brooding asteroid *Leptasterias groenlandica* (Steenstrup, 1857) could be explained as resulting from range expansion to contiguous waters as biogeographical barriers shift through time. However, it is difficult to apply the same reasoning to other wide-ranging species such as the large brittle-star *Ophiophrixus spinosus* (Storm, 1881), since the substrate type for most records is unknown and direct evidence for the mode of larval development is missing. The presence of two soft bottom viviparous species in the archipelago of Madeira (the Mediterranean holothurian *Phyllophorus urna* Grube, 1840 and the NW African ophiuroid *Ophioconis vivipara* Mortensen, 1925) is also hard to explain. Islands in the Madeira archipelago are roughly 640 km from the NW African coasts and as a true oceanic volcanic system, these islands were never linked to continental shores. Thus, the fauna from this archipelago must have derived solely by long-distance dispersal. How can the presence of these viviparous species in Madeira be explained, if rafting in soft-bottom animals is not plausible? As both species brood internally lecithotrophic larvae, is there a possibility that, occasionally, planktonic larvae are shed into the environment before metamorphosis? Data on *O*. *vivipara* is scarce, as this species is known from very few records and there is some historical confusion with a closely related species, *O*. *forbesi* (Madsen, 1970), a species with wider geographical distribution and habitat preferences (Koehler 1909; Tortonese 1965; Hernández *et al*. 2013). The assertion of viviparity in this species was based on Mortensen (1925)'s observations of similar sized young in the bursa of two adult females. The presence of young in an adult bursa may suggest (but does not prove) viviparity, as it could be interpreted as a result of crevice-seeking behaviour by young stages (Hotchkiss 1982). In contrast, *P*. *urna* is relatively better known and besides being a typical inhabitant of Mediterranean detritic environments, is also known from sea-grass communities, which may imply that this holothurian may be somehow capable of dispersal through rafting.

Sea-grass shoots, although known to survive long-distance dispersal (Harwell & Orth 2002), are, however, poor transporters due to their relatively low buoyancy. Sea-grass shoots are able to carry, at most, very small passengers and for very limited distances, as decomposition takes its toll, progressively lessening both size and buoyancy (Thiel & Gutow 2005b). Apparently, species associated with sea-grass beds do not seem to experience any advantage for dispersal compared with any other typical soft sediment species. Empirical data have shown that small-scale transportation of small invertebrates such as ophiuroids by detached sea grass is possible, but less effective than through macroalgae (Holmquist 1994). On the other hand, coastal sea grass systems are not homogeneous macrophyte structures and may contain variable amounts of macroalgae (and other substrata of complex morphology) at times rivalling the abundance of sea grasses themselves (Virnstein & Carbonara 1985; Virnstein & Howard 1987). Faunal comparisons between crustacean and gastropod species on their affinity for drifting macroalgae in sea grass beds were found to be similar (Virnstein & Howard 1987), as drifting algae mats appear to provide an alternative habitat for soft-bottom communities (Virnstein & Carbonara 1985; Norkko *et al*. 2000). Most data are available on faunal groups other than echinoderms and thus we are left to speculate if sea-grass associated species in this group could also opportunistically move up into, and survive in a drifting algal mat.

Our results also show differences between the general representative nature of each echinoderm group in oceanic systems and continental shores. For example, irregular echinoids and holothurians are under-represented in islands, but not asteroids. The different relation with substrate type might provide a partial answer. For example, sea star species from island faunas were characterised by less restrictive habitat requirements, with no clear preference for either soft or hard bottoms, despite a general trend in this class to favour sandy environments. In contrast, both irregular echinoids and holothurians show a close relation with soft bottoms. Additionally, holothurians show a more restricted bathymetrical range when compared with other classes, which might have reduced their capability of inhabiting oceanic systems as a whole. In addition to the potential constrains experienced by sediment fauna discussed above, glaciation cycles in the Pleistocene may have affected shallow-water species restricted to fine-sediment habitats in oceanic islands. During these glacial episodes, sandy and muddy environments habitats were considerably reduced by falling sea level. Due to the reduced shelf width, the mobile sediment was transported offshore, spilled over the insular shelf edge and lost to the abyssal depths (see Ávila *et al.* 2008, 2015, 2018).

Data on habitat preferences become increasingly unreliable with depth. For the deeper shelf, data collection derives primarily from indirect methods (such as trawls, dredges, grabs, corers, etc.) and for logistical reasons largely derive from soft bottoms. Bulk samples even when complemented by direct methods of observation (*e.g.,* use of footage or underwater high definition photography taken by ROVs) seldom disclose information on microhabitats particularly for small cryptic species, which tend to be either ignored or underestimated. Also, commensal relationships between species (*e.g.,* between obligatory epibiont echinoderms and their host species) are typically not recorded. Hence, comparisons of within vs. between habitat diversity may be highly biased by different sampling efforts, even when using an over-simplistic method such as used herein to categorise habitat relationships and potential for long-distance dispersion.

Biotic similarities between areas: Parsimony Analysis of Endemicity and Probable Directions of Faunal Flows

The patterns arising from both PAE and probable directions of faunal flow analysis were for the most part consistent. The expected decrease of shared species between two areas with increasing geographical distance was also shown by previous biogeographic echinoderm studies (*e.g.,* Price *et al*. 1999; Peréz-Ruzafa *et al*. 2013). Most areas show a close relationship with nearby areas, and this was most striking in oceanic islands. In these systems, faunal affinities were always towards the nearby continental shores (with the exception of Ascension Island; see Fig. 7.12), regardless of present-day prevailing sea-surface currents. Also, our analysis does not reveal any evidence at a specific level indicative of longitudinal flow across the Atlantic via continuous oceanic currents. Stöhr *et al*. (2012) stated that largest differences between regional and intra-regional ophiuroid faunas tend to be at the species-level, as all families and most genera are longitudinally widespread. This is consistent with the failure to produce a consensus tree on genus-based distributional data (data not shown), a possible direct consequence of an older longitudinal spread.

On the shelves and shores of continental regions, it is expected that temperate areas function as transitional or 'buffer' zones between cold arctic waters and tropical equatorial waters. As previously stated, faunas in these waters are expected to be characterised by a mixture between these two latitudinal zones, with little or no endemism. For the most part, the western areas of Virginia and Nova Scotia present the same general characteristics as their counterparts in the East Atlantic, *i.e.*, maintaining close relationships with both north (boreal to arctic faunal component) and southwest waters (temperate to subtropical component; Fig. 7.12). In contrast to the East Atlantic temperate areas, however, both Virginia and Nova Scotia show comparable low diversity levels. Although located at the north edge of the warm Gulf Current, NE American shores are at present highly influenced by the cold Labrador Current (Franz & Merrill 1980). For continental shelf species, Cape Hatteras and Cape Cod are not barriers *per se*, but instead are limited by thermal discontinuities associated with the confluence of surface currents that, in turn, are influenced by the shelf configuration. The stratified nature of their waters and highly seasonal thermal conditions may limit the distribution of some faunal groups, whether species ranges are linked to summer or winter latitudinal temperature differences (Franz *et al*. 1981). Furthermore, large estuarine systems also dominate the NE American littoral (*e.g.,* Chesapeake Bay, Delaware Bay and Hudson-Raritan Estuary). Comparable lower habitat diversity dominated by sandy bottoms combined with salinity differences, on one side may extricate specific faunal components such as those associated with hard substrates, and on the other side, may hamper the establishment of typical stenohaline echinoderms.

Macaronesia is a biogeographical term used for the volcanic archipelagos in the Northeast Atlantic, which traditionally includes the Azores, Madeira, Selvagens, Canaries, and Cabo Verde (Whittaker & Fernández-Palacios 2007). More recently, however, it has been suggested by some authors that, at least from a marine point of view, Cabo Verde should be excluded (Almada *et al*. 2001; Ávila *et al*. 2012, 2016). Our results agree with this proposition, by showing a close relation of Cabo Verdean echinoderm species with those from the Central African coasts, clearly contrasting with the remaining NE Atlantic archipelagos, in which the main influences derived from the Mediterranean Sea and NW African shores.

Ocean circulation in the North Atlantic is influenced by a large-scale asymmetric gyre, flowing to the north on the western side (the Gulf Stream) and to the south on the central eastern side, in a complex multi-branched current system (Santos *et al*. 1995). The Gulf Stream influence is felt in Macaronesian waters by the eastward flow of two sub-branches: the North Atlantic Current and the Azores Current. These eventually converge east of the Azores, joining the southward flow of Madeira and Canaries currents. In spite of the general sea-surface currents from west to east, the Azores, Madeira, Selvagens and Canaries archipelagos show a close relationship with the east continental coasts, *i.e*. Europe and NW Africa (Fig. 7.13). The contrast between patterns generated by faunal flows and present sea-surface currents is particularly significant in the isolated archipelago of the Azores. Two main factors have been proposed to explain this apparent biogeographical paradox: longer distances and differences in the local hydrological conditions (Santos *et al*. 1995); and 'windows of opportunity' correlated with the disruptive impact of glacial terminations on the usual sea-surface currents (Ávila *et al*. 2009, 2015, 2019). Notwithstanding, occasional reports of young stages from West Atlantic species in Azorean coasts support that downstream dispersal does indeed occur (Ávila 2000). Furthermore, phylogenetic data have shown that downstream colonisation from the insular Azores to continental Iberian coast can also occur (Ó Foighil *et al*. 2001). Additionally, Madeira *et al*. (2017) reviewed the echinoderms of the Azores, and realised that several species considered among recent faunal lists as native to the insular shallow-waters were actually based on single records of immature animals collected sometimes at depths well beyond their natural limits [*e.g., Eucidaris tribuloides*, *Ophionereis reticulata* (Say, 1825)]. Often references on local faunas simply list species, offering no further details on the number or size of the specimens, making it impossible to discern which records were based solely on immature animals (*i.e*. which may not actually represent breeding populations). This is particularly problematic in remote oceanic systems, as their fauna are less diverse and potentially less well studied (particularly at depths greater than 50 m).

The general eastward affinity (*i.e.* countercurrent faunal pattern) observed among NE Atlantic oceanic systems (Fig. 7.13), was portrayed by Mironov & Krylova (2006) as a mixture of species dispersing under different current patterns at different geological time scales. In other words, a combination made from more recent arrivals derived from periodical eddy-driven anomalies in the Azorean front and from 'ghosts of the past' (*sensu* Benzie 1999), species representative of possible past favourable oceanographic conditions prior to the formation of the Gulf Current, or during 'windows of opportunity' (*sensu* Ávila *et al*. 2015, 2019). Presently, it is not clear whether the direction of surface current patterns in the NE Atlantic displayed a westward general flow, prior to the closure of the Panama Isthmus and the formation of the Gulf Current (Molnar 2008). Regardless, the fossil record in the Azores archipelago suggests an old eastern fauna affinity, as confirmed by Madeira *et al*. (2011), who reviewed the early Pliocene echinoid fauna from Santa Maria Island. Of the four echinoids identified to the specific level, all but *Clypeaster altus* still occur as members of extant fauna of tropical (*Eucidaris tribuloides* and *Echinoneus cyclostomus*) to temperate (*Echinocyamus pusillus*) regions in the Atlantic. The tropical species do not clearly attest to affinities to either side of the Atlantic by the absence of older or contemporaneous fossil records in other regions or by their amphi-Atlantic (*E. tribuloides*) or cosmopolitan (*E. cyclostomus*) extant distribution. Though, a closely related *Eucidaris* fossil species, *E. zeamays* (Sismonda, 1842) is known from the Mediterranean, Paratethyan (Kroh 2005), and Portuguese Miocene (Pereira 2008). On the other hand, the two clypeasteroids species vouch for a much clear relationship, as both are known from the NE Atlantic and Mediterranean fossil record (Néraudeau *et al*. 2001, 2003; Pereira 2008). *E. pusillus* (O.F. Müller, 1776) is also known from the extant fauna of both eastern basins, including the Azores. Though in desperate need of revision, the echinoid fossil record from Middle-Miocene in the Madeira Archipelago appears to indicate a similar eastern Atlantic affinity (Pereira 2008). The fossil record of Santa Maria Island also shows that by the late Pleistocene, the older tropical fauna was completely replaced by a sub-tropical to warm-temperate species, with *E. pusillus* as the sole survivor from the Early Pliocene epoch (Madeira *et al*. 2011, 2017). For the most part, the Pleistocene echinoderm fossil record displays the same key elements of the extant Azorean fauna from rocky shores, with the echinoids *Arbacia lixula,* *Paracentrotus lividus*, and *Sphaerechinus granularis* as the most common elements. Only the former species is known to range to the western side, occurring also in southern Brazilian shallow-waters today.

With few exceptions, phylogeographic studies targeting echinoderm species have shown little or no genetic structuring between Macaronesian and continental shores, suggesting an almost panmictic metapopulation scenario (*e.g., Arbacia lixula*: Wangensteen *et al*. 2012; *Ophidiaster ophidianus* (Lamarck, 1816): Micael *et al*. 2014). These studies also indicate that the populations in the Macaronesian archipelagos were derived from rapid range expansions during the Pleistocene. The shallow-water sea star *Marthasterias glacialis* (Linnaeus, 1758) was one of the few exceptions to this pattern, revealing some genetic differentiation (Pérez-Portela *et al*. 2010).

The connection between the east continental and insular shores in NE Atlantic is similar to that between the archipelagos, supporting the expected 'stepping-stone' or 'island hopping' dispersal across the islands and seamounts (Fig. 7.13). However, the Lusitanian seamounts appear to function as well as faunal 'sinks' from the nearby continental and insular shores, with no clear directional flow, which is consistent with the results obtained in a similar analysis by Ávila *et al*. (2012) on rissoid gastropods. The isolated position of the Lusitanian seamount in the resulting PAE dendrogram (Fig. 7.12) may also reflect unique geomorphological features among the analysed areas. On average, the available habitat area at moderate depths in these seamounts is proportionally more restrictive than in the nearby Macaronesian islands. Therefore, shallow-water species (*i.e.*, ≤200 m) make up only a small fraction of these seamounts' fauna, encompassing a small number of exclusively eurybathic species. On the other hand, if the analysis is focused only on the NE Atlantic insular shores, the Canary Islands emerge as a faunal redistributor with the expected northwest flow progressively weakened by counter-flows between adjacent archipelagos (Canaries-Madeira-Azores). Features of this seven-island Canaries archipelago such as a relatively old age (25 Ma; Ávila *et al*. 2016), relative close proximity with African continent (98 km from Fuerteventura Island), long coastline (1,501 km), and wide range (spreading over 450 km to the west), may all have contributed to its relevant evolutionary and biogeographic role.

The area enclosed by Macaronesian archipelagos covers a large spectrum of islands with contrasting features in terms of isolation, geological age, geomorphology and coastal area, hydrology and climate conditions (for a summary see Table 1 of Ávila *et al*. 2016). Thus, it is expected that a pattern will arise from the sum of these differences between and within the islands of each archipelago hand in hand with the overall faunal affinities related to this biogeographical unit in the NE Atlantic. In sum, our results agree with Mironov & Krylova (2006) who classified NE Atlantic insular systems (both islands and seamounts) as recipient areas with strong mixing of faunas of different origins. It is necessary to note that, unlike any other archipelagos in the NE Atlantic, most of what is known about the echinoderm fauna of the Madeira archipelago from the lower infralittoral and circalittoral zones is from a single publication on soft bottoms around Madeira Island by Jesus & Abreu (1998). This may have led to the overrepresentation of certain elements in the archipelago fauna, which in turn may have influenced the observed arrangement of the NE Atlantic archipelagos in the PAE trees (Fig. 7.12).

Ascension and Saint Helena are two of the most isolated islands in the Atlantic, separated from each other by 1,290 km and from the nearest African continental shores by 1,500 and 1,870 km, respectively. The central position of Saint Helena in the South Atlantic was somewhat more evident in our analysis by the almost homogeneous faunal contributions from both sides of the Atlantic, with slightly higher representation of tropical West Atlantic and Ascension elements. Additionally, it has been suggested that Saint Helena may represent an important 'stepping-stone' for the Atlantic colonisation of species from the Indian Ocean (Vermeij & Rosenberg 1993; Briggs & Bowen 2012). However, the present study does not include the most southern shores of the Atlantic, thus further faunal affinities of Saint Helena were left untested. In contrast, the fauna from Ascension Island is characterised by an almost exclusive contribution from tropical West Atlantic. Lubbock (1980) suggested that the observed pattern is a reflection of the higher diversity of the western tropical shores when compared with eastern African shores. The close relation of the Brazilian Saint Peters and Saint Paul Rocks and Trindade and Martin Vaz Archipelago with nearest tropical west American continental shores (Fig. 7.12) is in agreement with the results of previous studies (Albuquerque & Guille 1991; Barboza *et al*. 2015; Martins *et al*.

2016). Similar to the Azores, the occasional current reversal caused by extension to surface waters of the Atlantic Equatorial Undercurrent was indicated as a primary immigration route in Saint Peters and Saint Paul Rocks and possible also in Ascension Island (Edwards & Lubbock 1983). These studies also indicate that the presence of islands and seamounts between the continental and insular shores also may have favoured an eastward faunal flow, particularly during periods of low sea level that characterised Pleistocene glaciations.

7.5. Conclusions

Echinoderms are a conspicuous presence in the coastal waters at virtually all latitudes. Due to the extensive knowledge regarding their highly diverse life strategies, echinoderms proved to be an excellent group to test biogeographic and diversity patterns in the Atlantic.

Our analysis shows that shallow-water echinoderm faunas in the Atlantic tend to be closely related to those in nearby areas, simultaneously showing marked latitudinal gradients in terms of species richness, species geographical range, endemism, bathymetrical zonation, modes of larval development, and asexual reproduction. The Northern Atlantic arctic and boreal areas turned out to be closely related, whereas the temperate and tropical areas grouped separately on each side of the Atlantic, with no evidence of a recent trans-Atlantic faunal flow. The tropical West Atlantic is a key area around which the surrounding southwestern Atlantic areas cluster together. In the east, the Iberian and West central Africa coasts appear to be important faunal sources to the temperate/subtropical and tropical east faunas, respectively. To the north, a major northward faunal flow toward the Arctic waters was detected. We did, however, detect an overall heterogeneity of available data (*e.g.,* habitat, depth, reproduction) for certain faunal groups (*e.g.,* shallow vs. deep shelf fauna). Data deficiency at the local scale reduced branch support in the PAE analysis and caused unresolved sister-group relationships for some regions.

The present study and the taxonomic survey it is based on (Madeira *et al., submitted*) provide a baseline for future studies on Atlantic echinoderms, enabling research on their response to increasing human pressure and climate change. Range shifts and local extirpations may be promoted by these processes, specifically in remote oceanic islands, where small changes can have swift and critical impacts on local faunas.

ACKNOWLEDGMENTS

P.M. benefited from PhD grant SFRH/BD/61146/2009 (FCT – Fundação para a Ciência e Tecnologia, Portugal) and by the SYNTHESYS Project (http://www.synthesys.info/, which is financed by European Community Infrastructure Action under the FP6 and FP7 programmes). S.P.A. acknowledges his IF/00465/2015 research contract funded by Fundação para a Ciência e a Tecnologia (Portugal), and a SYNTHESYS grant (DE–TAF–1071) to study the palaeontological collections of the Museum für Naturkunde, Berlin. This work was funded by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE, and by National Funds through FCT under the UID/BIA/50027/2013, POCI-01-0145-FEDER-006821 and under DRCT-M1.1.a/005/Funcionamento-C-/2016 (CIBIO-A) project from FRCT. This work was also supported by FEDER funds (in 85%) and by funds of the Regional Government of the Azores (15%) trough Programa Operacional Açores 2020, in the scope of the project “AZORESBIOPORTAL – PORBIOTA”: ACORES-01-0145-FEDER-000072.

6.5. References

Abreu-Pérez, M., Solís-Marín, F.A. & Laguarda-Figueras, A. (2005) Catálogo de los equinodermos (Echinodermata: Asteroidea y Ophiuroidea) nerítico-bentónicos del Archipiélago Cubano. *Revista de Biología Tropical*, 53 (Suppl. 3), 29–52.

Agassiz, A. (1881) Report on the Echinoidea dredged by HMS “Challenger” 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger, Zoology*, 3, 1–321.

Ahearn, C.G. (1995) Catalog of the type of specimens of seastars (Echinodermata: Asteroidea) in the National Museum of Natural History, Smithsonian Institution. *Smithsonian Contributions to Zoology*, 572, 59 pp.

Albuquerque, M.N. & Guille, A. (1991) Ophiuroidea (Echinodermata) ao largo do Brasil: Bancos dos Abrolhos, Cadeia Submarina Vitória-Trindade e Plataforma Continental adjacente. *Boletim do Museu Nacional: Zoologia, Nova série*, 353, 1–29.

Albuquerque, M.N., Campos-Creasey, L.S., Guille, A. (2001) Two new species of Amphiuridae (Echinodermata, Ophiuroidea) from the southeastern coast of Brazil. *Zoosystema,* 23(3), 591–604.

Aliani, S. & Molcard, A. (2003) Hitch-hiking on floating marine debris: macrobenthic species in the Western Mediterranean Sea. *Hydrobiologia*, 503, 59–67.

Allee, W.C. (1931) Animal Aggregations: A Study in General Sociology, University of Chicago Press, Chicago, ix+431 pp.

Almada, V.C., Oliveira, R.F., Gonçalves, E.J., Almeida, A.J., Santos, R.S. & Wirtz, P. (2001) Patterns of diversity of the North-Eastern Atlantic blenniidfish fauna (Pisces: Blennnidae). *Global Ecology and Biogeography*, 10(4), 411–422.

Alvà, V. (1991) On three species of Mediterranean echinoderms. *Scientia Marina*, 55(2), 450–462.

Alvà, V. & Jangoux, M. (1992) Brooding and marsupium structure in the cucumariid holothuroid *Neocnus incubans* (Echinodermata). *In*: L. Scalera-Liaci & Canicatti, C. (Eds.), *Echinoderm Research 1991*, Balkema, Rotterdam, pp. 121–123.

Alvà V. & Vadon, C. (1989) Ophiuroids from the western coast of Africa (Namibia and Guinea-Bissau). *Scientia Marina*, 53, 827–845.

Alves, F.M.A., Chicharro, L.M., Serrão, E. & Abreu, A.D. (2001) Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). *Scientia Marina*, 65, 383–392.

Alves, L.S.S., Pereira, A., & Ventura, C. (2002) Sexual and asexual reproduction of *Coscinasterias tenuispina* (Echinodermata: Asteroidea) from Rio de Janeiro, Brazil. *Marine Biology*, 140(1), 95–101.

Alvarado, J.J. & Solís-Marín, F. (2013). *Echinoderm research and diversity in Latin America*. Springer-Verlag, Berlin.

Améziane, N., Bourseau, J.P., Heinzeller, T. & Roux, M. (1999) Les genres *Cyathidium* et *Holopus* au sein des Cyrtocrinida (Crinoidea; Echinodermata). *Journal of Natural History*, 33, 439–470.

Aminin, D.L., Menchinskaya, E.S., Pisliagin, E.A., Silchenko, A.S., Avilov, S.A. & Kalinin, V.I. (2015) Anticancer activity of sea cucumber triterpene glycosides. *Marine Drugs*, 13(3), 1202–1223.

Anadón, R. (1977) Equinodermos recogidos durante la campaña «Atlor VII» en las costas noroccidentales de África (Noviembre 1975). *Resultados Expediciones Científicas del Buque Oceanográfico «Cornide De Saavedra»*, 6, 165–168.

Ancona Lopez, A.A. (1965) Sobre *Pentacta peterseni* sp. nov. (Echinodermata – Holothuroidea). *Boletim da Faculdade Filosofia, Ciências Letras,* Universidade São Paulo, Zoologia, 25, 315–320.

Anisimova, N. & S.J. Cochrane (2003) An annotated checklist of the echinoderms of the Svalbard and Franz Josef Land archipelagos and adjacent waters. *Sarsia*, 88, 113–135.

Arriaga-Ochoa, J.A., Solis-Marin, F.A., Laguarda-Figueras, A. & Solis-Weiss, V. (2012) First record of *Lissothuria antillensis* (Echinodermata: Holothuroidea) from the Gulf of Mexico. *Revista Mexicana de Biodiversidad*, 83(1), 291–293.

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Blazewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandćo, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.-Y., Cheng, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J.F., Dawson, M.N., De Clerck, O., Decock, W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M.A., Turon, X., Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G.C., Wilson, S.P. & Costello, M.J. (2012) The Magnitude of Global Marine Biodiversity - Supplemental Information. *Current Biology*, 22, 1–91.

Augier, H. (1985) Premier contribution a l'etude et a la cartigraphe des biocenoses marines benthiques de l'ile de Madere. *Boletim do Museu Municipal do Funchal (Hist. Nat.)*, 37(168), 86–129.

Ávila, S.P. (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago. Life and Marine Sciences*, Supplement 2 (Part A), 99–131.

Ávila, S.P. (2013) Unravelling the patterns and processes of evolution of marine life in oceanic islands: a global framework. *In*: Fernández-Palácios, J.M., L. Nascimento, J.C. Hernández, S. Clemente, A. González & J.P. Díaz-González (Eds.), *Climate Change perspectives from the Atlantic: past, present and future*. Universidad de La Laguna, Tenerife, pp. 95–125.

Avila, S. P., Madeira, P., Silva, C.M., Cachao, M., Landau, B., Quartau, R. & Martins, A.M. (2008) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science*, 23(8), 777–785.

Ávila, S.P., Silva, C.M., Schiebel, R., Cecca, F., Backeljau, T. & Martins, A.M.F. (2009) How did they get here? Palaeobiogeography of the Pleistocene marine molluscs of the Azores. *Bulletin of the Geological Society of France*, 180, 201–213.

Ávila, S.P., Goud J. & Martins A.M.F. (2012) Patterns of diversity of the Rissoidae (Mollusca: Gastropoda) in the Atlantic and the Mediterranean region. *The Scientific World Journal*, 1–30.

Ávila, S. P., Melo, C., Silva, L., Ramalho, R. S., Quartau, R., Hipólito, A., Cordeiro, R., Rebelo, A.C., Madeira, P., Rovere, A., Hearty, P.J., Henriques, D., Da Silva, C.M., Martins, A.M.F. & Zazo, C. (2015) A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews*, 114, 126–148.

Ávila, S.P., Melo, C., Berning, B., Cordeiro, R., Landau, B. & Silva, C.M. da (2016) *Persististrombus coronatus* (Mollusca: Strombidae) in the early Pliocene of Santa Maria Island (Azores: NE Atlantic): palaeoecology, palaeoclimatology and palaeobiogeographic implications on the NE

Atlantic Molluscan Biogeographical Provinces. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441, 912–923.

Ávila, S.P., Cordeiro, R., Madeira, P., Silva, L., Medeiros, A., Rebelo, A.C., Melo, C., Neto, A.I., Haroun, R., Monteiro, A., Rijsdijk, K. & Johnson, M.E. (2018) Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands. *Marine Pollution Bulletin*, 126, 101–112.

Ávila, S.P., Melo, C., Sá, N., Quartau, R., Rijsdijk, K., Ramalho, R.S., Berning, B., Cordeiro, R., De Sá, N.C., Pimentel, A., Baptista, L., Medeiros, A., Gil, A. & Johnson, M.E., 2019. Towards a 'Sea-Level Sensitive Marine Island Biogeography' model: the impact of glacio-eustatic oscillations in global marine island biogeographic patterns. *Biological Reviews,* DOI: 10.1111/brv.12492.

Bacallado, J.J., Moreno, E. & Pérez-Ruzafa, A. (1985) Echinodermata (Canary Islands) provisional Check-list. *In*: Keegan, B.F. & O'Connor, B.D.S. (Eds.) *Echinodermata; Proceedings of the 5th International Echinoderm Conference, Galway, September 1984*. A.A. Balkema, Rotterdam. pp. 149–151.

Baillon, S., Hamel, J.-F. & Mercier, A. (2011) Comparative study of reproductive synchrony at various scales in deep-sea echinoderms. *Deep-Sea Research I*, 58, 260–272.

Baker, A.N., Clark, H.E.S. & McKnight, D.G. (2001) New species of the brittlestar genus *Astrogymnotes* H.L. Clark, 1914, from New Zealand and Japan (Echinodermata: Ophiuroidea). *Journal of the Royal Society of New Zealand*, 31(2), 299–306.

Baker, H.G. (1955) Self-compatibility and establishment after'long-distance'dispersal. *Evolution*, 9(3), 347–349.

Baker, H.G. (1967) Support for Baker's law—as a rule. *Evolution*, 21(4), 853–856.

Balser, E.J. (2004) And then there were more: cloning by larvae of echinoderms. *In*: Heinzeller T. & Nebelsick, J.H. (Eds.) *Echinoderms: München*, Taylor & Francis, London, pp 3–9.

Balser, E.J., Ruppert, E.E. & Jaeckle, W.B. (1993) Ultrastructure of the coeloms of auricularia larvae (Holothuroidea, Echinodermata) – Evidence for the presence of an axocoel. *Biological Bulletin*, 185(1), 86–96.

Barbosa, S.S., Klanten, O.S., Jones, H. & Byrne, M. (2012) Selfing in *Parvulastra exigua*: an asterinid sea star with benthic development. *Marine biology*, 159(5), 1071–1077.

Barboza, C.A.M., Mendes, F.M., Dalben, A. & Tommasi, L.R. (2010) Echinodermata, Ophiuroidea, *Gorgonocephalus* Leach, 1815: First report of the genus for the Brazilian continental margin. *Check List*, 6(2), 289–291.

Barboza, C.A.M., Mattos, G. & Paiva, P.C. (2015) Brittle stars from the Saint Peter and Saint Paul Archipelago: morphological and molecular data. *Marine Biodiversity Records*, 8(e16), 1–9, doi: 10.1017/S1755267214001511.

Barker, M.F. (1978) Structure of the organs of attachment of brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea). *Journal of Experimental Marine Biology and Ecology*, 33(1), 1–36.

Bartsch, I. (1987) Notes on Ophiuroidea (Echinodermata) from the Northeastern Atlantic Ocean. I. Ophiacanthidae. *Spixiana*, 10, 115–130.

Bas, C. (2009) The Mediterranean: A synoptic overview. *Contributions to Science*, 5, 25–39.

Bernasconi, I. (1955) Equinoideos y asteroideos de la colección del Instituto Oceanográfico de la Universidad de San Pablo: primera contribución. *Boletim do Instituto Oceanográfico*, 6(1–2), 51–77.

Benavides-Serrato, M., O'Loughlin, P.M. & Rowley, C. (2007). A new fissiparous micro-asteriid from southern Australia (Echinodermata: Asteroidea: Asteriidae). *Memoirs of Museum Victoria*, 64, 71–78.

Benavides-Serrato, M., Borrero-Pérez, G.H. & Diaz-Sanchez, C.M. (2011) *Equinodermos del Caribe colombiano I: Crinoidea, Asteroidea y Ophiuoridea*. Serie de Publicaciones Especiales de Invemar, Santa Marta, 22, 384 pp.

Benavides-Serrato, M., Borrero-Pérez, G.H. & Diaz-Sanchez, C.M. (2012) *Equinodermos del Caribe colombiano II: Echinoidea y Holothuroidea*. Serie de Publicaciones Especiales de Invemar, Santa Marta, 30, 250 pp.

Benzie, J.A. (1999). Genetic structure of coral reef organisms: ghosts of dispersal past. *American Zoologist*, 39(1), 131–145.

Besteiro, C. & Urgorri, V. (1988) Inventario dos Equinodermos de Galicia (Echinodermata). *Cadernos da Área de Ciencias Biolóxicas (Inventarios)*. Publicacións do Seminario de Estudos Galegos, Edicións do Castro, Sada (A Coruña), 1, 51 pp.

Bianchi, C.N., Morri, R.H.C., Sartoni, G. & Wirtz, P. (1998) Sublittoral epibenthic communities around Funchal (Ilha da Madeira, NE Atlantic). *Boletim do Museu Municipal do Funchal (Hist. Nat.)*, supplement 5, 59–80.

Bianchi, C.N., Morri, R.H.C. & Wirtz, P. (2000) The subtidal epibenthic Communities off Puerto del Carmen (Lanzarote, Canary Islands). *Arquipelago*, *Life and Marine Sciences*, Supplement 2(A), 145–155.

Bluhm, B.A., Piepenburg, D. & von Juterzenka, K. (1998) Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. *Polar Biology*, 20, 325–334.

Bohn, J.M. (2004) Remarks on some Holothuroidea described by Heller from the eastern Adriatic Sea. *In*: Heinzeller, T. & Nebelsick, J.H. (Eds.) *Echinoderms: München. Proceedings of the 11th international echinoderm conference*, Munich, Germany, 6–10 October 2003. A.A. Balkema, Leiden, pp. 517–519.

Borges, M. (2006) *Taxonomia, distribuição e biologia reprodutiva de Ophiuroidea (Echinodermata) das regiões Sudeste e Sul do Brasil*. PhD thesis (unpublished), Universidade Estadual Paulista, Instituto de Biociências, São Paulo, vii+143.

Borges, M. & Amaral, A.C.Z. (2006) Classe Ophiuroidea. *In*: Amaral, A.C.Z., Rizzo, A.E. & Arruda, E.P. (Eds.), *Manual de identificação dos invertebrados marinhos da região sudeste-sul do Brasil*, Edusp, Editora da Universidade de São Paulo, 1, 288 pp.

Borges, M. & Campos, L.D.S. (2011) *Ophiomusium acuferum* (Ophiolepididae) and *Ophiomisidium pulchellum* (Ophiuridae) (Ophiuroidea: Echinodermata), redescription based on the Brazilian specimens. *Zoologia (Curitiba)*, 28(2), 219–225.

Borges, M., Monteiro, A.M.G. & Amaral, A.C.Z. (2002) Taxonomy of Ophiuroidea (Echinodermata) from the continental shelf and slope of the Southern and Southeastern Brazilian Coast. *Biota Neotropica*, 2(2), 1–69.

Borrero-Pérez, G.H., Benavides-Serrato, M., Solano, Ó. & Navas G.R. (2008) Brittle-stars (Echinodermata: Ophiuroidea) from the continental shelf and upper slope of the Colombian Caribbean. *Revista Biología Tropical*, 56 (3), 169–204.

Borrero-Pérez, G.H., Pérez-Ruzafa, A., Marcos, C. & González-Wangüemert, M. (2009) The taxonomic status of some Atlanto-Mediterranean species in the subgenus *Holothuria* (Echinodermata: Holothuroidea: Holothuriidae) based on molecular evidence. *Zoological Journal of the Linnean Society*, 57, 51–69.

Briggs, J.C. & Bowen, B.W. (2012). A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, 39(1), 12–30.

Brito, I.M. (1971) Contribuição ao conhecimento dos equinodermos da Ilha da Trindade, Brasil. *Arquivos do Museu Nacional do Rio de Janeiro*, 54, 261–265.

Brogger, M.I. & O’Hara, T.D. (2015) Revision of some ophiuroid records (Echinodermata: Ophiuroidea) from Argentina. *Zootaxa*, 3972(3), 432–440.

Brooks, W. & Grave, C. (1899) *Ophiura brevispina*. *National Academy of Sciences*, 8(4), 79–100.

Broszeit, S., Davenport, J. & McAllen, R. (2010) First documented record of *Rhabdomolgus ruber* (Echinodermata: Holothuridea) in Irish waters. *Marine Biodiversity Records*, 3(e64), 1–3, doi: 10.1017/S1755267210000485.

Brown, J., Downes, K., Mrowicki, R.J., Nolan, E.L., Richardson, A.J., Swinnen, F. & Wirtz, P. (2016) New records of marine invertebrates from Ascension Island (central Atlantic). *Arquipelago, Life and Marine Sciences*, 33, 71–79.

Buchanan, J.B. (1958) The bottom fauna communities across the continental shelf off Accra, Ghana (Gold Coast]. *Proceedings of the Zoological Society of London*, 130(1), 1–56.

Buhl-Mortensen, L. & Mortensen P.B. (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. *In*: Freiwald A, Roberts JM (Eds.), *Cold-water Corals and Ecosystems*, Springer-Verlag Berlin Heidelberg, pp. 849–879.

Cadenat, J. (1938) Liste des echinodermes recueillis pendant la cinquieme croisiere du navire de recherches President-Theodore-Tissier. *Revue des Travaux de l’Institut des Peches Maritimes*, 11, 349–375.

Campbell, D.B. & Turner, R.L. (1984) *Echinaster graminicola*, a new species of spinulosid sea star (Echinodermata: Asteroidea) from the west coast of Florida. *Proceedings of the Biological Society of Washington*, 97(1), 167–178.

Carrera-Rodríguez, C.J. & Tommasi, L.R. (1977) Asteroidea de la plataforma continental de Rio Grande do Sul (Brasil), coleccionados durante los viajes del N/Oc. "Prof. W. Besnard" para el Proyecto Rio Grande do Sul. *Boletim do Instituto Oceanográfico*, São Paulo, 26(1), 51–130.

Carvalho, A.L.P.S. & Ventura, C.R.R. (2002) The reproductive cycle of Asterina stellifera (Möbius) (Echinodermata: Asteroidea) in the Cabo Frio region, southeastern Brazil. *Marine Biology*, 141, 947–954.

Caso, M.E. (1990) Un nuevo asteroideo del Caribe Mexicano *Astropecten caribemexicanenesis* sp. nov. y comparación con la especie afín *Astropecten nitidus* Verrill. *Anales del Instituto de Ciencias del Mar y Limnología*, 17, 107–130.

Cherbonnier, G. (1949) Note préliminaire sur quelque holothuries rapportées par le Navire École Belge MERCATOR. *Bulletin Muséum National Histoire Naturelle*, Paris, 2 série, 21(2), 255–257.

Cherbonnier, G. (1957a) Holothuries des cotes de Sierra Leone. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 29(6), 485–492.

Cherbonnier, G. (1958a) Holothuries des cotes de Sierra Leone (2e note). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 30, 101–108.

Cherbonnier, G. (1958b) Holothuries des cotes de Sierra Leone (3e note). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 30(2), 191–197.

Cherbonnier, G. (1958c) Holothuries des cotes de Sierra Leone (4e note). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série. 30, 394–299.

Cherbonnier, G. (1958d) Holothuries des cotes de Sierra Leone (5e et dern. note). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 30, 371–378.

Cherbonnier, G. (1959a) Échinodermes de la Guyane Française (Crinoides, Astérides, Ophiurides, Échinides, Holothurides) (4e note). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 31(4), 367–372.

Cherbonnier, G. (1959b) Echinides: Expédition Océanographique Belege dans les Eaux Cotiérs Africaines de l'Atlantique Sud. 1948–1949. *Institut Royal des Sciences Naturelles de. Belgique, Résultats Scientifiques*, 3(6), 37–59.

Cherbonnier, G. (1963a) Note sur *Leptosynapta bergensis* (Ostergren), espèce critique d'holoturie apode. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 35(4), 420–440.

Cherbonnier, G. (1963b) Echinodermes des côtes du Cameroun récoltés par A. Crosnier en Décembre 1962 – Janvier 1963. *Bulletin Muséum National Histoire Naturelle*, Paris, 2 série, 35(2), 179–193.

Cherbonnier, G. (1964) Note préliminaire sur les holothuries de l'Atlantique Sud. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 36(4), 532–536.

Cherbonnier, G. (1965a) Holothurides. *Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique Sud (1948–1949): résultats scientifiques*, Brussels, 3(2), 23 pp.

Cherbonnier, G. (1965b) Holothuries récoltées par A. Crosnier dans le Golfe de Guinée. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 36(5), 647–676.

Cherbonnier, G. (1966) Note sur une nouvelle holothurie dendrochirote de Golfe de Guinée: *Psolus tropicus* nov. sp. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série. 37(6), 1024–1029.

Cherbonnier, G. (1969a) Étude critique de L'Astérie *Anseropoda lobiancoi* (Ludwig). *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 41(4), 946–951.

Cherbonnier, G. (1969b) Échinodermes récoltés par la «Thalassa» au large de côtes d'espagne et du Golfe de Gascogne (3–12 Aout 1967). *Bulletin Muséum National Histoire Naturelle*, Paris, 2 série, 41(1), 343–361.

Cherbonnier, G. (1970) Échinodermes récoltés par la «Thalassa» au large de côtes d'espagne et du Golfe de Gascogne (18–25 Aout 1968). *Bulletin Muséum National Histoire Naturelle*, Paris, 2ª série, 41(5), 1266–1277.

Cherbonnier, G. (1972) *Thyone bacescoi*, nouvelle espèce d'Holothurie dendrochirote (Echinoderme) des côtes de Mauritanie. *Bulletin Muséum National Histoire Naturelle,* Paris. 3 série, Zoologie, 30(24), 291–294.

Cherbonnier, G. (1973) Sur une nouvelle espèce d'holothurie dendrochirote du Golfe de Guinéee: *Hemioedema multipodia* n. sp. *Bulletin Muséum National Histoire Naturelle*, Paris. 3 série. Zoologie, 170(115), 1161–1165.

Cherbonnier, G. (1984) Redescription et nouvelle position générique de Holothurie dendrochirote *Euthyonidiella atlantica* (Ludwig et Heding). *Bulletin Muséum National Histoire Naturelle*, Paris. 4a série. Zoologie, 6(4), 853–856.

Cherbonnier, G. (1988) Espèces nouvelles ou peu connues de Rhopalodinidae (Échinodermes, Holothuries). *Bulletin Muséum National Histoire Naturelle*, Paris. 4a série. Zoologie, 10(3), 429–448.

Cherbonnier, G. & Guille, A. (1968) Sur une nouvelle Holothurie dendrochirote de Méditerranée: *Phyllophorus drachi* nov. sp. *Bulletin Muséum National Histoire Naturelle*, Paris. 2 série, 40(3), 630–633.

Cherbonnier, G. & Nataf, G. (1973) *Astropecten* des côtes occidentales d'Afrique. *Bulletin Muséum National Histoire Naturelle*, Paris. 3 série. Zoologie, 181 (120), 1233–1302.

Chesher, R.H. (1966a) The R/V Pillsbury deep-sea biological expedition to the Gulf of Guinea, 1964–1965, 10: report on the Echinoidea collected by the R/V Pillsbury in the Gulf of Guinea. *Studies in Tropical Oceanography*, 4(1), 209–223.

Chesher, R.H. (1966b) Redescription of the echinoid species Paraster floridiensis (Spatangoida: Schizasteridae). *Bulletin of Marine Science*, 16(1), 1–19.

Chesher, R.H. (1968a) *Lytechinus williamsi*, a new sea urchin from panama. *Breviora*, Museum of Comparative Zoology, 305, 1–15.

Chesher, R.H. (1968b) The Systematics of Sympatric Species in West Indian Spatangoids: A Revision of the Genera *Brissopsis*, *Plethotaenia*, *Paleopneustes*, and *Saviniaster*. *Studies in Tropical Oceanography*, 7, 168 pp.

Chesher, R.H. (1969) Contribution to the biology of *Meoma ventricosa* (Echinoidea: Spatangoida). *Bulletin of Marine Science*, 19(1), 72–110.

Chesher, R.H. (1970) Evolution in the Genus *Meoma* (Echinoidea: Spatangoida) and a Description of a New Species from Panama. (Biological results of the University of Miami deep-sea expeditions. 68. *Bulletin of Marine Science*, 20, 731–761.

Chesher, R.H. (1972) Biological results of the University of Miami Deep-Sea Expeditions. 86. A new *Paraster* (Echinoidea: Spatangoida) from the Caribbean. *Bulletin of Marine Science*, 22, 10–25.

Cihangir, H.A. & Papadopoulou, M.A.P. (2012) Spatial and temporal variation of echinoderm assemblages from soft bottoms of the Çanakkale Strait (Turkish Strait System) with a taxonomic key of the genus Amphiura (Echinodermata: Ophiuroidea). *Turkish Journal of Zoology*, 36(2), 147–161.

Cisneros, A.G., 2016. *Estructura, distribución e historia evolutiva de las poblaciones de estrellas de mar echinaster sepositus y Coscinasterias tenuispina*. Ph. D. Thesis, Universitat de Barcelona, 209 pp.

Cisternas, P. Selvakumaraswamy, P. & Byrne, M. (2004) Evolution of development and the Ophiuroidea – revisited. *In*: Heinzeller, T. & Nebelsick, J.H. (Eds.) *Echinoderms: München*. Taylor & Francis, London, pp. 521–526.

Clark, A.H. (1914) Echinoderma II: Crinoidea. *In*: Michaelsen, W. (Ed.) *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. L. Friederichsen & Co. Hamburg, 1(2), 305–318.

Clark, A.H. (1921) Report on the Echinoidea Collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *University of Iowa Studies in Natural History*, 9(5), 103–121.

Clark, A.H. (1931) A monograph of the existing crinoids. The comatulids. Superfamily Comasterida. *Bulletin of the U.S. National Museum*, 82(1), 815 pp.

Clark, A.H. (1934) A new genus of brittle stars from Puerto Rico. *Smithsonian Miscellaneous Collections*, 91(13), 1–3.

Clark, A.H. (1949) Echinoderms from the mid-Atlantic dredged by lhe Atlantis in the summer of 1948. *Journal of the Washington Academy of Sciences*, 39, 371–377.

Clark, A.H. & Clark, A.M. (1967) A Monograph of the Existing Crinoids. Part 5 Suborders Oligophreata (concluded) and Macrophreata. *United States National Museum Bulletin*, 82, 1–860.

Clark, A.M. (1953) A revision of the genus Ophionereis (Echinodermata, Ophiuroidea). *Proceedings of the Zoological Society of London*, 123(1), 65–94.

Clark, A.M. (1976) *The echinoderms of southern Africa*. British Museum (Nat. Hist), London, 766, 277 pp.

Clark, A.M. (1977). Notes on deep-water Atlantic Crinoidea. *Bulletin of the British Museum, Natural History. Zoology*, 31(4), 159–186.

Clark, A.M. & Downey, M.E. (1992) Starfishes of the Atlantic. *Natural History Museum Publications*. Ed. Chapman & Hall, London, 794 pp.

Clark, A.M. & Mah, C. (2001) An index of names of recent Asteroidea, part 4. Forcipulatida and Brisingida. *In*: Jangoux, M. & Lawrence, J.M. (Eds.). *Echinoderm Studies*, 6, 229–347.

Clark, H.L. (1900) The Echinoderms of Porto Rico. *Bulletin of the U.S. Fisheries Commision*. 20(2), 233–263.

Clark, H.L. (1907a) The Cidaridae. *Bulletin of the Museum of Comparative Zoology*, 51(7), 165–230.

Clark, H.L. (1907b) The apodous holothurians. A monograph of the Synaptidae and Molpadiidae. *Smithson Contributions to Knowledge*, 35, 1–231

Clark, H.L. (1915) Catalogue of recent ophiurans. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 25 (4), 165–376.

Clark, H.L. (1918) Brittle-Stars, New and Old. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 62, 265–338.

Clark, H.L. (1922) The Echinoderms of the Challenger Bank, Bermuda. *Proceedings of the American Academy of Arts and Sciences*, 57(13), 353–362.

Clark, H.L. (1925) *A catalogue of the Recent sea urchins (Echinoidea) in the British Museum (Natural History)*. Trustees of the British Museum, London. The Oxford University Press, London, 1–250 pp.

Clark, H.L. (1933) A Handbook of the Littoral Echinoderms of Porto Rico and the Other West Indian Islands. *Scientific Survey of Porto Rico and the Virgin Islands*, New York Academy of Sciences: New York, 16(1), 1–147.

Clark, H.L. (1939) Two new ophiurans from the Smithsonian-Hartford Expedition, 1937. *Proceedings of the United States National Museum*, 86(3054), 415–418.

Clark, H.L. (1941) Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The echinoderms (other than Holothurians). *Memorias de la Sociedad cubana de Historia natural, "Felipe Poey"*. 15(1), 1–154.

Clark, H.L. (1942) The echinoderm fauna of Bermuda. *Bulletin of the Museum of Comparative Zoology*, 89(8), 367–391.

Clarkson, E. (1998) *Invertebrate palaeontology and evolution*. 4th edition, Blackwell Science Ltd, Malden, Massachusetts, 452 pp.

Colman, J. (1946) Marine biology in St. Helena. *Proceedings of the Zoological Society of London*, 116(2), 266–281.

Contins, M. & Ventura, C.R.R. (2011) Embryonic, larval, and post-metamorphic development of the sea urchin *Cassidulus mitis* (Echinoidea; Cassiduloida): an endemic brooding species from Rio de Janeiro, Brazil. *Marine Biology*, 158, 2279–2288.

Copley, J.T.P, Tyler, P.A., Sheader, M., Murton, B.J. & German, C.R. (1996) Megafauna from sublittoral to abyssal depths along the Mid-Atlantic Ridge south of Iceland. Oceanologica Acta, 19(5), 549–559.

Coppard S.E., Zigler, K.S. & Lessios, H.A. (2013) Phylogeography of the sand dollar genus *Mellita*: Cryptic speciation along the coasts of the Americas. *Molecular Phylogenetics and Evolution*, 69(3), 1033–1042

Crump, R.G. & Emson, R.H. (1983) The natural history, life history and ecology of the two British species of Asterina. *Field Studies*, 5 (5), 867–882.

Danielssen, D.C. & Koren, J. (1881) North Altantic Echinodermata. *Journal of Natural History*, 8(43), 66–69.

Deichmann, E. (1930) The Holothurians of the Western Part of the Atlantic Ocean. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 71, 43–236.

Deichmann, E. (1936) The Arctic Species of *Molpadia* (Holothuroidea), and some Remarks on Heding's Attempt to subdivide the Genus. *Annals and Magazine of Natural History*, 10(17), 452–464.

Denisenko, S.G., Denisenko, N.V., Lehtonen, K.K., Andersin, A.B. & Laine, A.O. (2003) Macrozoobenthos of the Pechora Sea (SE Barents Sea): community structure and spatial distribution in relation to environmental conditions. *Marine Ecology Progress Series*, 258, 109–123.

Devaney, D.M. (1974) Shallow-Water Echinoderms from British Honduras, with a Description of a New Species of Ophiocoma (Ophiuroidea). *Bulletin of Marine Science*, 24(1), 122–164.

Dilman A.B. (2006) Asteroid fauna of the Reykjanes Ridge. *In*: Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*, KMK Scientific Press, Russian Academy of Sciences, P.P. Shirshov Institute of Oceanology, Moscow, pp. 177–192.

Dilman A.B. (2008) Asteroid fauna of the northern Mid-Atlantic Ridge with description of a new species *Hymenasterides mironovi* sp. nov. *Marine Biology Research*, 4, 1–2, 131–151.

Dilman A.B. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Asteroidea. *Invertebrate Zoology*, 11(1), 25–42.

Döderlein, L. (1920) Die Asteriden der Siboga-Expedition. 2. Die Gattung *Luidia* und ihre Stammesgeschichte. *Siboga Expedition*, 46, 193–291.

Dolmatov, I.Y. (2014) Asexual reproduction in holothurians. *The Scientific World Journal*, 527234, 1–13.

Domanski, P.A. (1984) Giant larvae: prolonged planktonic larval phase in the asteroid *Luidia sarsi*. *Marine Biology*, 80, 189–195.

Domínguez-Godino, J., Slater, M., Colin, H. & M. González-Wangüemert (2015) A new species for sea cucumber ranching and aquaculture: Breeding and rearing of *Holothuria arguinensis*. *Aquaculture*, 438, 122–128.

Downey, M.E. (1973) Starfishes from the Caribbean and the Gulf of Mexico. *Smithsonian Contributions to Zoology*, 126, 1–158.

Duggen, S., Hoernle, K., Van Den Bogaard, P., Rüpke, L. & Morgan, J.P. (2003). Deep roots of the Messinian salinity crisis. *Nature*, 422(6932), 602–606.

Eckelbarger, K.J. & N.W. Riser (2013) Derived sperm morphology in the interstitial sea cucumber *Rhabdomolgus ruber*, with observations on oogenesis and spawning behavior. *Invertebrate Biology*, 132, 270–281.

Edgar, G.J. (1987) Dispersal of faunal and floral propagules associated with drifting Macrocystis pyrifera plants. *Marine Biology*, 95(4), 599–610.

Edwards, A. & Lubbock, R. (1983) Marine zoogeography of St Paul's Rocks. *Journal of Biogeography*, 65–72.

Eléaume, M., N. Ameziane & T.K. Baumiller (2003) Developmental mode, egg size, larval size and some evolutionary considerations in comatulids (Crinidea: Echinodermata). *In*: J.-P. Féral and B. David (Eds.). *Echinoderm Research 2001, Proceedings of the sixth European Conference, Banyuls-sur-mer, 3-7 September 2001*, Swets & Zeitlinger, Lisse, 307–315.

Emlet, R.B. (1995) Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution*, 49(3), 476–489.

Emson, R.H. & Wilkie, I.C., 1980. Fission and autotomy in echinoderms. *Oceanography and Marine Biology: an Annual Review*, 18, 155–250.

Engle, V.D. & Summers, J.K. (2000) Biogeography of benthic macroinvertebrates in estuaries along the Gulf of Mexico and western Atlantic coasts. *Hydrobiologia*, 436, 17–33.

Entrambasaguas, L. (2008) *Estudio faunístico y ecológico de los equinodermos del archipiélago de Cabo Verde*. Universidad de Murcia. Departamento de Ecología e Hidrología, PhD thesis (unpublished), 301pp.

Farran, G.P. (1913) The deep-water Asteroidea, Ophiuroidea and Echinoidea of the West Coast of Ireland. *Department of Agriculture and technical instruction for Ireland, fisheries branch, scientific investigations*, 1912, 6, 1–66.

Fell, H.B. (1945) A Revision of the Current Theory of Echinoderm Embryology. *Transactions of the Royal Society of New-Zealand*, 75(2), 20–38.

Fisher, W.K. (1930) Asteroidea of the North Pacific and Adjacent Waters, Part. 3: Forcipulata (concluded). *Bulletin of the United States National Museum*, 76, 1–356.

Fisher, W.K. (1941) Asteroidea. *Discovery Reports,* 20, 69–306.

Floeter, S.R. & Gasparini, J.L. (2000) The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology*, 56(5), 1099–1114.

Foighil, D.Ó., Jennings, R., Park, J.K. & Merriwether, D.A. (2001) Phylogenetic relationships of mid-oceanic ridge and continental lineages of *Lasaea* spp. (Mollusca: Bivalvia) in the northeastern Atlantic. *Marine Ecology Progress Series*, 213, 165–175.

Forbes E (1843) On the radiata of the eastern Mediterranean. *Transactions of the Linnean Society of London*, 19, 143–153.

Franz, D.R. & Merrill, A.S. (1980) The origins and determinants of distribution of molluscan faunal groups on the shallow continental-shelf of the northwest Atlantic. *Malacologia*, 19(2), 227–248.

Franz, D.R., Worley, E.K. & Merrill, A.S. (1981) Distribution patterns of common seastars of the middle Atlantic continental shelf of the northwest Atlantic (Gulf of Maine to Cape Hatteras). *The Biological Bulletin*, 160(3), 394–418.

Fraser, C.I., Nikula, R. & Waters, J.M. (2011) Oceanic rafting by a coastal community. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1706), 649–655.

Fredriksen, S., De Backer, A. Boström, C. & Christie, H. (2010) Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Marine Biology Research,* 6, 189–200.

Freire, C.A. d. O. & Grohmann, P.A. (1989) *Leptosynapta brasiliensis*: a new species of synaptid holothurian (Echinodermata) from a sandy beach in southeastern Brazil. *Revista Brasileira de Zoologia*, 6(4), 719–723.

Froglia C. (1975) Segnalazione de *Pseudothyone sculponea* Cherbonnier nel Adriatico (Echinodermata, Holothurioidea). *Annali Museo Civico di Storia Naturale "Giacomo Doria"*, 80, 259–262.

Gage, J.D., Billett, D.S.M., Jensen, M. & Tyler, P.A. (1983) Echinoderms of the Rockall Trough and adjacent areas. I. Crinoidea, Asteroidea and Ophiuroidea. *Bulletin of the British Museum (Natural History)*, *Zoology*, 45, 263–308.

Gage, J.D., Billett, D.S.M., Jensen, M. & Tyler, P.A. (1985) Echinoderms of the Rockall Trough and adjacent areas. 2. Echinoidea and Holothurioidea. *Bulletin of the British Museum (Natural History)*, *Zoology*, 48(4), 173–214.

Gage, J.D. & Tyler, P.A. (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge, UK, Cambridge University Press, 504 pp.

Gagnon, J.-M. & K.D. Gilkinson (1994) Discrimination and distribution of the sea urchins *Strongylocentrotus droebachiensis* (O.F. Müller) and *S. pallidus* (G.O. Sars) in the Northwest Atlantic. *Sarsia*, 79, 1–11.

Garrido, M.J., Hernández, M., Espino, F., Herrera, R. & Tavío, O. (2004) *Hacelia superba* H.L. Clark, 1921 and *Chaetaster longipes* Retzius, 1805 (Echinodermata: Echinodea) new records for Canary Islands. *Arquipélago, Life and Marine Sciences*, 21A, 87–88.

Gebruk, A.V., Tyler, P.A. & Billett, D.S.M. (1997) Pelagic juveniles of the deep-sea elasipodid holothurians: New records and review. *Ophelia*, 46(2), 153–164.

Gebruk, A.V., Solis-Marin, F.A., Billett, D.S.M., Rogacheva, A.V. & Tyler, P.A. (2012) Review of the genus *Zygothuria* Perrier, 1898 and the Atlantic group of species of the genus *Mesothuria* Ludwig, 1894 (Synallactidae: Holothuroidea) with description of the new species *Mesothuria milleri* sp. nov. *Journal of Natural History*, 46(5–6), 265–348.

Gebruk, A.V., Smirnov, A.V. & Rogacheva, A.V. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Holothuroidea. *Invertebrate Zoology*, 11(1), 156–180.

George, S.B. (1990) Population and seasonal differences in egg quality of *Arbacia lixula* (Echinodermata: Echinoidea). *Invertebrate Reproduction & Development*, 17, 111–121.

Ghiselin, M.T. (1969) The Evolution of Hermaphroditism among Animals. *The Quarterly Review of Biology*, 44(2), 189–208.

Gillespie, J.M. & McClintock, J.B. (2007) Brooding in Echinoderms: How Can Modern Experimental Techniques Add to Our Historical Perspective? *Journal of Experimental Marine Biology and Ecology,* 342, 191–201.

Gislén, T. (1933) A small Collection of Crinoids from St. Helena. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 67. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening*, 93(3), 475–485.

Gladfelter, W.B. (1978) General ecology of the cassiduloid urchin Cassidulus caribbearum. *Marine Biology*, 47(2), 149–160.

Glück, F.U., Stöhr, S., Bochert, R. & Zettler, M.L. (2012) Brittle stars (Echinodermata: Ophiuroidea) from the continental shelf off Angola and Namibia. *Zootaxa*, 3475, 1–20.

Godet L., Le Mao, P., Cindy, G. & Frederic, O. (2010) Marine invertebrate fauna of the Chausey archipelago: an annotated checklist of historical data from 1828 to 2008. *Cahiers de Biologie Marine*, 51(2), 147–165.

Gondim A.I., Dias, T.L.P. & Christoffersen, M.L. (2013a) *Diadema ascensionis* Mortensen, 1909 (Echinodermata: Echinoidea) is not restricted to Oceanic Islands: evidence from morphological data. *Brazilian Journal of Biology*, 73(2), 431–435.

Gondim, A.I., Alonso, C., Dias, T.L.P., Manso, C.L.C. & Christoffersen, M.L. (2013b) A taxonomic guide to the brittle-stars (Echinodermata, Ophiuroidea) from the State of Paraíba continental shelf, Northeastern Brazil. *ZooKeys*, 307, 45–96.

Gondim, A.I., Christoffersen, M.L. & Dias, T.L.P. (2014) Taxonomic guide and historical review of starfishes in northeastern Brazil (Echinodermata, Asteroidea). *ZooKeys*, 449, 1–56.

Gondim, A.I., Dias, T.L.P., Christoffersen, M.L. & Stöhr, S. (2015) Redescription of *Hemieuryale pustulata* von Martens, 1867 (Echinodermata, Ophiuroidea) based on Brazilian specimens, with notes on systematics and habitat association. *Zootaxa*, 3925(3), 341–360.

González-Irusta, J.M., González-Porto, M., Sarralde, R., Arrese, B., Almón, B. & Martín-Sosa, P. (2015) Comparing species distribution models: a case study of four deep sea urchin species. *Hydrobiologia*, 745(1), 43–57.

Grantham, B.A., Eckert, G.L. & Shanks, A.L. (2003) Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications*, S108–S116.

Grainger, E.H. (1966) Sea stars (Echinodermata: Asteroidea) of Arctic North America. *Bulletin of Fisheries Research Board of Canada*, 152, 1–70.

Gray, *I.E.*, Downey, M.E. & Cerame-Vivas, M.J. (1968) Sea stars of North Carolina. *Fishery Bulletin*, 67(1), 127–163.

Greef, R. (1882) Echinodermen, beobachtet auf einer Reise nach der Guinea-Insel Sao Thome. *Zoologischer Anzeiger*, 5, 114–120, 135–139, 156–159.

Grieg, J.A. (1932) Echinodermata. *Report of the scientific results of the Michael Sars North Atlantic deep sea expedition 1910*, 3(2), 1–47.

Guille, A. (1981) Echinodermes: Ophiurides. Résultats des Campagnes MUSORSTOM. I – Philippines (18–28 March 1976). *Mémoires du Muséum national d'Histoire naturelle. Série A, Zoologie,* 91, 413–456.

Guille A. & Albuquerque, M.N. (1990) Stratégie de dispersion et insularité: Les Ophiures littorales de la chaîne des seamounts Vitoria-Trindade (Brésil). Résultats preliminaires. *In*: Ridder, C. De, Dubois, C., Lahaye, M.C. & Jangoux, M. (Eds.), *Echinoderm Research - Proceedings of the Second European Conference on Echinoderms, Brussels*, 18–21, September 1989. A.A. Balkema Publishers, Rotterdam, 125–129.

Guillou, M. & Diop, M. (1988) Ecology and demography of a population of *Anseropoda placenta* (Echinodermata: Asteroidea) in the Bay of Brest, Brittany. *Journal of the Marine Biological Association of the United Kingdom*, 68, 41–54.

Gukov, A.Y. (2011) Monitoring of the Bottom Biocenoses of the Novosibirsk Polynya. *Oceanology*, 51(3), 471–476.

Haedrich, R.L. & Maunder, J.E. (1985) The Echinoderm Fauna of the Newfoundland Continental Slope. *In*: B.F. Keegan & B.D.S. O'Connor (Eds.) *Echinodermata, Proceedings of the Fifth International Echinoderm Conference, Galway, September 1984*. A.A. Balkema, Rotterdam, 35–46 pp.

Haesaerts, D., Jangoux, M. & Flammang, P. (2006) Adaptations to benthic development: functional morphology of the attachment complex of the brachiolaria larva in the sea star *Asterina gibbosa*. *Biological Bulletin*, 211(2), 172–182.

Halpern, J.A. (1972) Pseudarchasterinae (Echinodermata, Asteroidea) of the Atlantic. *Proceedings of the Biological Society of Washington*, 85(30), 359–384.

Hamel, J.F. & Mercier, A. (1995) Prespawning behavior, spawning, and development of brooding starfish Leptasterias polaris. *Biological Bulletin*, 188(1), 32–45.

Harvey, E.B. (1956) *The American Arbacia and other sea urchins*. Princeton University Press. Princeton, viii+298.

Harvey, R., Gage, J.D., Billett, D.S.M., Clark, A.M. & Paterson, G.L.J. (1988) Echinoderms of the Rockall Trough and adjacent areas. 3. Additional records. *Bulletin British Museum Natural History*, Zoology, 54, 153–198.

Harwell, M.C. & Orth, R.J. (2002) Long-distance dispersal potential in a marine macrophyte. *Ecology*, 83(12), 3319–3330.

Harzhauser, M., Piller, W.E. & Steininger, F.F. (2002) Circum-Mediterranean Oligo–Miocene biogeographic evolution–the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183(1-2), 103-133.

Harzhauser, M., Kroh, A., Mandic, O., Piller, W. E., Göhlich, U., Reuter, M. & Berning, B. (2007) Biogeographic responses to geodynamics: a key study all around the Oligo–Miocene Tethyan Seaway. *Zoologischer Anzeiger*, 246(4), 241-256.

Heding, S.G. (1928) Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 46. Synaptidae. *Videnskabelige Meddelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, 85, 105–323.

Heding, S.G. (1931) *Uber die Synaptiden des Zoologischen Museums zu Hamburg.Zool. Jahrb. Jena (Syst.)*, 61, 637–698.

Heding, S.G. (1935a) Holothurioidea, Part 1: Apoda, Molpadioidea, Gephyrothurioidea. *The Danish Ingolf Expedition*, Hagerup, Copenhagen, 4 (9), 1–84.

Heding, S.G. (1935b) The Scoresby Sound Committee's 2nd East Greenland Expedition in 1932 to King Christian IX's Land. Echinoderms. *Meddelelser Grønland*. 104, 1–68.

Heding, S.G. (1936) Echinoderms. 6 & 7 Thule Expeditions til Sydostgronland 1931–1933. *Meddelelser Grønland*. 108, 34 pp.

Heding, S.G. (1942) Holothurioidea, Part 2: Aspidochirota, Elasipoda, Dendrochirota. *The Danish Ingolf Expedition*, Hagerup, Copenhagen, 4(13), 1–39.

Hendler, G. (1975) Adaptational significance of the patterns of ophiuroid development. *American Zoologist*, 15, 691–715.

Hendler, G. (1979) Sex-reversal and viviparity in *Ophiolepis kieri*, n. sp. with notes on viviparous brittlestars from the Carribbean (Echinodermata: Ophiuroidea). *Proceedings of the Biological Society in Washington*, 92(4), 783–795.

Hendler, G. (1988) Western Atlantic *Ophiolepis* (Echinodermata: Ophiuroidea): a description of *O. pawsoni* new species, and a key to the species. *Bulletin of Marine Science*, 42(2), 265–272.

Hendler, G. (1995) New species of brittle stars from the western Atlantic, *Ophionereis vittata*, *Amphioplus sepultus*, and *Ophiostigma siva*, and the designation of a neotype for *Ophiostigma isocanthum* (Say) (Echinodermata: Ophiuroidea). *Contributions in Science, Natural History Museum of Los Angeles County*, 458, 1–19.

Hendler, G. (2005) Two New Brittle Star Species of the Genus *Ophiothrix* (Echinodermata: Ophiuroidea: Ophiotrichidae) from Coral Reefs in the Southern Caribbean Sea, with notes on their Biology. *Caribbean Journal of Science*, 41(3), 583–599.

Hendler, G. (2011) New light on the nomenclature, taxonomy, and biology of *Hemipholis* species (Echinodermata: Ophiuroidea: Ophiactidae). *Zootaxa*, 3048, 44–52.

Hendler, G. & Littman, B.S. (1986) The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. *Coral Reefs*, 5, 31–34.

Hendler, G. & Miller, J.E. (1984) *Ophioderma devaneyi* and *Ophioderma ensiferum*, new brittlestar species from the Western Atlantic (Echinodermata: Ophiuroidea). *Proceedings of the Biological Society in Washington*, 97(2), 442–461.

Hendler G. & Pawson, D.I. (2000) Echinoderms of the Rhomboidal Cays, Belize: Biodiversity, Distribution, and Ecology. *Atoll Research Bulletin*, 479, 275–299.

Hendler, G. & Turner, R.L. (1987) Two new species of *Ophiolepis* (Echinodermata: Ophiuroidea) from the Caribbean Sea and Gulf of Mexico: with notes on ecology, reproduction, and morphology. *Contributions in Science, Natural History Museum of Los Angeles County*, 395, 1–14.

Herapath, W.B. (1865) On the genus *Synapta*, with some new British species. *Quarterly journal of microscopical science NS,* 5, 1–7.

Hernández J.C., Clemente, S., Tuya, F., Pérez-Ruzafa, A., Sangil, C., Moro-Abad, L. & Bacallado-Aránega, J.J. (2013) Echinoderms of the Canary Islands, Spain. *In*: Alvarado J.J. & Solis-Marin F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*. Springer Berlin Heidelberg, pp. 471–510.

Hernández-Díaz, Y.Q., Solís-Marín, F.A., Simões, N., Sanvicente-Añorve, L. (2013) First record of Ophioderma ensiferum (Echinodermata: Ophiuroidea) from the southeastern continental shelf of the Gulf of Mexico and from an anchialine cave. *Revista Mexicana de Biodiversidad*, 84(2), 676–681.

Hernández-Herrejón, L.A., Solís-Marín, F.A. & Laguarda-Figueras, A. (2008) Ofiuroideos (Echinodermata: Ophiuroidea) de las aguas mexicanas del golfo de México. *Revista Biología Tropical*, 56(3), 83–167.

Hérouard, E. (1902) Holothuries Provenant Des Campagnes De La Princesse-Alice. *Résultats Campagnes Scientifiques du Prince de Monaco*, xxi+62 pp.

Hérouard, E. (1923) Holothuries provenant des campagnes des yachts Princesse-Alice et Hirondelle ii (1898–1915). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 66, 1–161.

Hérouard, E. (1929) Holothuries de la côte Atlantique du Maroc et de Mauritaine. *Bulletin de la Société des Sciences Naturelles du Maroc*, 9, 36–70.

Herrero-Pérezrul, M.D., Granja-Fernández, R., Hoyos-Padilla, M. & Reyes-Bonilla, H. (2014) New record of the basket star *Gorgonocephalus eucnemis* (Ophiuroidea: Gorgonocephalidae) at the Pacific coast of Mexico. *Marine Biodiversity Records*, 7 (e33), 1–3, doi: 10.1017/S1755267214000323.

Higgins, R.C. (1975) Observations on the morphology of *Echinocardium cordatum* (Echinoidea: Spatangoida) from diverse geographical areas. *Journal of Zoology*, 177, 507–515.

Highsmith, R.C. (1985) Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series*, 25, 169–175.

Høisæter, T. (1990) An annotated check-list of the echinoderms of the Norwegian coast and adjacent waters. *Sarsia*, 75, 83–106.

Holmquist, J.G. (1994) Benthic macroalgae as a dispersal mechanism for fauna: influence of a marine tumbleweed. *Journal of Experimental Marine Biology and Ecology*, 180(2), 235–251.

Hotchkiss, F.H. (1982) Ophiuroidea (Echinodermata) from Carrie Bow Cay, Belize. *Smithsonian Contributions to the Marine Sciences*, 12, 387–412.

Hsü, K.J., Ryan, W.B.F. & Cita, M.B. (1973) Late Miocene desiccation of the Mediterranean. *Nature*, 242(5395), 240–244.

Imaoka, T., Irimura, S., Okutani, T., Oguro, C., Oji, T. & Kanazawa, K. (1991) Echinoderms from Continental Shelf and Slope around Japan. *Japan Fisheries Resource Conservation Association.* 2, 1–204.

Jablonski, D. & Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews*, 58, 21–89.

Jackson, J.B.C. (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. *Bulletin of Marine Science*, 39(2), 588–606.

Jeffery, C.H. & Emlet, R.B. (2003) Macroevolutionary consequences of developmental mode in temnopleurid echinoids from the Tertiary of southern Australia. *Evolution*, 57(5), 1031–1048.

Jesus, D. & Abreu, A.D. (1998) Contribution to the knowledge of the soft bottom echinoderms of Madeira Island. *Boletim do Museu Municipal do Funchal (História Natural)*, 50(286), 59–69.

Jesus, D.C. & Fonseca, L.C. (1999) First records of 13 echinoderm species on the southwest coast of Portugal. *Boletín Instituto Español de Oceanografía*, 15 (1–4), 343–349.

Jokiel, P.L. (1989) Rafting of reef corals and other organisms at Kwajalein Atoll. *Marine Biology*, 101(4), 483–493.

Kasyanov, V.L., Kryuchkova, G.A., Kulikova V.A. & Medvedeva, L.A. (1998) Larvae of marine bivalves and echinoderms. *Smithsonian Institution Libraries,* Washington, DC*,* 288 pp.

Kenchington, E.L., Cogswell, A.T., MacIsaac, K.G., Beazley, L., Law, B.A. & Kenchington, T.J. (2014) Limited depth zonation among bathyal epibenthic megafauna of the Gully submarine canyon, northwest Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography*, 104, 67–82.

Klitgaard, A.B. (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. *Sarsia*, 80, 1–22.

Knott, K.E., Balser, E.J., Jaeckle, W.B. & Wray, G.A. (2003) Identification of asteroid genera with species capable of larval cloning. *The Biological Bulletin*, 204(3), 246–255.

Koehler, R. (1896) Échinodermes. Résultats scientifiques de la Campagne du 'Caudan' dans le Golfe de Gascogne. *Annales de l'Université de Lyon*, 26, 33–127.

Koehler, R. (1898) Echinides et Ophiures provenant des campagnes du yacht Hirondelle (Golfe de Gascogne, Açores, Terre-Neuve). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 12, 78 pp.

Koehler, R. (1906) Ophiures. *Expeditions Scientifiques du Travailleur et du Talisman*, 8, 245–311.

Koehler, R. (1909) Echinodermes provenant des campagnes du yacht Princesse-Alice (Astéries, Ophiures, Echinides et Crinoïdes). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco*, 34, 1–317.

Koehler, R. (1914a) A Contribution to the Study of Ophiurans of the United States National Museum. *Bulletin of the United States National Museum*, 84, 1–173.

Koehler, R. (1914b) Echinoderma I: Asteroidea, ophiuroidea et Echnoidea. *In*: Michaelsen, W. (Ed.) *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. L. Friederichsen & Co., Hamburg, 1(2), 127–303.

Koehler, R. (1921) *Echinodermes. Faune de France, 1*. Librairie de la Faculte des Sciences, Paris, 216 pp.

Komatsu, M. Moritaki, T. & Suzuki, N. (2004) Development of an apodous holothuroid, *Oestergrenia variabilis* (Theel, 1886). *In*: Heinzeller, T. & Nebelsick, J.H. (Eds.) *Echinoderms: München. Proceedings of the 11th international echinoderm conference*, Munich, Germany, 6–10 October 2003. A.A. Balkema, Leiden, pp. 589–590.

Kornprobst, J.M. (2014) *Encyclopedia of Marine Natural Products, 2nd, Greatly Enlarged Edition*. Wiley-Blackwellm, Weinheim, 1731 pp.

Koukouras, A., Sinis, A.I., Bobori, D., Kazantzidis, S. & Kitsos, M.-S. (2007) The echinoderm (Deuterostomia) fauna of the Aegean Sea, and comparison with those of the neighbouring seas. *Journal of Biological Research*, 7, 67–92.

Kramers, P.G. (1971) New records of the holothurians, *Thyone serrifera* Oestergren (Dendrochirotida) and *Leptosynapta bergensis* (Oestergren) (Apodida). *Zoologische Mededelingen*, Leiden, 45, 193–195.

Krau, L. (1952) Sôbre uma nova espécie de echinoidea *Clypeaster oliveirai* (ordem Clypeastroida). *Memórias do Instituto Oswaldo Cruz*, 50, 703–712.

Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J. & Wilson, D.S. (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature*, 400(6745), 652–655.

Kroh, A. & Mooi, R. (2018) World Echinoidea database. Available from http://www.marinespecies.org/echinoidea/ at VLIZ. Accessed 2018-01-11. doi: 10.14284/170.

Kroh, A., Madeira, P. & Haring, E. (2011) Species distributions: virtual or real – the case of *Arbaciella elegans* (Echinoidea: Arbaciidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 99–105.

Laguarda-Figueras, A., Solís-Marín, F.A., Durán-González, A., Hernández-Pliego, P. & Del Valle-García, R. (2001) Holoturoideos (Echinodermata: Holothuroidea) of the Mexican Caribbean: Puerto Morelos, Quintana Roo, México. *Avicennia*, 14, 7–46.

Laguarda-Figueras, A., Abreu, M., Torres-Vega, J., Solís-Marín, F.A. & Durán-González, A. (2004) Ofiuroideos (Echinodermata: Ophiuroidea) del Caribe Mexicano: Puerto Morelos. *Avicennia*, 17, 13–34.

Laguarda-Figueras, A., Gutierrez-Castro, A., Solis-Marin, F.A., Duran-Gonzalez, A. & Torres-Vega, J. (2005a) Equinoideos (Echinodermata: Echinoidea) del Golfo De Mexico. *Revista de Biología Tropical*, 53(3), 69–108.

Lawrence, J.M. (2001) *Edible sea urchins: biology and ecology*. Elsevier, Amsterdam, 419 pp.

Lawrence, J.M. & Herrera, J. (2002) Stress and deviant reproduction in echinoderms. *Zoological Studies*, 39(3), 151–171.

Lawrence, J.M., Durán-González, A., Solís-Marín, F.A., Herrera, J. & Ventura, C.R.R. (2013) Distribution of *Luidia clathrata* and *Luidia lawrencei* (Echinodermata: Asteroidea) along the coast of the western Atlantic Ocean, the Gulf of Mexico and the Caribbean Sea. *Cahiers de Biologie Marine*, 54, 525–529.

Lessios, H.A., Lockhart, S., Collin, R., Sotil, G., Sanchez-Jerez, P., Zigler, K.S., Perez, A.F., Garrido, M.J., Geyer, L.B., Bernardi, G., Vacquier, V.D., Haroun, R. & Kessing, B.D. (2011) Phylogeography and bindin evolution in *Arbacia*, a sea urchin genus with an unusual distribution, *Molecular Ecology*, 21, 130–144.

Levitan, D.R. & Young, C.M. (1995) Reproductive success in large populations: empirical measures and theoretical predictions of fertilization in the sea biscuit Clypeaster rosaceus. *Journal of Experimental Marine Biology and Ecology*, 190, 221–241

Lima, E.J B. & Fernandes, M.L.B. (2009) Diversidade de equinodermos (Echinodermata) no Estado de Pernambuco (Brasil). *Revista Brasileira de Zoociências*, 11(1), 55–63.

Lima, M.L.F., Correia, M.D., Sovierzoski, H.H. & Manso, C.L.C. (2011) New records of Ophiuroidea (Echinodermata) from shallow-waters off Maceió, State of Alagoas, Brazil. *Marine Biodiversity Records*, 4(e97), 1–10, doi: 10.1017/S175526721100090X.

Ljungman, A.V. (1872) Förteckning öfver uti Vestindien af Dr A. Goës samt under korvetten Josefinas expedition i Atlantiska Oceanen samlade Ophiurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 1871, 28(5), 615–658

Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., Garcia, H.E., Baranova, O.K., Zweng, M.M., Paver, C.R., Reagan, J.R., Johnson, D.R., Hamilton, M. & Seidov, D. (2013) *World Ocean Atlas 2013, Volume 1: Temperature*. *In*: Levitus, S. & Mishonov, A. (Eds.), NOAA Atlas NESDIS 73, 40 pp, https://www.nodc.noaa.gov/OC5/woa13/woa13data.html

Loosanoff, V.L. (1964) Variations in the time and intensity of setting of the starfish, *Asterias forbesi*, in Long Island Sound during a twenty-five-year period. *Biological Bulletin*, 126, 423–439.

Lopes, E.M. & Ventura, C.R.R. (2016) Development of the Sea Star *Echinaster (Othilia) brasiliensis*, with Inference on the Evolution of Development and Skeletal Plates in Asteroidea. *Biological Bulletin*, 230(1), 25–34.

Loeuff, P. Le (1993) La faune benthique des fonds chalutables du plateau continental de la Guinée: premiers résultats en référence à la faune de la Côte-d'Ivoire. *Revue d'Hydrobiologie Tropicale*, 26(3), 229–252.

Loeuff, P. Le & Intès, A. (1968) La faune benthique du plateau continental de Cote d'Ivoire. *Document Scientifique et Technique du Centre – ORSTOM de Brest*, 25, 106 pp.

Lubbock, R. (1980) The shore fishes of Ascension Island. *Journal of Fish Biology*, 17(3), 283–303.

Lyman, T. (1878) Ophiurans. Reports on the dredging operations of the US coast survey Str. "Blake". *Bulletin of the Museum of Comparative Zoology*, 5(9), 217–238.

Lyman, T. (1882) Report on the Ophiuroidea. *Report on the Scientific Results of the Voyage of H.M.S. Challenger 1873–1876. Zoology*, 5(14), 1–386.

Lyman, T. (1883) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Carribbean Sea (1878–79), and on the east coast of the United States, during the summer of 1880, by the U.S. coast survey steamer 'Blake', commander J.R. Bartlett, U.S.N., commanding.

XX.– Report on the Ophiuroidea. *Bulletin of the Museum of Comparative Zoology at Harvard*, 10(6), 227–287.

Macpherson, E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society B*, 269, 1715–1720.

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61 (3), 243–264.

Madeira, P., Kroh, A., Melo, C., Cordeiro & Ávila, S.P. (2017) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic). *In*: Ávila, S.P. & Melo, C. (Eds.). RCANS *2017 - 6th Regional Committee on Neogene Atlantic Stratigraphy, Ponta Delgada, São Miguel Island, Azores, July, 10-13, University of the Azores (Abstract Book)*, p. 44.

Madsen, F.J. (1950) The echinoderms collected by the Atlantide Expedition, 1945–46. 1. Asteroidea. *Atlantide Reports*, 1, 167–222.

Madsen, F.J. (1970) West African Ophiuroids. *Atlantide Reports*, 11, 151–243.

Madsen, F.J. (1987) The *Henricia sanguinolenta* complex (Echinodermata, Asteroidea) of the Norwegian Sea and adjacent waters. A re-evaluation, with notes on related species. *Steenstrupia*, 13(5), 201–268.

Mah, C.L. (2015) A new Atlantic species of *Evoplosoma* with taxonomic summary and *in situ* observations of Atlantic deep-sea corallivorous Goniasteridae (Valvatida; Asteroidea). *Marine Biodiversity Records*, 8(5e), 1–15, doi: 10.1017/S1755267214001407.

Mah, C.L. & Blake, D.B. (2012) Global Diversity and Phylogeny of the Asteroidea (Echinodermata). *PLoS One*, 7(4), 1–22, doi: 10.1371/journal.pone.0035644.

Mah, C.L., Neill, K., Eléaume, M. & Foltz, D. (2014) New Species and global revision of Hippasteria (Hippasterinae: Goniasteridae; Asteroidea; Echinodermata). *Zoological Journal of the Linnean Society*, 171, 422–456.

Manso, C.L.C. (2004) Echinodermata da Bacia de Camamu, Bahia, Brasil. *Biologia Geral e Experimental*, 5(1), 19–25.

Manso, C.L.C. (2010) Deep-water Ophiuroidea (Echinodermata) from off Chile in the Eastern South Pacific. *Biota Neotropica*, 10(2), 185–199.

Manso, C.L.C., Alves, O.F. de S. & Martins L.R. (2008) Echinodermata da Baía de Todos os Santos e da Baía de Aratu (Bahia, Brasil). *Biota Neotropica*, 8(3), 179–196.

Manso, C.L.C., Gondim, A.I. & Ventura, C.R.R. (2014) New records of Ophiuroidea (Echinodermata) of the Brazilian coast, with notes on its taxonomy and distribution. *Marine Biodiversity Records*, 7(e124), 1–7, doi: 10.1017/S1755267214001237.

Marques, V.M. (1980) Echinodermes recueillis pedant la mission «Hesperides 76» du N/O Jean Charcot. *Arquivo do Museu Bocage*, 2ª série, 7(7), 95–107.

Marques, V.M., Calvário, J., Marques, J., Reis, C. & Santos, R. (1982) Contribuição para o estudo dos povoamentos bentónicos (substrato rochoso) da costa ocidental portuguesa. Zona intertidal. *Oecologia aquatic*, 6, 119–145.

Marshall, D.J., Krug, P.J., Kupriyanova, E.K., Byrne, M. & Emlet, R.B. (2012) The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution, and Systematics*, 43, 97–114.

Martínez, S. (2009) Shallow-water Asteroidea and Ophiuroidea of Uruguay: composition and biogeography. *Revista de Biología Tropical*, 56 (Suppl. 3), 205–214.

Martínez-Melo, A., Solís-Marín, F.A. & Laguarda-Figueras, A. (2014) New record of the irregular sea urchin *Rhynobrissus cuneus* (Echinoidea: Brissidae). *Revista Mexicana de Biodiversidad*, 85, 617–620.

Martins, L. (2013. *Estudo Taxonômico dos Holothuroidea (Echinodermata) de águas rasas da costa Brasileira*. Master tesis (unpublished), Universidade Federal da Bahia, Brazil, 119 pp.

Martins, L., Souto, C., Braga, J. & Tavares, M. (2016) Echinoidea and Holothuroidea (Echinodermata) of the Trindade and Martin Vaz Archipelago, off Brazil, with new records and remarks o1n taxonomy and species composition. *Journal of the Marine Biological Association of the United Kingdom*, 1–35, doi: 10.1017/S0025315416001569.

Martynov, A. (2010) Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. *Zootaxa*, 2697, 1–154.

Martynov, A.V. & Litvinova N.M. (2008) Deep-water Ophiuroidea of the northern Atlantic with descriptions of three new species and taxonomic remarks on certain genera and species. *Marine Biology Research*, 4, 76–11.

Massin, C. (1993) The Holothurioidea (Echinodermata) collected during the Tyro Mauritania–II expedition 1988. *Zoologische Mededelingen*, Leiden, 67, 397–429.

Massin, C., Robar-Matheson, A., Hamel, J.-F. & Mercier, A. (2014) First records of *Thyone inermis* and *Labidoplax buskii* (Echinodermata: Holothuroidea) in Canadian waters. *Marine Biodiversity Records*, 7(e128), 1–5, doi: 10.1017/S1755267214001249.

Mastrototaro, F. & Mifsud, C. (2008) Some observations on the morphology of *Sclerasterias richardi* a rarely encountered Mediterranean Sea star (Echinodermata: Asteriidae). *Mediterranean Marine Science*, 9(2), 103–109.

Mastrototaro F, D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P., Gherardi, M. Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C., Boero, F., Taviani, M., Tursi, A. (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): An update. *Deep Sea Research Part II: Topical Studies in Oceanography*, 57, 412–430.

McClary, D.J. & Mladenov, P.V. (1990) Brooding biology of the sea star *Pteraster militaris* (O.F. Müller): energetic and histological evidence for nutrient translocation to brooded juveniles. *Journal of Experimental Marine Biology and Ecology*, 142, 183–199.

McClintock, J.B., Hopkins, T., Marion, K., Watts, S. & Schinner, G. (1993) Population structure, growth and reproductive biology of the gorgonocephalid brittlestar *Asteroporpa annulata*. *Bulletin of Marine Science*, 52, 925–936.

McEdward, L. & Janies, D. (1997) Relationships among development, ecology, and morphology in the evolution of echinoderm larvae and life cycles. *Biological Journal of the Linnean Society*. 60, 381–400.

McEdward, L.R. & Miner, B.G. (2001) Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology*, 79, 1125–1170.

McKenzie, J.D. (1991) The taxonomy and natural history of north European dendrochirote holothurians (Echinodermata), *Journal of Natural History*, 25, 123–171.

Mecho, A., Billett, D.S.M., Ramírez-Llodra, E., Aguzzi, J., Tyler, P.A. & Company, J.B. (2014) First records, rediscovery and compilation of deep-sea echinoderms in the middle and lower continental slope of the Mediterranean Sea. *Scientia Marina*, 78(2), 281–302.

Mercier, A., Pawson, D.L., Pawson, D.J. & Hamel, J-F. (2010) First record of the sea cucumber *Trachythyone nina* (Echinodermata: Holothuroidea) in Canadian waters, with a redescription of the species and notes on its distribution and biology. *Marine Biology Research*, 6(3), 315–320.

Messing, C.G. (1985) Submersible observations of deep-water crinoid assemblages in the tropical western Atlantic Ocean. *In*: Keegan, B.F. & O'Connor, B.D.S. (Eds.) Proceedings 5th international Echinoderm Conference, Galway. A.A. Balkema, Amsterdam, p. 185–193.

Messing, C.G. (2013) A revision of the genus *Atelecrinus* PH Carpenter (Echinodermata: Crinoidea). *Zootaxa*, 3681(1), 1–43.

Messing, C.G. & Dearborn, J.H. (1990) Marine Flora and Fauna of the Northeastern United States Echinodermata: Crinoidea *NOAA Technical Report NMFS*, NOAA/National Marine Fisheries Service, 90, 29 pp.

Metaxas, A., Scheibling, R.E., Robinson, M.C., Young, C.M. (2008) Larval Development, Settlement, and Early Post-Settlement Behavior of the Tropical Sea Star Oreaster Reticulatus. *Bulletin of Marine Science*, 83(3), 471–480.

Meyer, D.L., Messing, C.G. & Macurda Jr., D.B. (1978) Biological results of the University of Miami deep-sea expeditions. 129. Zoogeography of tropical western Atlantic Crinoidea (Echinodermata). *Bulletin of Marine Science*, 28(3), 412–441.

Micael, J., Alves, M.J., Costa, A.C. & Jones, M.B. (2009) Exploitation and Conservation of Echinoderms. *Oceanography and Marine Biology: An Annual Review*, 47, 191–208.

Micael, J., Rodrigues, P., Costa, A.C. & Alves, M.J. (2014) Phylogeography and genetic diversity of *Ophidiaster ophidianus* (Echinodermata: Asteroidea) — evidence for a recent range expansion in the Azores. *Journal of the Marine Biological Association of the United Kingdom*, 94, 1475–1484.

Mifsud, C., M. Taviani & S. Stohr (2009) Remarks on Echinodermata from the South Central Mediterranean Sea based upon collections made during the MARCOS cruise (10 to 20th April, 2007). *Mediterranean Marine Science*, 10(2), 63–71.

Mileikovsky, S.A. (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Marine Biology*, 10(3), 193–213.

Miller, J.E. (1984) Systematics of the ophidiasterid sea stars *Copidaster lymani* A.H. Clark, and *Hacelia superba* H.L. Clark (Echinodermata: Asteroidea) with a key to species of Ophidiasteridae from the Western Atlantic. *Proceedings of the Biological Society of Washington*, 97(1), 194–208.

Miller, J.E. & Turner, R.L. (1986) *Psolus pawsoni* (Echinodermata: Holothuroidea), a new bathyal sea cucumber from the Florida east coast. *Proceedings of the Biological Society of Washington*, 99(3), 478–485.

Miloslavich, P., Díaz, J.M., Klein, E., Alvarado, J.J., Díaz, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J.J., Weil, E., Cortés, J., Bastidas, A.C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A. & Ortiz, M. (2010) Marine biodiversity in the Caribbean: regional estimates and distribution patterns. PloS one, 5(8), 1–25, doi: 10.1371/journal.pone.0011916.

Mironov, A.N. (2006a) Echinoids from seamounts of the north-eastern Atlantic, onshore/offshore gradients in species distribution. *In*: Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*, KMK Scientific Press, Russian Academy of Sciences, P.P. Shirshov Institute of Oceanology, Moscow, pp. 96–133.

Mironov, A.N. (2006b) Centers of marine fauna redistribution. *Entomological Review*, 86, S32–S44.

Mironov, A.N. (2008) Pourtalesiid sea urchins (Echinodermata: Echinoidea) of the northern Mid-Atlantic Ridge. *Marine Biology Research*, 4, 3–24.

Mironov, A.N. (2014) Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Echinoidea. *Invertebrate Zoology*, 11(1), 120–129.

Mironov, A.N. & Dilman, A.B. (2010) Effect of the East Siberian barrier on the echinoderm dispersal in the Arctic Ocean. *Oceanology*, 50, 342.

Mironov, A.N. & Krylova, E.M. (2006) Origin of the fauna of the Meteor Seamounts, north-eastern Atlantic. *In*: Mironov, A.N., Gebruk, A.V. & Southward, A.J. (Eds.) *Biogeography of the North Atlantic Seamounts*, pp. 22–57.

Mladenov, P.V. (1996) Environmental factors influencing asexual reproductive processes in echinoderms. *Oceanologica acta*, 19(3–4), 227–235.

Mlandenov, P.V. & Emson, R.H. (1988) Density, size structure and reproductive characteristics of fissiparous brittle stars in algae and sponges: evidence for interpopulational variation in levels of sexual and asexual reproduction. *Marine Ecology Progress Series*, 42, 181–194.

Mladenov P.V., Carson, S.F. & Walker, C.W. (1986) Reproductive ecology of an obligately fissiparous population of the sea star *Stephanasterias albula* (Stimpson). *Journal of Experimental Marine Biology and Ecology*, 96, 155–175.

Molnar, P. (2008) Closing of the Central American Seaway and the Ice Age: A critical review. *Paleoceanography*, 23(PA2201), 1–15, doi:10.1029/2007PA001574

Mooi, R. (1990a) A New “Living Fossil” Echinoid (Echinodermata) and the Ecology and Paleobiology of Caribbean Cassiduloids. *Bulletin of Marine Science*, 46(3), 688–700.

Mooi, R. (1990b) Living Cassiduloids (Echinodermata: Echinoidea): a key and annotated list. *Proceedings of the Biological Society of Washington*, 103(1), 63–85.

Morrone, J.J. (1994) On the identification of areas of endemism. *Systematic Biology*, 43(3), 438–441.

Moreno-Batet E. & Bacallado, J.J. (1980) Sur une collection d’astéries del’Archipel des Canaries. *In*: Jangoux, M. (Ed.) *Proceedings of the European colloquium on Echinoderms, Brussels, 3–8th September 1979, Amsterdam*, A.A. Balkema, pp. 123–126.

Mortensen, T. (1903) Echinoidea (Part 1). *The Danish Ingolf–Expedition 1895–1896*, Bianco Luno, Copenhagen, 4(1), 1–198.

Mortensen, T. (1913) On the development of some British echinoderms. *Journal of the Marine Biological Association of the United Kingdom*, 10 (1), 1–18.

Mortensen, T. (1921) *Studies of the Development and Larval Forms of Echinoderms*. G.E.C. Gad, Copenhagen, 294 pp.

Mortensen, T. (1925) Echinodermes du Maroc et de Mauritanie. *Bulletin de la Société des sciences naturelles du Maroc*, 5(4–5), 178–187.

Mortensen, T. (1927a*) Handbook of the echinoderms of the British Isles*. Oxford University Press, viii (8)+471 pp.

Mortensen, T. (1927b) Sur les échinides recueillis par l’expédition du “Travailleur” et du “Talisman.”. *Archives du Muséum d’Histoire Naturelle*, 2(6), 21–34.

Mortensen, T. (1928) *A Monograph of the Echinoidea. I. Cidaroidea*. C.A. Reitzel & Oxford University Press, Copenhagen & London, 551 pp.

Mortensen, T. (1933a) Ophiuroidea. *The Danish Ingolf Expedition*, 4(8), 1–121.

Mortensen, T. (1933b) The echinoderms of St. Helena (Other than crinoids), Papers from Dr. Th. Mortensen’s Pacific Expedition 1914–16. 66. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening, 93(3), 401–473.

Mortensen, T. (1935) *A Monograph of the Echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta*. C.A. Reitzel & Oxford University Press, Copenhagen & London, 647 pp.

Mortensen, T. (1936) Echinoidea and Ophiuroidea. *Discovery Reports*, 12, 199–348.

Mortensen, T. (1940) *A Monograph of the Echinoidea. III, 1. Aulodonta, with Additions to Vol. II (Lepidocentroida and Stirodonta)*. C.A. Reitzel, Copenhagen, 370 pp.

Mortensen, T. (1941) Echinoderms of Tristan da Cunha. *Results of the Norwegian scientific expedition to Tristan da Cunha 1937–1938*, Det Norske Videnskaps Akademi, Oslo, 7, 1–10 pp.

Mortensen, T. (1943a.) *A Monograph of the Echinoidea. III, 3. Camarodonta. II. Echinidæ, Strongylocentrotidæ, Parasaleniidæ, Echinometridæ*. C.A. Reitzel, Copenhagen, 446 pp.

Mortensen, T. (1943b) *A Monograph of the Echinoidea. III, 2. Camarodonta. I. Orthopsidæ, Glyphocyphidæ, Temnopleuridæ and Toxopneustidæ*. C.A. Reitzel, Copenhagen, 553 pp.

Mortensen, T. (1948) A Monograph of the Echinoidea. IV, 2. Clypeasteroida. Clypeasteridæ, Arachnoidæ, Fibulariidæ, Laganidæ and Scutellidæ. C.A. Reitzel, Copenhagen, 471 pp.

Mortensen, T. (1951a) *A Monograph of the Echinoidea. V, 2. Spatangoida II. Amphisternata II. Spatangidæ, Loveniidæ, Pericosmidæ, Schizasteridæ, Brissidæ.* C.A. Reitzel, Copenhagen, 593 pp.

Mortensen, T. (1951b) Report on the Echinoidea collected by the "Atlantide" Expedition. *Atlantide Report*, 2, 293–303.

Morton, B., Britton, J.C. & de Frias Martins, A.M. (1998) *Ecologia Costeira dos Açores*. Sociedade Afonso chaves, Ponta Delgada, x+249 pp.

Moyse, J. & Tyler, P.A. (1995) Sea urchins, starfish and sea cucumbers (Phylum Echinodermata). *In*: Hayward, P.J. & Ryland, J.S. (Eds.) *Handbook of the marine fauna of North-West Europe*. Oxford University Press, pp. 662–686.

Murillo, F.J., Serrano, A., Kenchington, E. & Mora, J. (2015) Epibenthic assemblages of the tail of the grand bank and Flemish cap (northwest Atlantic) in relation to environmental parameters and trawling intensity. *Deep Sea Research Part I: Oceanographic Research Papers*, 109, 99–122.

Muths, D., Davoult, D., Gentil, F. & Jollivet, D. (2006) Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. *Molecular Ecology*, 15, 3303–3318.

Nataf, G. & Cherbonnier, G. (1973) Les Astérides d'Afrique occidentale, utilisation du microscope électronique à balayage pour une étude systématique des *Luidia*. *Bulletin du Museum National D'Histoire Naturelle*, 3ª série, Zoologie, Paris, 107(81), 69–102.

Nataf, G. & Cherbonnier, G. (1975) Troisieme contribution a la connaissance des Asterides de la cote occidentale d'Afrique. *Bulletin du Museum National D'Histoire Naturelle*, 3ª série, Zoologie, Paris, 311(218), 813–834.

Navarro, P.G., García-Sanz, S. & Tuya, F. (2012) Reproductive biology of the sea cucumber *Holothuria sanctori* (Echinodermata: Holothuroidea). *Scientia Marina*. 76(4), 741–752.

Néraudeau, D., Barbe, S., Mercier, D. & Roman, J. (2003) Signatures paléoclimatiques des échinides du Néogène final Atlantique à faciès redonien. *Annales de Paléontologie*, 89, 153–170.

Néraudeau, D., Goubert, E., lacour, D. & Rouchy, J.M. (2001) Changing biodiversity of Mediterranean irregular echinoids from the Messinian to present-day. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 175, 43–60.

Netto, L.F., Hadel, V.F. & Tiago, C.G. (2005) Echinodermata from São Sebastião Channel (São Paulo, Brazil). *Revista Biología Tropical*, 53 (3), 207–218.

Nobre, A. (1938) *Equinodermes de Portugal (3rd Edition)*. Companhia Editora do Minho, Barcelos, Portugal, 215 pp.

Norkko, J., Bonsdorff, E. & Norkko, A. (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. *Journal of Experimental Marine Biology and Ecology*, 248(1), 79–104.

Obuchi, M., Fujita, Y., Nakano, Y., Uehara, T. & Motokawa, T. (2010) Reproductive biology and early life history of the hermaphroditic feather star *Dorometra sesokonis* (Echinodermata: Crinoidea). *Marine biology*, 157(6), 1191–1201.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. & Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, 104(4), 1266–1271.

O'Hara, T. (1998) Origin of Macquarie Island echinoderms. *Polar Biology*, 20(2), 143–151.

Okanishi, M. & Fujita, T. (2011) A taxonomic review of the genus *Astrocharis* Koehler (Echinodermata: Ophiuroidea: Asteroschematidae) with a description of a new species. *Zoological Science*, 28, 148–157.

Okanishi, M., Olbers, J.M. & Fujita, T. (2013) A taxonomic review of the genus Asteromorpha Lütken (Echinodermata: Ophiuroidea: Euryalidae). *The Raffles Bulletin of Zoology,* 61(2), 461–480.

O'Loughlin, P.M. (1994) Brood-protecting and fissiparous cucumariids (Echinodermata, Holothurioidea). *In*: Guille, F. & Roux, M. (Eds.) *Echinoderms through time*, Balkema, Rotterdam, pp. 539–547.

O'Loughlin, P.M. & Ahearn, C. (2005) A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific oceans. *Memoirs of Museum Victoria*, 62(2), 147–179.

O'Loughlin, P.M. & Rowe, F.W.E. (2006) A systematic revision of the asterinid genus *Aquilonastra* O'Loughlin, 2004 (Echinodermata: Asteroidea). *Memoirs of Museum Victoria*, 63(2), 257–287.

O'Loughlin, P.M. & Waters, J.M. (2004) A molecular and morphological revision of genera of Asterinidae (Echinodermata: Asteroidea). *Memoirs of Museum Victoria*, 61(1), 1–40.

Östergren, H. (1902) The Holothurioidea of Northern Norway. *Bergens Museum Aarbog*, 9, 1–34.

Paim, F.G., Guerrazzi, M.C. & Borges, M. (2015) Descriptive and illustrated diagnosis of Ophiuroidea fauna (Echinodermata) in the shallow-waters of North-eastern Brazil. *Marine Biodiversity Records*, 8(e86), 1–17, doi: 10.1017/S1755267215000652.

Palacio, F.J. (1980) Revisión zoogeográfica marina del sur del Brasil. *Boletim do Instituto Oceanográfico de São Paulo*, 31(1), 69–92.

Pálmason, G. (1974) The insular margins of Iceland. *In*: Burk, C.A. & Drake, C.L. (Eds.), The *Geology of Continental Margins*, Springer Verlag, pp. 375–379.

Pannell, J.R., Auld, J.R., Brandvain, Y., Burd, M., Busch, J.W., Cheptou, P.O., Conner, J.K., Goldberg, E.E., Grant, A.-G., Grossenbacher, D.L., Hovick, S.M., Igic, B., Kalisz, S., Petanidou, T., Randle, A.M., de Casas, R.R., Pauw, A., Vamosi, J.C. & Winn, A.A. (2015) The scope of Baker's law. *New Phytologist*, 208, 656–667.

Paterson, G.L.J. (1985) The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History)*, Zoology Series, 49(1), 1–162.

Paterson, G.L.J., P.A. Tyler & J.D. Gage (1982) The taxonomy and zoogeography of the genus *Ophiocten* (Echinodermata: Ophiuroidea) in the North Atlantic Ocean. *Bulletin of the British Museum (Natural History)*, *Zoology*, 43(3), 109–128.

Pawson, D.L. (1967) The psolid holothurian genus *Lissothuria*. *Proceedings of the United States National Museum*, 122(3592), 1–17.

Pawson, D.L. (1968) A new psolid sea cucumber from the Virgin Islands. *Proceedings of the Biological Society of Washington*, 81, 347–350.

Pawson, D.L. (1976a) Two new sea cucumbers (Echinodermata: Holothuroidea) from the eastern United States. *Proceedings of the Biological Society of Washington*, 89(34), 405–410.

Pawson, D.L. (1976b) Shallow-water sea cucumber (Echinodermata: Holothuroidea) from Carrie Bow Cay, Belize. *Proceedings of The Biological Society of Washington*, 89(31), 369–382.

Pawson, D.L. (1977) Marine Flora and Fauna of the Northeastern United States. Echinodermata: Holothuroidea. *NOAA Technical Report NMFS*, 405, 15 pp.

Pawson, D.L. (1978) The Echinoderm Fauna of Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to the Marine Sciences*, 2, 31 pp.

Pawson, D.L. (2007a) Phylum echinodermata. *Zootaxa*, 1668, 749–764.

Pawson, D.L. (2007b) *Narcissia ahearnae*, a new species of sea star from the Western Atlantic (Echinodermata: Asteroidea: Valvatida). *Zootaxa*, 1386, 53–58.

Pawson, D.L., Vance, D.J. & Haern, C. (2001) Western Atlantic sea cucumbers of the Order Molpadiida (Echinodermata: Holothuroidea). *Bulletin of the Biological Society of Washington*, 10, 311–327.

Pawson, D.L. & Miller, J.E. (1983) Systematics and ecology of the sea-urchin genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans. *Smithsonian Contributions to the Marine Sciences*, 20, 1–15.

Pawson, D.L. & Pawson, D.J. (2013) Bathyal sea urchins of the Bahamas, with notes on covering behavior in deep sea echinoids (Echinodermata: Echinoidea). *Deep Sea Research Part II: Topical Studies in Oceanography*, 92, 207–213.

Pawson, D.L., Pawson, D.J. & King, R.A. (2010) A taxonomic guide to the Echinodermata of the South Atlantic Bight, USA: 1. Sea cucumbers (Echinodermata: Holothuroidea). *Zootaxa*, 2449, 1–48.

Pawson, D.L., Vance, D.J., Messing, C.G., Solís-Marin, F.A. & Mah, C.L. (2009) Echinodermata of the Gulf of Mexico. *In*: Felder D.L. & Camp, D.K. (Eds.) *Gulf of Mexico: origin, waters, and biota, vol. 1, Biodiversity*. Texas A & M University Press, College Station, pp. 1177–1204.

Pearse, J.S. (1994) Cold-water echinoderms break ‘Thorson’s rule’. *In*: Young, C.M. & Eckelbarger, K.J. (Eds.) *Reproduction, larval biology, and recruitment of the deep-sea benthos*. New York: Columbia University Press, 26–43.

Pechenik, J.A. (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, 177, 269–297.

Peck, J.R., Yearsley, J.M. & Waxman, D. (1998) Explaining the geographic distributions of sexual and asexual populations. *Nature*, 391(6670), 889–892.

Pereira, P. (2008). *Echinoids from the Neogene of Portugal mainland: Systematics, Palaeoecology, Palaeobiogeography*. Ph. D. thesis, University of Lisbon, 200 pp.

Pérès, J.M. (1964) Contribution à l'étude des peuplements benthiques du golfe Ibéro–Marocaine. Campagne de la Calypso en mer d'Alboran et dans la Baie Ibéro–Marocaine (1958), 20. *Annales de l'Institut Oceanographique*, 41, 3–30.

Pérez-Portela, R., Villamor, A. & Almada, V. (2010) Phylogeography of the sea star *Marthasterias glacialis* (Asteroidea, Echinodermata): deep genetic divergence between mitochondrial lineages in the north-western mediterranean. *Marine Biology*, 157(9), 2015–2028.

Pérez-Ruzafa, A., Marcos, C. & Bacallado, J.J. (1992a) Holoturias (Echinodermata: Holothuroidea) de las Islas Canarias: I. Consideraciones Generales y Orden Aspidochirotida. *Revista de la Academia Canaria de Ciencias*, 4(3–4), 139–162.

Pérez-Ruzafa, A., Marcos, C. & Bacallado, J.J. (1992b) Holoturias (Echinodermata: Holothuroidea) de las Islas Canarias: II. Ordenes Dendrochirotida, Elasipodida, Apodida y Molpadida. *Revista de la Academia Canaria de Ciencias*, 4(3–4), 163–185.

Pérez-Ruzafa, A., Entrambasaguas, L. & Bacallado, J.J. (1999) Fauna de equinodermos (Echinodermata) de los fondos rocosos infralitorales del archipielago de Cabo Verde. *Revista de la Academia Canaria de Ciencias*, 11 (3–4), 43–62.

Pérez-Ruzafa, A., Entrambasaguas, L., Espejo, C., Marcos, C. & Bacallado, J.J. (2002) Fauna de equinodermos (Echinodermata) de los fondos rocosos infralitorales del archipiélago de Salvajes (Océano Atlantico). *Revista de la Academia Canaria de Ciencias*, 14 (3–4), 277–296.

Pérez-Ruzafa, A.P., J.J.B. Aránega, I.A. García & J.R.D. Díaz (2003) División Echinodermata. *In*: Moro, L., J.L. Martìn, M.J. Garrido & I. Izquierdo (Eds.) *Lista de especies marinas de Canarias (algas, hongos, plantas y animales)*. Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias, 112–113.

Pérez-Ruzafa, A., Alvarado, J.J., Solís-Marín, F.A., Hernández, J.C., Morata, A., Marcos, C., Abreu-Pérez, M., Aguilera, O., Alió, J., Bacallado-Aránega, J.J., Barraza, E., Benavides-Serrato, M., Benítez-Villalobos, F., Betancourt-Fernández, L., Borges, M., Brandt, M., Brogger, M.I., Borrero-Pérez, G.H., Buitrón-Sánchez, B.E., Campos, L.S., Cantera, J.R., Clemente, S., Cohen-Renfijo, M., Coppard, S.E., Costa-Lotufo, L., Valle-García, R. del, Díaz de Vivar, M.E., Díaz-Martínez, J.P., Díaz, Y., Durán-González, A., Epherra, L., Escolar, M., Francisco, V., Freire, C.A., García-Arrarás, J.E., Gil, D.G., Guarderas, P., Hadel, V.F., Hearn, A., Hernández-Delgado, E.A., Herrera-Moreno, A., Herrero-Pérezrul, M.D., Hooker, Y., Honey-Escandón, M.B.I., Lodeiros, C., Luzuriaga, M., Manso, C.L.C., Martín, A., Martínez, M.I., Martínez, S., Moro-Abad, L., Mutschke, E., Navarro, J.C., Neira, R., Noriega, N., Palleiro-Nayar, J., Pérez, A.F., Prieto-Ríos, E., Reyes, J., Rodríguez-Barreras, R., Rubilar, T., Sancho-Mejías, T.I., Sangil, C., Silva, J. R.M.C., Sonnenholzner, J.I., Ventura, C.R.R., Tablado, A., Tavares, Y., Tiago, C.G., Tuya, F., Williams, S.M. (2013) Latin America Echinoderm Biodiversity and Biogeography: Patterns and Affinities. *In*: Alvarado, J.J. & Solis-Marin, F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*, 511–542.

Perrier, M.E. (1894) Stellérides. *Expéditions Scientifiques du Travailleur et du Talisman*, Masson, Paris, 1–431.

Perrier, R. (1902) Holothuries. *Expéditions Scientifiques du Travailleur et du Talisman pendant les Années 1880, 1881, 1882, 1883. Ouvrage publié sous les auspices du ministère de l'instruction publique sous la direction de A. Milne-Edwards de 1888 à 1890 et continué par E. Perrier*. Masson et Cie, Editeurs, Paris, 7, 273–554

Petzelt, C. (2005) Are echinoderms of interest to biotechnology? *In*: Matranga, V. (Ed.) *Echinodermata*. Berlin, Heidelberg, New York, Springer-Verlag, pp. 1–6.

Pfaller, J.B., Frick, M.G., Reich, K.J., Williams, K.L. & Bjorndal, K.A. (2008) Carapace epibionts of loggerhead turtles (*Caretta caretta*) nesting at Canaveral National Seashore, Florida. *Journal of Natural History*, 42(13–14), 1095–1102.

Picton, B. (1993) *A field guide to the shallow-water echinoderms of the British Isles*. IMMEL Publishing Lda, 96 pp.

Piepenburg, D., Chernova, N.V., von Dorrien, C.F., Gutt, J., Neyelov, A.V., Rachor, E., Saldanha, L., Schmid, M.K. (1996) Megabenthic commmunities in the waters around Svalbard. *Polar Biology*, 16(6), 431–446.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, 100(910), 33–46.

Pianka, E.R. (1989) Latitudinal gradients in species diversity. *Trends in Ecology and Evolution*, 8, 223–224.

Poulin, E., Féral, J. P., Forensa, M., Cornudella, L. & Alva, V. (1999). Selfing and outcrossing in the brood protecting ophiuroid *Amphipholis squamata*. *In:* Candia-Carnaveli, M.D. & Bonasoro, F. (Eds.) *Echinoderm Research 1998: Proceeding of the 5th European Conference on Echinoderms,* A.A. Balkema, Rotterdam pp. 147–150.

Pomory, C.M. (2003) A guide to the shallow-water echinodermata of the Texas Coast. *Contributions in Marine Science*, 36, 1–188.

Pomory, C.M.; Carpenter, J.H.; Winter, J.H. (2011) *Amphicutis stygobita*, a new genus and new species of brittle star (Echinodermata: Ophiuroidea: Ophiurida: Amphilepididae) found in Bernier Cave, an anchialine cave on San Salvador Island, Bahamas. *Zootaxa*, 3133, 50–68.

Prata J. & Christoffersen M.L. (2012) *Holothuria* (*Semperothuria*) *surinamensis* Ludwig, 1875 (Echinodermata: Holothuroidea): Record of the species for the northeast coast of Brazil. *Check List*, 8(4), 768–770.

Prata, J., Manso, C.L.C. & Christoffersen, M.L. (2014) Aspidochirotida (Echinodermata: Holothuroidea) from the northeast coast of Brazil. *Zootaxa*, 3889 (1), 127–150.

Prato, E. & Pastore, M. (2012) Occurrence of *Marginaster capreensis* (Echinodermata: Asteroidea: Poraniidae) inthe Taranto seas (Ionian Sea, Italy). *Marine Biodiversity Records*, 5(e72), 1–3, doi: 10.1017/S1755267212000474.

Price, A.R.G., Keeling, M.J., O'Callaghan, C.J. (1999) Ocean-scale patterns of 'biodiversity' of Atlantic asteroids determined from taxonomic distinctness and other measures. *Biological Journal of the Linnean Society*, 66, 187–203.

Purcell, S.W., Samyn, Y. & Conand, C. (2012) Commercially important sea cucumbers of the world. *FAO Species Catalogue for Fishery Purposes*, Rome, 6, 180 pp.

Quartau, R., Hipólito, A., Romagnoli, C., Casalbore, D., Madeira, J., Tempera, F., Roque, C., Chiocci, F.L. (2014) The morphology of insular shelves as a key for understanding the geological evolution of volcanic islands: insights from Terceira Island (Azores). *Geochemistry, Geophysics, Geosystems*, 15, 1801–1826.

Rathbun, R. (1879) A list of the Brazilian Echinoderms, with notes on their distribution. *Transactions of the Connecticut Academy*, 5, 139–158.

Raff, R.A. & Byrne, M. (2006) The active evolutionary lives of echinoderm larvae. *Heredity*, 97(3), 244–252.

Rathbun, R. (1886) Catalogue of the collection of recent echini in the U.S. National Museum (corrected to July 1, 1886). *Proceedings of the United States National Museum*, 9, 255–309.

Reitzel, A.M. & A. Heyland (2007) Reduction in morphological plasticity in echinoid larvae: relationship of plasticity with maternal investment and food availability. *Evolutionary Ecology Research*, 9, 109–121.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 514–527.

Riera, R., Rodríguez, M., Ramos, E., Monterroso, Ó. & Delgado, J.D. (2013) Hard and soft-bottom macrozoobenthos in subtidal communities around an inactive harbour area (Gran Canaria, Canary Islands). *Vie et milieu – Life and environment*, 63 (1), 23–34.

Rochette, R., Hamel, J.-F. & Himmelman, J.H. (1994) Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status. Marine. *Ecology Progress Series*, 106, 93–100.

Rodriguez, A., Hernández, J.C., Clemente, S. & Coppard, S.E. (2013) A new species of *Diadema* (Echinodermata: Echinoidea: Diadematidae) from the eastern Atlantic Ocean and a neotype designation of *Diadema antillarum* (Philippi, 1845). *Zootaxa*, 3636(1), 144–170.

Rodríguez-Barreras, R. (2014) The shallow-water echinoids (Echinodermata: Echinoidea) of Cuba. *Marine Biodiversity Records*, 7(e86), 1–8, doi: 10.1017/S175526721400092X.

Rodriguez-Barreras, R. & Messing, C. (2013) A New List of Cuban Crinoids (Echinodermata: Crinoidea). *Caribbean Journal of Science*, 47(2–3), 198–212.

Rogacheva, A. (2007) Revision of the Arctic group of species of the family Elpidiidae (Elasipodida, Holothuroidea). *Marine Biology Research*, 3(6), 367–396.

Rogers, A.D. (1999) The Biology of *Lophelia pertusa* (Linnaeus 1758) and Other Deep-Water Reef-Forming Corals and Impacts from Human Activities. *International Review of Hydrobiology*, 84, 315–406.

Rosen, B.R. & Smith, A.B. (1988) Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method. *Geological Society Special Publication*, 37(1), 275–306.

Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the United States of America*, 95 (7), 3699–3702.

Roy, K., Jablonski, D. & Valentine, J.W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society B*, 267 (1440), 293–299.

Rueda, J.L., Gil, J., González-García, E., Farias, C., López-González, N. & Díaz-del-Río-Español, V. (2011) First record of *Hacelia superba* H.L. Clark, 1921 (Echinodermata: Asteroidea) in the European continental margin. *Marine Biodiversity Records*, 4 (e96), 1–5, doi: 10.1017/S175526721100087X.

Saldanha, L. (1995) *Fauna Marinha Atlântica*. Publicações Europa-America, Mem Martins, 364 pp.

Salvini-Plawen, L.V. (1972) Zur Taxonomie und Ökologie mediterraner Holothuroidea-Apoda. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 23, 459–466.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M. & Isidro, E.J. (1995) Marine research, resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *5*(4), 311–354.

Scheltema, R.S. (1986) Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among Central Pacific islands. *Bulletin of Marine Science*, 39, 241–256.

Schipper, C.A., Dubbeldam, M.C., Feist, S., Rietjens, I.M.C.M. & Murk, T.A.J. (2008) Cultivation of the heart urchin *Echinocardium cordatum* and validation of its use in marine toxicity testing for environmental risk assessment. *Journal of Experimental Marine Biology and Ecology*, 364(1–2), 11–18.

Schoener, A. (1972) Fecundity and possible mode of development of some deep-sea ophiuroids. *Limnology and Oceanography*, 17(2), 193–199.

Schoppe, S. (1996) *Ophiothrix synoecina* New Species (Echinodermata: Ophiuroidea) from the Caribbean Coast of Colombia. *Bulletin of Marine Science*, 58(2), 429–437.

Schultz, H. (2006) *Sea Urchins. A guide to worldwide shallow-water shallow-water species*. Heinke & Peter Schultz Partner Scientific Publications, 3rd edition, 484 pp.

Schwartz, F.J. & Porter, H.J. (1977) Fishes, macroinvertebrates, and their ecological interrelationships with a calico scallop bed off North Carolina. *Fishery Bulletin*, 75(2), 427–446.

Serafy, D.K. (1971) A redescription of *Clypeaster pallidus* H.L. Clark, 1914, and a description of juveniles of *C. rosaceus* (Linnaeus, 1758) (Echinodermata; Echinoidea). *Bulletin of Marine Science*, 83, 780–786.

Serafy, D.K. (1979) Echinoids (Echinodermata: Echinoidea). *Memoirs of the Hourglass Cruises*, 5(3), 1–120.

Serafy, D.K. & Fell, F.J. (1985) Marine Flora and Fauna of the Northeastern United States. Echinodermata: Echinoidea. *NOAA Technical Report NMFS*, 33, 27 pp.

Shibata, D., Hirano, Y. & Komatsu, M. (2011) Life cycle of the multiarmed sea star *Coscinasterias acutispina* (Stimpson, 1862) in laboratory culture: sexual and asexual reproductive pathways. *Zoological science*, 28(5), 313–317.

Sladen, W.P. (1889) Report on the Asteroidea collected by H.M.S. Challenger during the years 1873–1876. *Challenger series of reports, Zoology*, 30, 893 pp.

Smirnov, A.V. (1994) Arctic Echinoderms: Composition, Distribution and History of the Fauna. *In*: Guille, F. & M. Roux (Eds.) *Echinoderms through time*, A.A. Balkema, Rotterdam, Rotterdam, pp. 135–142.

Sneli, J.-A. (1999) Echinodermata, Asteroidea in the Faroe region. *Fróðskaparrit*, 47, 229–259.

Solis-Marin, F.A. & Laguarda-Figueras, A. (2010) A new species of starfish (Echinodermata: Asteroidea) from an anchialine cave in the Mexican Caribbean. *Revista Mexicana de Biodiversidad*, 81, 663–668.

Solís-Marín, F.A., Alvarado, J.J., Abreu-Pérez, M., Aguilera, O., Alió, J., Bacallado-Aránega, J.J., Barraza, E., Benavides-Serrato, M., Benítez-Villalobos, F., Betancourt-Fernández, L., Borges, M., Brandt, M., Brögger, M.I., Borrero-Pérez, G.H., Buitrón-Sánchez, B.E., Campos, L.S., Cantera, J., Clemente, S., Cohen-Renjifo, M., Coppard, S., Costa-Lotufo, L.V., del Valle-García, R., Díaz, Y., Díaz de Vivar, M.E., Díaz-Martínez, J.P., Durán-González, A., Epherra, L., Escolar, M., Francisco, V., Freire, C.A., García-Arrarás, E., Gil, D.G., Guarderas, P., Hadel, V.F., Hearn, A., Hernández, J.C., Hernández-Delgado, E.A., Herrera-Moreno, A., Herrero-Pérezrul, M.D., Hooker, Y., Honey-Escandón, M.B.I., Lodeiros, C., Luzuriaga, M., Manso, C.L.C., Martín, A., Martinez, M.I., Martínez, S., Moro-Abad, L., Mutschke, E., Navarro, J.C., Neira, R., Noriega, N., Palleiro-Nayar, J.S., Pérez, A.F., Pérez-Ruzafa, A., Prieto-Rios, E., Reyes, J., Rodríguez, R., Rubilar, T., Sancho-Mejía, T., Sangil, C., Silva, J.R.M.C., Sonnenholzner, J.I., Ventura, C.R., Tablado, A., Tavares, Y., Tiago, C.G., Tuya, F. & Williams, S.M. (2013) Appendix. In: Alvarado J.J. & Solís-Marín F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*. Springer Berlin Heidelberg, pp. 543–65

Solís-Marín, F.A., Laguarda-Figueras, A., Durán-González, A., Arriaga-Ochoa, J.A., Caballero-Ochoa, A.A. & Valdés-de Anda, M. (2014) First record and geographic distribution of *Ophiambix devaneyi* (Echinodermata: Ophiuroidea) in the Gulf of Mexico. *Revista Mexicana de Biodiversidad*, 85(3), 961–964.

Solís-Marín, F.A., Pineda-Enríquez, T., Hernández-Díaz, Y.Q., Yepes-Gaurisas, D., González-Gándara, C., Granados-Barba, A. & Simões, F.N.D.M. (2015) First records and range extension of *Ophioblenna antillensis* (Echinodermata: Ophiuroidea) in the Gulf of Mexico. *Revista Mexicana de Biodiversidad*, 86, 306-309.

Sponer, R. & Roy, M.S. (2002) Phylogeographic analysis of the brooding brittle star *Amphipholis squamata* (Echinodermata) along the coast of New Zealand reveals high cryptic genetic variation and cryptic dispersal potential. *Evolution*, *56*(10), 1954–1967.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, 133(2), 240–256.

Stevens, G.C. (1996) Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography,* 23(2), 149–15.

Stevenson, A. & Rocha, C. (2012) Evidence for the bioerosion of deep-water corals by echinoids in the Northeast Atlantic. *Deep-Sea Research I*, 71, 73–78.

Stöhr, S. (2003) A new fissiparous amphiurid brittlestar (Echinodermata: Ophiuroidea) from southwest of Iceland. *Sarsia*, 88 (6), 373–378.

Stöhr, S. (2005) Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society*, 143, 543–576.

Stöhr, S. (2011) New records and new species of Ophiuroidea (Echinodermata) from Lifou, Loyalty Islands, New Caledonia. *Zootaxa*, 3089, 1–50.

Stöhr, S. & Alme, Ø. (2014) Sometimes two arms are enough—an unusual life-stage in brittle stars (Echinodermata: Ophiuroidea). *Zootaxa*, 3994(3), 425–432.

Stöhr, S., O'Hara, T. & Thuy, B. (2012) Global diversity of Ophiuroidea. *PloS One*, 7(3), 1–14, doi: 10.1371/journal.pone.0031940

Strathmann, R. (1978) Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. *Journal of Experimental Marine Biology and Ecology*, 34(1), 23–27.

Strathmann, R., Strathmann, M. & Emson, R. (1984) Does Limited Brood Capacity Link Adult Size, Brooding, and Simultaneous Hermaphroditism? A Test with the Starfish *Asterina phylactica*. *The American Naturalist*, 123(6), 796–818.

Studer, T. (1882) Übersicht über die Ophiuriden, welche während der Reise S.M.S. "Gazelle" um die Erde 1874–76 gesammelt wurden. *Physikalische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 34, 1–37.

Sumida, P.Y.G., Tyler, P.A., Lampitt, R.S. & Gage, J.D. (2000) Reproduction, dispersal and settlement of the bathyal ophiuroid Ophiocten gracilis in the NE Atlantic Ocean. *Marine Biology*, 137(4), 623–630.

Swofford, D.L. (2002) PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4, Sinauer, Sunderland, Massachusetts, USA, 142 pp.

Tâmega, F.T.S., Spotorno-Oliveira, P. & Figueiredo, M.A.O. (2013) *Catalogue of the benthic marine life from Peregrino oil field, Campos Basin, Brazil*. Instituto Biodiversidade Marinha, Rio Janeiro, Brazil, 140 pp.

Thandar, A.S. (2001) The holothuroid family Rhopalodinidae – its composition, distribution, phylogeny and taxonomic status. *African Zoology*, 36(2), 229–243.

Thandar, A.S. (2013) *Trachythyone flaccida*, a new sea cucumber species from southern Angola (Echinodermata: Holothuroidea: Dendrochirotida: Cucumariidae) with key to the genus. *Zootaxa*, 3693(3), 395–400.

Thandar, A.S. & Mjobo, S. (2014) On some sea cucumbers from Ghana (Echinodermata: Holothuroidea) with descriptions of a new genus and one new species. *Zootaxa*, 3900(2), 243.

Thandar, A.S., Zettler, M.L. & Arumugam, P. (2010) Additions to the sea cucumber fauna of Namibia and Angola, with descriptions of new taxa (Echinodermata: Holothuroidea). *Zootaxa*, 2655, 1–24.

Thiede, J. (1978) A glacial Mediterranean. *Nature*, 276, 680–683.

Thiel, M. & Gutow, L. (2005a) The ecology of rafting in the marine environment II. The rafting organisms and community. *Oceanography and Marine Biology: an annual review*, 43, 279–418.

Thiel, M. & Gutow, L. (2005b) The ecology of rafting in the marine environment. I. The floating substrata. *Oceanography and Marine Biology: an annual review*, 42, 181–264.

Thiel, M. & Haye, P.A. (2006) The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. *Oceanography and Marine Biology: an annual review*, 44, 323–429.

Thomas, L.P. (1962) The Shallow-water Amphiurid Brittle Stars (Echinodermata, Ophiuroidea) of Florida. *Bulletin of Marine Science*, 12(4), 623–694.

Thordarson, T. & Larsen, G. (2007) Volcanism in Iceland in historical time: Volcano types, eruption styles and eruptive history. *Journal of Geodynamics*, 43, 118–152.

Thorson, G. (1950) Reproduction and larval ecology of marine bottom invertebrates. *Biological Review*, 25, 1–45.

Todd, C.D. (1998) Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, 376, 1–21.

Tommasi, L.R. (1966) Lista dos echinóides recentes do Brasil. *Contribuições Avulsas do Instituto Oceanografico, Universidade de Sao Paulo, sér. Oceanografia biológica*, 11, 1–50.

Tommasi, L.R. (1969a) Nota sôbre os fundos detríticos do circalitoral inferior da plataforma continental brasileira ao sul do Cabo Frio (RJ). *Boletim do Instituto Oceanográfico*, São Paulo, 18(1), 55–62.

Tommasi L.R. (1969b) Lista dos Holothuroidea recentes do Brasil. *Contribuições Avulsas do Instituto*. Universidade de São Paulo, 15, 1–50.

Tommasi, L.R. (1970a) Os Ofiuroides recentes do Brasil e de regioes Vizinhas. *Contribuições Avulsas do Instituto Oceanografico*, Universidade de São Paulo, 20, 1–146.

Tommasi, L.R. (1970b) Lista de asteróides recentes do Brasil. *Contribuições do Instituto Oceanográfico*, Universidade de São Paulo, 18, 1–61.

Tommasi, L.R. (1971) Equinodermes do Brasil. I. Sobre algumas novas espécies e outras pouco conhecidas, para o Brasil. *Boletim do Instituto Oceanográfico*, São Paulo, 20, 1–21.

Tommasi, L.R. (1972) Equinodermes da região entre o Amapá (Brasil) e a Florida (E.U.A.) II. Echinozoa. *Boletim do Instituto Oceanográfico*, São Paulo, 21, 15–67.

Tommasi, L.R. (1974) Equinodermes do Brasil. III. Observações sobre algumas espécies coletadas durante as viagens do N/Oc. “Almirante Saldanha”. São Paulo. *Boletim do Instituto Oceanográfico*, São Paulo, 23, 1–15.

Tommasi, L.R. (2004) Classes Asteroidea, Crinoidea, Holothuroidea & Echinoidea. *In*: Amaral, A.C.Z. & Rossi-Wongtschowski, C.L. (Eds.) Biodiversidade bentônica da região Sudeste-Sul do Brasil, plataforma externa e talude superior, *Série documentos Revizee*: Score SuL, Instituto Oceanográfico, São Paulo, pp. 161–163.

Tommasi, L.R. & Lima-Verde, J.S. (1970) Observações sôbre Cassidulus mitis Krau, 1960 (Cassiduloida, Echinoidea). *Boletim do Instituto Oceanográfico*, São Paulo, 18(1), 1–9.

Tommasi, L.R. & Oliveira, E. de (1976) Equinodermes do Brasil. V. Sobre algumas espécies coletadas durante viagens do N/Oc. “Prof. W. Besnard”. *Boletim Instituto Oceanografica, São Paulo*, 25 (1), 77–100.

Tortonese, E. (1965) Fauna D’Italia – Echinodermata. Edizioni Calderini, Bologna, xiii+422 pp.

Tilquin, A. & Kokko, H. (2016) What does the geography of parthenogenesis teach us about sex? *Philosophical Transactions of the Royal Society B*, 371(1706), 1–16.

Turner, R.L. & B.D. Graham (2003) *Calocidaris micans* (Cidaridae) and *Pseudoboletia maculata* (Echinoidea) of the Gulf of Mexico. *Proceedings of The Biological Society of Washington*, 116, 61–81.

Tuya, F., Cisneros-Aguirre, J., Ortega, L., & Haroun, R.J. (2007) Bathymetric segregation of sea urchins on reefs of the Canarian Archipelago: role of flow-induced forces. *Estuarine, Coastal and Shelf Science*, 73, 481–488.

Tuwo, A. & Conand, C. (1992) Reproductive biology of the holothurian *Holothuria forskali* (Echinodermata). *Journal of the Marine Biological Association of the United Kingdom*, 72, 745–758.

Tyler, P.A. & Gage, J.D. (1980) Reproductive patterns in deep sea Ophiuroids from the North East Atlantic. *In*: Jangoux, M. (Ed.). *Echinoderms: Present and Past. Proceedings of the European Colloquium on Echinoderms Brussels, 3 – 8 September 1979. Internationale Revue der gesamten Hydrobiologie und Hydrographie*, A.A. Balkema, Rotterdam, pp. 417–420.

Tyler, P.A. & Gage, J.D. (1984) The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, North-East Atlantic Ocean). *Marine Biology*, 80(1), 63–74.

Tyler, P.A., Emson, R.H., Sumida, P. & Howell, K. (2005) Ophiuroid distribution at sublittoral and bathyal depths round the Faroe Islands, NE Atlantic Ocean. *BIOFAR Proceedings*, 175–194.

Tzetlin, A.B., Mokievsky, V.O., Melnikov, A.N., Saphonov, M.V., Simdyanov, T.G. & Ivanov, *I.E*. (1997) Fauna associated with detached kelp in different types of subtidal habitats of the White Sea. *Hydrobiologia*, 355, 91–100.

Uthicke, S., Schaffelke, B. & Byrne, M. (2009) A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs*, 79(1), 3–24.

Valle-García, R., Solís-Marín, F.A., Abreu-Pérez, M., Laguarda-Figueras, A. & Durán- González, A. (2005) Catálogo de los equinodermos (Echinodermata: Crinoidea, Echinoidea, Holothuroidea) nerítico-bentónicos del Archipiélago Cubano. *Revista de Biología Tropical*, 53(3), 9–28.

Ventura, C.R.R., Lima, R.P.N., Nobre, C.C., Veríssimo, I. & Zama, P.C. (2006) Capítulo 9. Filo Echinodermata. *In*: Lavrado, H.P. & Ignacio, B.L. (Eds.) *Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira*. Museu Nacional, Rio de Janeiro, 18, 339–389.

Ventura C.R.R., Veríssimo, I., Nobre, C.C. & Zama, P.C. (2007) Filo Echinodermata. *In*: Lavrado, H.P. & Viana, M.S. (Eds.) *Atlas de invertebrados marinhos da região central da zona econômica exclusiva brasileira. Parte 1*. Museu Nacional, Rio de Janeiro, 25, 339–389.

Vermeij, G.J. & Rosenberg, G. (1993) Giving and receiving: the tropical Atlantic as donor and recipient region for invading species. *American Malacological Bulletin*, 10(2), 181–194.

Vernon, J.D., Mcclintock, J.B., Hopkins, T.S., Watts, S.A. & Marion, K.R. (1993) Reproduction of Clypeaster ravenelii (Echinodermata: Echinoidea) in the northern Gulf of Mexico. *Invertebrate Reproduction & Development*, 24(1), 71–78.

Verrill, A.E. (1885a) Notice of recent additions to the marine invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. part V – Annelida, Echinodermata, Hydroida, Tunicata. *Proceedings of the United States National Museum*, 8, 424–447.

Verrill, A.E. (1885b) Results of the explorations made by the steamer "Albatross", off the northern coast of the United States, in 1883. *Report of Commissioner of Fish and Fisheries*, 503–699.

Verrill, A.E. (1895) Distribution of the echinoderms of northeastern America. *American Journal of Science*, 291, 199–212.

Verrill, A.E. (1899) Report on the Ophiuroidea collected by the Bahama expedition in 1893. *Bulletin from the Laboratories of Natural History of the State University of Iowa*, 5(1), 1–86.

Virnstein, R.W. & Carbonara, P.A. (1985) Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. *Aquatic Botany*, 23(1), 67–82.

Virnstein, R.W. & Howard, R.K. (1987) Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. II. Comparisons between drift algae and three species of seagrasses. *Bulletin of Marine Science*, 41(1), 13–26.

Vogt, P. & Jung, W. (2007) Origin of the Bermuda volcanoes and the Bermuda Rise: history, observations, models, and puzzles. *Geological Society of America*, 430, 553–591.

Walenkamp, J.H.C. (1976) The Asteroids of the coastal waters of Surinam, *Zoologische Verhandelingen*, 147, 1–89.

Walenkamp, J.H.C. (1979) Asteroidea (Echinodermata) from the Guyana Shelf. *Zoologische Verhandelingen*, 170, 1–97.

Wangensteen, O.S., Turon, X., Pérez-Portela, R. & Palacín, C. (2012) Natural or naturalized? Phylogeography suggests that the abundant sea urchin *Arbacia lixula* is a recent colonizer of the Mediterranean. *PLoS One*, 7(9), 1–16, doi: 10.1371/journal.pone.0045067.

Waters, J.M. & Roy, M.S. (2003) Global phylogeography of the fissiparous sea star genus *Coscinasterias. Marine Biology*, 142, 185–191.

Watrous, J.E. & Wheeler, Q.D. (1981) The out-group comparison method of character analysis. *Systematic Zoology*, 30, 1–11.

Wenner, E.L., Hinde, P., Knott, D.M. & Van Dolah, R.F. (1984) A temporal and spatial study of invertebrate communities associated with hard-bottom habitats in the South Atlantic Bight. *NOAA Technical Report NMFS*, 18, 1–104.

Wirtz, P. (2001) *Madeira Marine Life*. Francisco Ribeiro & Filhos, Lda., Funchal, Madeira, 192 pp.

Wirtz, P. (2006) Ten invertebrates new for the marine fauna of Madeira. *Arquipélago. Life and Marine Sciences*, 23A, 75–78.

Wirtz, P. & Debelius, H. (2003) *Mediterranean and Atlantic invertebrate guide*. ConchBooks, Hackenheim, 305 pp.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: ecology, evolution and conservation*, 2nd edn. Oxford University Press, Oxford, 416 pp.

WoRMS Editorial Board (2017) World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2017-01-15. doi: 10.14284/170.

Wray, G.A. (1996) Parallel evolution of nonfeeding larvae in echinoids. *Systematic Biology*, 45(3), 308–322.

Young, C.M. (2003) Reproduction, development and life-history traits. *Ecosystems of the World*, 381–426.

Young, C.M. & George, S.B. (2000) Larval development of the tropical deep-sea echinoid *Aspidodiadema jacobyi*: phylogenetic implications. *The Biological Bulletin*, 198(3), 387–395.

Young, C.M., R., Emlet, R.B., Li, Y., Qian, H., Arellano, S.M., Van Gaest, A., Bennett, K.C., Wolf, M., Smart, T.I. & Rice, M.E. (2012) Dispersal of Deep-Sea Larvae from the Intra-American Seas: Simulations of Trajectories Using Ocean Models. *Integrative and Comparative Biology*, 52(4), 483–496.

Young, C.M., Sewell, M.A., Tyler, P.A., Metaxas, A. (1997) Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiversity and Conservation*, 6, 1507–1522.

Zaixso, H.E. & Lizarralde, Z.I. (2000) Distribución de equinodermos en el golfo San José y sur del golfo San Matías (Chubut, Argentina). *Revista de biología marina y oceanografía*, 35(2), 127–145.

Zibrowius, H. (1978) Nouvelles observations de l'Ophiure Gorgonecéphale, *Astrospartus mediterraneus*, sur la côte méditerranéenne de France. Bibliographie annotée et répartition. *Scientific Reports of Port-Cros national Park*, 4, 157–169.

Ziesenhenne, F.C. (1955) A review of the genus *Ophioderma* M. & T. *Essays in the natural sciences in honour of Captain Alan Hancock*, 185–201.

Zulliger, D.E. & Lessios, H.A. (2010) Phylogenetic relationships in the genus *Astropecten* Gray (Paxillosida: Astropectinidae) on a global scale: molecular evidence for morphological convergence, species-complexes and possible cryptic speciation. *Zootaxa*, 2504, 1–19.+

Supplementary Material

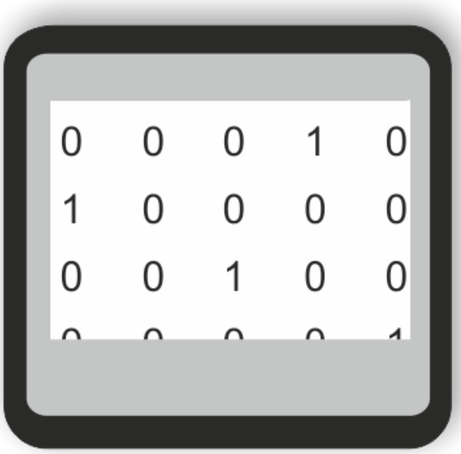


Table S7.1. Echinoderm species from the North and Central Atlantic and the Mediterranean Sea

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Acrocnida brachiata	1-40	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Acrocnida semisquamata	5-80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Acrocnida spatulispina	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinopyga agassizii	0-54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
Agassizia excentrica	43-900	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Allopatiria ocellifera	6-55	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allostichaster capensis	0-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Allostichaster hartii	113-338	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Allothyone mexicana	0-6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphicutis stygobita	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphilepis ingolfiana	182-4829	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Amphilepis norvegica	70-2940	0	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphilimna olivacea	60-490	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0
Amphiodia guillermosoberoni	0-4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiodia habilis	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiodia planispina	1-56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiodia pulchella	1-71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Amphiodia riisei	1-311	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiodia trychna	0-160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Amphiophiura coronata	173-904	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiophiura fasciculata	87-527	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Amphioplus abditus	0-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Amphioplus aciculatus	10-84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphioplus albidus	0-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphioplus archeri	0-9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphioplus aurensis	8-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphioplus brasiliensis	48-130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphioplus camamuensis	36-51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphioplus cincta	0-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphioplus congensis	5-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphioplus coniortodes	1-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphioplus lucyae	0-600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphioplus macilentus	97-210	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Amphioplus occidentalis	10-73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphioplus sepultus	0-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphioplus suspectus	14-64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphioplus thrombodes	0-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphioplus tumidus	30-587	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Amphipholis bananensis	0-297	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphipholis goesi	25-510	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphipholis januarii	1-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Amphipholis nudipora	5-250	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Amphipholis squamata	0-1962	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1
Amphipholis torelli	10-580	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Amphipholizona delicata	15-600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura atlantica	27-480	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Amphiura atlantidea	62-95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura bihamula	166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiura borealis	150-800	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura callida	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiura capensis	0-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Amphiura cherbonnieri	12-130	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura chiajei	2-1250	0	1	0	1	0	0	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphiura complanata	10-810	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura crassipes	3-120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphiura dacunhae	134-135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Amphiura delamarei	43-200	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura diducta	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiura fibulata	2-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Amphiura filiformis	5-1665	0	1	1	1	0	0	1	1	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphiura flexuosa	5-810	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphiura fragilis	155-2640	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Amphiura grandisquama	2-2870	1	1	1	1	1	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	1
Amphiura griegi	60-810	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura incana	10-110	0	1	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura intricata	1-8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura kinbergi	3-300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura lacazei	12-175	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura latispina	10-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphiura mediterranea	0-90	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura muelleri	134-600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphiura otteri	198-3200	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Amphiura palmeri	6-479	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Amphiura princeps	0-133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Amphiura rathbuni	29-510	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiura rosae	51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphiura sarsi	55-1098	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura securigera	13-600	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura semiermis	82-1448	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura senegalensis	76-90	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura stepanovi	70-205	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura stimpsoni	1-986	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Amphiura sundevalli	3-820	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Amphiura ungulata	15-79	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Analcidometra armata	3-148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Anseropoda lobiancoi	40-100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anseropoda placenta	10-500	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Antedon bifida	0-450	1	1	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Antedon duebenii	0-168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Antedon hupferi	0-120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Antedon mediterranea	0-420	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antedon petasus	10-326	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthenoides peircei	20-844	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Apollonaster yucatanensis	60-1174	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Araeosoma belli	130-1020	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Araeosoma fenestratum	148-1270	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Arbacia dufresnii	0-315	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arbacia lixula	0-55	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Arbacia punctulata	0-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Aslia lefevrii	0-30	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aslia pygmaea	0-37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Aspidodiadema jacobyi	170-720	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asterias forbesi	0-613	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Asterias rubens	0-900	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Asterina gibbosa	0-126	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asterina pancerii	0-40	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asterina phylactica	0-18	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asterina stellifera	0-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Asterinides folium	0-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0
Asterinides hartmeyeri	0-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asterinides pilosa	11-256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asterinides pompom	3-6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteronyx loveni	100-4721	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Asteroporpa annulata	37-305	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Asteroporpa lindneri	87-205	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroporpa pulchra	100-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema arenosum	33-1449	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema elongatum	98-708	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema intectum	90-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Asteroschema laeve	146-540	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema nuttingii	189–225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema oligactes	146-530	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asteroschema tenue	66–180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astichopus multifidus	1-37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astracme mucronata	70-691	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astrocaneum herrerai	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astrocnida isidis	20-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astrocyclus caecilia	20 a 677	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Astrogomphus vallatus	60-706	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astrogordius cacaoticus	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astropecten acutiradiatus	35-66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astropecten africanus	3-100	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten alligator	22-576	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astropecten americanus	110-641	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Astropecten antillensis	3-278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astropecten aranciacus	1-183	0	1	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten articulatus	0-550	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
Astropecten bispinosus	1-105	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten brasiliensis	7-45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Astropecten caribemexicanensis	50-51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astropecten cingulatus	0-1350	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0
Astropecten comptus	35-130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astropecten duplicatus	0-550	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Astropecten gruveli	9-120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten hermatophilus	15-165	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten huepferi	15-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten ibericus	33-120	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten irregularis	1-1000	0	1	1	1	1	0	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten jonstoni	1-90	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten leptus	70-650	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten liberiensis	5-30	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten mamillatus	7-97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Astropecten marginatus	6-130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Astropecten nitidus	11-686	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astropecten platyacanthus	1-64	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten sanctaehelenae	18-60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Astropecten spiniphorus	10-65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten spinulosus	1-55	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astropecten variegatus	20-55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Astropectinides mesactus	80-165	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Astrophyton muricatum	2-508	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astropyga magnifica	2-89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Astropyga nuptialis	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Astrospartus mediterraneus	40-265	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Bathybiaster loripes	80-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bathysalenia goesiana	90-616	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Benthophyllophorus conchilegum	182-345	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Blakiaster conicus	168-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Brisaster fragilis	14-1700	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Brisinga endecacnemos	183-2360	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brissopsis alta	25-310	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Brissopsis atlantica	2-3200	0	1	1	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0
Brissopsis elongata	3-270	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Brissopsis lyrifera	5-2250	1	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Brissus unicolor	0-240	1	1	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Calocidaris micans	100–624	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Caryometra tenuipes	165-914	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cassidulus caribaearum	0-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cassidulus infidus	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cassidulus mitis	2-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Caudina arenata	0-2500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cenocrinus asterius	140-585	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Centrostephanus longispinus	5-360	1	1	1	1	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0
Ceramaster granularis	40-2185	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Ceramaster grenadensis	106-2845	1	0	0	1	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Chaetaster longipes	30-1140	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Chaetaster nodosus	53-110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Cheiraster echinulatus	150-570	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cherbocnus cabindaensis	13-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cherbocnus ransoni	10-74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiridota ferruginea	70-301	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Chiridota laevis	0-700	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Chiridota peloria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Chiridota rotifera	0-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0
Cidaris abyssicola	36-800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Cidaris cidaris	20-2010	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Cidaris nuda	70-450	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cidaris rugosa	46-790	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Cladaster rudis	150-900	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Cladodactyla senegalensis	19	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clypeaster chesheri	20-101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster cyclopilus	23-487	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster durandi	105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster euclastus	36-530	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster lamprus	78-450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Clypeaster luetkeni	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster oliveirai	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Clypeaster pallidus	75-216	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Clypeaster prostratus	15-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Clypeaster rangianus	24-42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Clypeaster ravenelii	5-230	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Clypeaster rosaceus	0-285	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Clypeaster subdepressus	1-378	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Coccometra hagenii	14-1046	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Coccometra nigrolineata	40-987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Coelopleurus floridanus	65-2380	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Comactinia echinoptera	2-92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Comactinia meridionalis	3-373	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Comatonia cristata	14–366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Comissia venustus	24-236	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Conocrinus lofotensis	140-3135	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Conolampas sigsbei	120-800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Copidaster cavernicola	13-18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Copidaster lymani	9-34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Copidaster schismochilus	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Coronaster briareus	35-700	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Coronatum baiensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Coscinasterias tenuispina	0-165	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	0
Crinometra brevipinna	69-1097	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
Crossaster helianthus	110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Crossaster papposus	0-909	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Crossaster penicillatus	55-820	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Crossaster squamatus	73-1383	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Cryptopelta brevispina	20-145	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ctenantedon kinziei	9-49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ctenodiscus australis	70-4605	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ctenodiscus crispatus	10-2200	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Cucumaria frondosa	0-300	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Cucumaria paraglacialis	128	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cucumaria solangeae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Culcitopsis borealis	110-1170	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Cyathidium pourtalesi	171-249	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cycethra verrucosa	0-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Davidaster discoideus	1-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Davidaster rubiginosus	1-344	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Deichmannia unica	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Democrinus conifer	155-1750	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Democrinus rawsonii	66-652	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diadema africanum	0-70	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Diadema antillarum	0-70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Diadema ascensionis	0-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0
Diplasiaster productus	78-567	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diplopteraster multipes	91-1225	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Dipsacaster antillensis	113-897	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinarachnius parma	0-1625	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Echinaster brasiliensis	1-360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Echinaster echinophorus	0-55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Echinaster graminicola	0-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinaster guyanensis	13-106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinaster modestus	67-470	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Echinaster paucispinus	12-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinaster sentus	0-68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Echinaster sepositus	1-250	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinaster serpentarius	0-107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinaster spinulosus	1-238	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Echinocardium connectens	40-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Echinocardium cordatum	0-230	1	1	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0
Echinocardium fenauxi	20-128	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocardium flavescens	5-360	1	1	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocardium laevigaster	40-220	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Echinocardium mediterraneum	2-40	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocardium mortenseni	10-145	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocardium pennatifidum	0-275	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocucumis hispida	48-3257	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinocucumis multipodia	85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocucumis tenera	42-88	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinocyamus grandiporus	110-2310	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Echinocyamus pusillus	0-1250	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinolampas depressa	37-310	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Echinolampas rangii	20-1620	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinometra lucunter	0-45	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	0	1	1	0
Echinometra viridis	0-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Echinoneus cyclostomus	1-585	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Echinus esculentus	0-1264	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinus melo	25-1103	1	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinus tenuispinus	130-200.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ekmania barthii	10-600	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Elpidia glacialis	70-610	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Encope aberrans	12-90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Encope emarginata	0-128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Encope michelini	3-90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Endoxocrinus maclearanus	187-604	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Endoxocrinus parrae	154-832	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Eostichopus arnesoni	9-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Epitomapta roseola	0-37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Eremasterias' robusta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Euapta lappa	0-1350	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0
Eucidaris tribuloides	0-800	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	0
Eupatinapta acanthia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eupatinapta multipora	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Eupyrgus scaber	5-480	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eurhodia relicta	57-112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Euthyonacta solida	6-124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Euthyonidiella destichada	0-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Euthyonidiella dubia	14-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Euthyonidiella trita	0-4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ganeria falklandica	0-135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Genocidaris maculata	12-500	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0
Goniaster tessellatus	2-104	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0
Gorgonocephalus arcticus	5-1500	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0
Gorgonocephalus caputmedusae	150-1265	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gorgonocephalus chilensis	0-507	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gorgonocephalus eucnemis	8–1850	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Gorgonocephalus lamarckii	75-887	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Gracilechinus acutus	3-1280	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gracilechinus elegans	50-1710	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gracilechinus gracilis	70-450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Hacelia attenuata	1-190	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hacelia superba	40-487	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0
Hathrometra tenella	28-1783	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Havelockia exigua	25-48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Havelockia guttata	30-56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Havelockia scabra	10-1170.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Heliometra glacialis	4-1900	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Heliophora orbiculus	0-13	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Hemieuryale pustulata	18-330	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Hemioedema goreensis	10-34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemioedema gruveli	19	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemioedema multipodia	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemipholis cordifera	2-35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Henricia sexradiata	185-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Henricia simplex	0-183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Heterobrissus hystrix	38-1610	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hippasteria phrygiana	10-1405.	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Histampica duplicata	125-2870	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Holothuria arenicola	0-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0
Holothuria arguinensis	0-52	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria caparti	100-150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Holothuria cubana	0-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Holothuria dakarensis	1-54	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
Holothuria floridana	0-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holothuria forskali	0-850	1	1	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria glaberrima	0-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Holothuria grisea	0-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0
Holothuria helleri	0-102	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria impatiens	0-27	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Holothuria lentiginosa	8-467	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	0	1	0
Holothuria mammata	0-77	1	1	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria manningi	2-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0
Holothuria mexicana	0-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holothuria occidentalis	69-457	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holothuria parvula	0-4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Holothuria poli	0-250	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria princeps	0-73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Holothuria pseudofossor	2-370	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Holothuria rowei	3–20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holothuria sanctori	0-30	1	1	0	1	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Holothuria sinefibula	115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria surinamensis	0-42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0
Holothuria thomasi	3-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holothuria tubulosa	0-100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuria turrisimperfecta	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Horaeometra duplex	159-567	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hybometra senta	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hygrosoma petersii	200-3800	1	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0
Hymenaster pellucidus	13-3527	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Hymenodiscus coronata	100-2904	1	0	0	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hypalometra defecta	60-493	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hypselaster limicolus	30-340	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Icasterias panopla	8-680	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Isometra vivipara	79-242	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Isostichopus badionotus	0-70	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0
Korethraster hispidus	85-1150	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Labidoplax buskii	10-2117	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Labidoplax media	5-95	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Labidoplax thomsoni	7-325	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lanceophora lanceolata	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Leilaster radians	102-274	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leodia sexiesperforata	0-60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0
Leptasterias austera	33-64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Leptasterias canuti	5-10	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptasterias clavispina	9-55	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptasterias compta	32-275	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Leptasterias degerboelli	11-15	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptasterias floccosa	0-25	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptasterias groenlandica	0-276	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Leptasterias hispidella	91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Leptasterias hyperborea	7-380	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Leptasterias littoralis	0-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Leptasterias muelleri	0-500	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptasterias polaris	0-360	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Leptasterias tenera	18-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Leptometra celtica	46-1279	0	1	1	1	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptometra phalangium	40-1300	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptopentacta elongata	0-485	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptopentacta tergestina	8-170	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta bergensis	1-40	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta brasiliensis	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leptosynapta circopatina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta crassipatina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta cruenta	shallow	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta decaria	40-401	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta galliennii	0-30	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta imswe	lagoon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta inhaerens	0-173	1	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta longhursti	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta makrankyra	1-36	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta minuta	3-50	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptosynapta multigranula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta nannoplax	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta parvipatina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta roseogradia	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptosynapta tenuis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Leptychaster arcticus	35-2470	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Linckia bouvieri	0-60	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Linckia guildingi	0-298	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0
Linckia nodosa	0-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0
Linopneustes longispinus	55-710	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lipotrapeza capilla	140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Lissothuria antillensis	0-17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Lissothuria braziliensis	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lophaster furcifer	6-2555	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0
Luidia alternata	1-200	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
Luidia atlantidea	10-80	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Luidia barbadensis	73-430	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Luidia ciliaris	1-650	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Luidia clathrata	0-175	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0
Luidia heterozona	28-975	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Luidia lawrencei	6-469	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Luidia ludwigi	20-126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Luidia sagamina	20-975	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0
Luidia sarsii	9-1300	1	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Luidia senegalensis	1-64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Lytechinus callipeplus	22-350	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Lytechinus euerces	55-777.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Lytechinus variegatus	0-250	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Lytechinus williamsi	5-92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Marginaster capreensis	0.5-742	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marginaster pectinatus	166-450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Marthasterias glacialis	0-180	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mediaster bairdi	38-3509	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Mediaster pedicellaris	14-576	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Mellita quinquiesperforata	1-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Mellita tenuis	0-45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Meoma cadenati	31-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Meoma ventricosa	0-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Mesothuria intestinalis	20–2480	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0
Microcomatula mortenseni	91-183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Microphiopholis atra	2-48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
Microphiopholis gracillima	0-55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Microphiopholis subtilis	2-1530	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Mithrodia clavigera	15-71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Moira atropos	0-445	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Molpadia arctica	200-400	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Molpadia borealis	40-2000	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Molpadia cubana	24-1464	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Molpadia musculus	35-5205	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	1	0
Molpadia oolitica	42-1440	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Molpadia parva	125-2695	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Molpadia parvicauda	128-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Molpadia triforia	65-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Myriotrochus eurycyclus	8-449	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Myriotrochus rinkii	2-720	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Myriotrochus vitreus	0-700	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Narcissia ahearnae	53-135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Narcissia canariensis	15-170	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Narcissia trigonaria	5-91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Nemaster grandis	3-102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Neocnus incubans	0-2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neocomatella alata	60-510	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Neocomatella pulchella	10-567	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Neocrinus decorus	154-1220	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Neocucumis atlanticus	40-725	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neocucumis marionii	25-100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neolampas rostellata	95-1260	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Neopentadactyla mixta	0-200	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neopneustes micrasteroides	148-430	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Neothyonidium parvum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nudamphiura carvalhoi	15-117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ocnus brunneus	0-130	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocnus diomedeae	192-247	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ocnus glacialis	20-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ocnus lacteus	0-100	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocnus petiti	30-35	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocnus placominutus	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ocnus planci	0-250	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontaster hispidus	30-1160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Odontaster mediterraneus	24-1804	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontaster robustus	160-675	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Oestergrenia digitata	20-600	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oestergrenia marenzelleri	80-150	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha	55-417	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiacantha abyssicola	35-3500	1	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Ophiacantha anomala	140-2460	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0
Ophiacantha aspera	133-478	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiacantha brasiliensis	145-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophiacantha brevispina	90-417	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha cosmica	40-4005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1
Ophiacantha granulifera	184	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiacantha pentacrinus	160-1245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiacantha setosa	5-1480	1	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiacantha smitti	75-2282	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ophiacantha spectabilis	145-1750	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiacantha stellata	102-478	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiacantha varispina	184	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiacantha veterna	101-2460	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacanthella troscheli	133-793	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Ophiactis abyssicola	118-4721	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Ophiactis algicola	0-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Ophiactis balli	50-1765	0	1	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis brasiliensis	1-163	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiactis luetkeni	0-120	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiactis lymani	0-600	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0
Ophiactis muelleri	13-67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiactis nidarosiensis	102-560	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Ophiactis notabilis	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiactis plana	18-412	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiactis quinqueradia	0-640	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiactis rubropoda	0-8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiactis savignyi	1-550	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0
Ophiactis seminuda	80-140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiactis virens	0-90	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiambix devaneyi	146-494	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiarachnella africana	60-200	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiarachnella petersi	1-474	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiarachnella semicincta	69-104	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophidiaster alexandri	52-505	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0
Ophidiaster bayeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophidiaster bullisi	40-73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophidiaster guildingi	0-329	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0
Ophidiaster ophidianus	0-105	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Ophidiaster reyssi	128-350	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiernus adspersus	68-3650	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioblenna antillensis	1-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiobyrsella serpens	126-358	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiocamax hystrix	53-706	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiochondrella squamosa	175-602	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiochondrus convolutus	165-720	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiocnida loveni	0-48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiocnida scabriuscula	1-126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiocoma echinata	0-183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
Ophiocoma paucigranulata	1-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiocoma pumila	0-375	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Ophiocoma wendtii	1-384	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
Ophiocomella ophiactoides	1-18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
Ophiocomina nigra	0-400	1	1	0	1	0	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophioconis forbesi	20-230	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophioconis vivipara	20-300	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiocreas lumbricus	135-230	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiocryptus dubius	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiocten abyssicolum	100-1000	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiocten affinis	8-550	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiocten gracilis	198-1200	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Ophiocten sericeum	5–2222	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ophioderma anitae	0-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioderma appressa	0-364	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1	0
Ophioderma brevicauda	1-64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophioderma brevispina	1-223	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Ophioderma cinerea	0-1719	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Ophioderma devaneyi	54-139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophioderma divae	15-106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophioderma elaps	133-547	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioderma ensifera	11-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioderma guttata	0-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioderma januarii	0-118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Ophioderma longicauda	0-120	0	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophioderma phoenia	1-14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioderma rubicunda	1-110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Ophioderma squamosissima	3-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiogeron granulatus	95-627	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiohelus umbella	151	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiolepis affinis	7-110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiolepis ailsae	156-549	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiolepis elegans	1-329	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiolepis gemma	2-139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiolepis impressa	0-33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Ophiolepis kieri	2-4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiolepis paucispina	1-93	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0
Ophiolepis pawsoni	21-24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioleptoplax brasiliana	15-520	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophiolipus agassizii	142-309	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiolycus dentatus	164-450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ophiolycus purpureus	75-1480	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiomastus satelitae	115-600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophiomastus secundus	110-2050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiomisidium pulchellum	70-3063	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiomitra valida	16-538	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiomitrella clavigera	160-1952	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Ophiomitrella laevipellis	155-507.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiomusium acuferum	48-575.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiomusium anaelisae	180-258	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ophiomusium eburneum	35-1064	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiomusium testudo	126-926	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiomusium validum	108-2850	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiomyces frutectosus	50-1098	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiomyces grandis	150-1800	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiomyxa brevicauda	21-360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiomyxa flaccida	0-380	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Ophiomyxa pentagona	21-1095	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiomyxa stimpsonii	62-768	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiomyxa tumida	23-805	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Ophiomyxa vivipara	0-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Ophionephthys limicola	1-12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophionereis dolabriformis	14-99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophionereis olivacea	0-77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Ophionereis reticulata	0-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Ophionereis sexradia	18-128	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophionereis squamulosa	1-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophionereis vittata	10-126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopaepale goesiana	68-435	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopholis aculeata	0-1000	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Ophiophragmus acutispina	10-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiophragmus brachyactis	22-87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiophragmus cubanus	1-36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiophragmus filograneus	0-80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiophragmus luetkeni	0-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiophragmus moorei	1-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiophragmus pulcher	0-47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophiophragmus septus	1-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiophragmus wurdemani	2-11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Ophiophrixus spinosus	40-1383	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophioplax clarimundae	30-103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophioplax ljungmani	22-504	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioplax reducta	146-219	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopleura borealis	10-2500	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ophiopleura inermis	150-1875	1	1	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Ophioplinthaca spinissima	177-219	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioplinthus scutata	174	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioplocus januarii	0-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Ophioplus tuberculosus	175-165	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopristis hirsuta	150-1740	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila annulosa	10-100	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiopsila aranea	8-185	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiopsila fulva	29-315	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila guineensis	18-175	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiopsila hartmeyeri	12-161	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila maculata	42-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila platispina	18-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila polysticta	14-91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila riisei	0-91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopsila vittata	11-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiopteron atlanticum	11-120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiopus arcticus	50-2290	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Ophiopyren longispinus	100-1024	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Ophioscolex glacialis	35-2727	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Ophioscolex serratus	166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophioscolex tropicus	188-918	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiostigma abnorme	16-185	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
Ophiostigma isocanthum	0-244	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Ophiostigma siva	1-99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Ophiosyzygus disacanthus	127-278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix ailsae	50-98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Ophiothrix angulata	0-540	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Ophiothrix aristulata	70-530	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix brachyactis	1-6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix cimar	0-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix congensis	0-65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiothrix cotteaui	0-820	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiothrix fragilis	0-509	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiothrix hartfordi	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix lineata	0,7-57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix luetkeni	130-838	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiothrix maculata	114-410	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiothrix nociva	25-65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiothrix oerstedii	0-31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix pallida	33–1280	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix platyactis	0-43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix quinquemaculata	40-250	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiothrix rathbuni	5-600	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Ophiothrix roseocoerulans	0-55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Ophiothrix stri	0-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix suensoni	0-479	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Ophiothrix synoecina	0-4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiothrix trindadensis	0-98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Ophiothyreus goesi	144-540	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiotreta valenciennesi	123-1442	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Ophiozonella antillarum	171-926	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiozonella clypeata	148-275	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiozonella granulifera	70-1097	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiozonella molesta	68-2115	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiozonella nivea	102-1003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiozonella tessellata	109-547	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiura acervata	8-630	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiura albida	2-1030	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura carneaex	40-2857	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiura falcifera	73-1050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ophiura fallax	22-433	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Ophiura flagellata	96-2330	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura grubei	1-350	0	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiura imprudens	75-560	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura ljungmani	100-6398	1	1	0	1	0	0	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	1	0
Ophiura ophiura	0-704	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura robusta	0-1950	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Ophiura sarsii	3-3000	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Ophiura tenera	158-2999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiurochaeta littoralis	10-49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiurothamnus exigua	153-438	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Oreaster clavatus	3-38	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Oreaster reticulatus	0-800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0
Ova canaliferus	9-105	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeobrissus hilgardi	150-1025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Paleopneustes cristatus	76-805	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Paleopneustes tholoformis	90-645	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Panningia bispicula	32-74	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Panningia crosnieri	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Panningia curvata	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Panningia fastigata	30-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Panningia hyndmanni	15-1150	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panningia pseudocurvata	26-41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Paracaudina chilensis	0-1006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Paracentrotus gaimardi	0-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Paracentrotus lividus	0-100	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracolochirus mysticus	18-215	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Paracucumaria deridderae	23	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parastichopus regalis	5-800	1	1	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Parastichopus tremulus	20-1918	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratelecrinus orthotriremis	177-855	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Parathyone braziliensis	1-60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Parathyone surinamensis	0-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Parechinus angulosus	0-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Parvulastra exigua	0-3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Pawsonaster parvus	30-600	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Pawsonia saxicola	0-50	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinura vestita	182	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedicellaster typicus	20-223	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Peltaster placenta	10-1370	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Pentacta peterseni	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pentamera calcigera	10-100	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pentamera pulcherrima	0-27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Persephonaster echinulatus	196-724	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Phormosoma placenta	44-4100	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0
Phrixometra longipinna	146-1097	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phyllophorella drachi	90	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllophorus arenicola	6-158	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Phyllophorus granulatus	3-15	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllophorus mammulus	45-90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllophorus occidentalis	1-99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Phyllophorus pedinaequalis	200-700	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllophorus urna	2-150	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiobrissus africanus	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiobrissus costae	20-200	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Plagiobrissus grandis	1-409	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Plagiobrissus jullieni	13-300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plethotaenia angularis	150-645	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Plethotaenia spatangoides	150-619	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0
Plutonaster agassizi	70-4252	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0
Podocidaris sculpta	8-780	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Poliometra prolixa	20-1960	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pontaster tenuispinus	16-2620	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Porania pulvillus	5-680	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Poraniella echinulata	3-309	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Poraniomorpha bidens	52-1200	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Poraniomorpha hispida	90-1500	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Poraniomorpha tumida	9-1203	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Poraniopsis echinaster	0-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pourtalesia jeffreysi	50–3081	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Protankyra benedeni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Protankyra dubia	145-210	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Protankyra multidentata	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Protankyra ramiurna	shallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Prototrochus geminiradiatus	70-225	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammechinus microtuberculatus	4-100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psammechinus miliaris	0-100	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudarchaster gracilis	168-2940	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0
Pseudarchaster parelii	75-3540	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Pseudechinus magellanicus	0-820	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pseudoboletia maculata	1-450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0
Pseudocnella syracusana	7-100	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocnus grubei	3-145	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocnus koellikeri	50-685	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudostichopus	134-5453	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Pseudothyone belli	0-37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Pseudothyone raphanus	7-1150	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudothyone sculponea	25-120	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudothyone serrifera	50-1045	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psilaster andromeda	35-2965	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Psolus fabricii	0-1800	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Psolus megaloplax	90-360	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Psolus operculatus	150-274	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Psolus phantapus	1-400	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Psolus squamatus	7-1087	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Psolus tropicus	180-300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Psolus tuberculosus	73–243	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Psolus victoriae	50-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pteraster acicula	196-3712	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pteraster militaris	10-2152	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pteraster obscurus	19-600	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pteraster pulvillus	36-3696	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pteraster rugosus	91-466	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Quironia johnsoni	37-73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Rhabdomolgus ruber	0-21	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Rhopalodina celsa	22-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina compacta	9-35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina gracilis	35-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina intermedia	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina intesti	10-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina lageniformis	2-56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina pachyderma	9–14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina panningi	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina parvalamina	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina proceracolla	30–50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina turrisalta	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodina turrisdensa	25-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodinaria bocherti	24-32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Rhopalodinopsis capensis	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhopalodinopsis collalongus	21-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynobrissus cuneus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Rosaster alexandri	60-445	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Rotula deciesdigitatus	0-13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Schizaster doederleini	12-250	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Schizaster edwardsi	15-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Schizaster floridiensis	2-45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Schizaster orbignyanus	22-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Schizostella bifurcata	12-46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sclerasterias contorta	20-424	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0

Echinoderm species	**Depth (m)**	**AZO**	**MAD**	**LUS**	**CAN**	**CAP**	**SEL**	**WAF**	**IBE**	**BRI**	**FAR**	**SCA**	**ICE**	**GRE**	**MED**	**CAF**	**ASC**	**STH**	**ANG**	**ART**	**NSC**	**VIR**	**CRL**	**BER**	**TRO**	**STP**	**TRI**	**BRA**	**TCU**
Sclerasterias eustyla	185-275	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sclerasterias guernei	160-1000	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sclerasterias neglecta	160-485	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sclerasterias richardi	100-710	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sclerasterias tanneri	35-699	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Sclerodactyla briareus	0-180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Sigsbeia conifera	4-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sigsbeia murrhina	16-706	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Solaster caribbaeus	20-649	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Solaster endeca	0-549	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Solaster glacialis	30-790	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Solaster syrtensis	82-185	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Spatangus purpureus	0-900	**0**	0	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Spatangus raschi	146-1500	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spatangus subinermis	60-313	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerechinus granularis	0-120	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stegnaster wesseli	0-183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Stegophiura nodosa	0-565	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Stegophiura stuwitzii	10-80	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stephanasterias albula	3-2300	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0
Stereoderma colochiriformis	44-80	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stereoderma congoana	7–45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stereoderma kirchsbergii	36-135	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stereoderma unisemita	10-200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Stichastrella rosea	2-700	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stolus cognatus	0-9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Strongylocentrotus droebachiensis	0-1150	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Strongylocentrotus pallidus	5-1600	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Stylocidaris affinis	0-1000	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0
Stylocidaris lineata	66-630	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Stylometra spinifera	102-658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Synapta hispida	4-18	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synaptula hydriformis	1-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Synaptula secreta	litoral	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Taeniogyrus furcipraeditus	4-5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taeniogyrus venustus	1-81	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tamaria halperni	180-500	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tamaria passiflora	198-278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tethyaster grandis	67-139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tethyaster subinermis	40-1400	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Tethyaster vestitus	5-293	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0
Thandarum manoelina	12-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Echinoderm species	Depth (m)	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
Thyone adinopoda	63-92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Thyone bacescoi	25	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone cherbonnieri	3-63	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone crassidisca	6-45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Thyone deichmannae	6-366	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Thyone fusus	5-402	0	1	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone gadeana	80-1045	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone inermis	0-170	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone pawsoni	6-51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Thyone pseudofusus	6-46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Thyone roscovita	0-40	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyone tanyspiera	20-170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Thyonella gemmata	0-6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Thyonella pervicax	6-70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Thyonella sabanillaensis	4-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Thyonidium drummondii	5-923	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Thyonidium flavum	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyonidium hyalinum	4-200	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thyonidium seguroensis	1-210	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Trachythyone corbicula	145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachythyone crassipeda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Trachythyone fallax	38-70	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Trachythyone flaccida	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Trachythyone nina	132-1308	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Tremaster mirabilis	150-1060	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Tretocidaris bartletti	48-914	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Tretocidaris spinosa	50-72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Trigonocidaris albida	70-720	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tripneustes ventricosus	0-55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0
Trochoderma elegans	9-700	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Tropiometra carinata	0-84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
Tylaster willei	79-2920	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Urasterias lincki	5-2000	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Ypsilocucumis asperrima	43–720	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Table S7.2. Species not included in the analysis, owing to their uncertain taxonomic status, geographical and/or bathymetrical distributions in the studied area.

Species	Class	Uncertain taxonomical status	Uncertain geographical range	Uncertain bathymetrical range	Non-native
Aquilonastra burtoni (Gray, 1840)	Asteroidea				x
Aquilonastra yairi O'Loughlin & Rowe, 2006	Asteroidea			x	
Amphiura canadensis Verrill, 1899c	Ophiuroidea			x	
Amphiura deichmanni Tommasi, 1965	Ophiuroidea			x	
Amphiura exigua Verrill, 1899c	Ophiuroidea			x	
Amphiura joubini Koehler, 1912	Ophiuroidea	x			
Amphiura lymani Studer, 1885	Ophiuroidea				x
Arbaciella elegans Mortensen, 1910	Echinoidea		x	x	
Asteroschema vicinum Koehler, 1907	Ophiuroidea			x	
Astropecten richardi Perrier, 1875	Asteroidea	x		x	
Bathyplotes natans (Sars, 1868)	Holothuroidea	x			
Bathyplotes pourtalesii (Théel, 1886)	Holothuroidea	x			
Bathyplotes tizardi (Théel, 1882)	Holothuroidea	x			
Chiridota conceptacula Cherbonnier, 1963	Holothuroidea			x	
Clypeaster aloysioi (Brito, 1959)	Echinoidea			x	
Cucumaria vicaria Sluiter, 1910	Holothuroidea			x	
Dougaloplus libera (Koehler, 1907a)	Ophiuroidea			x	
Elpidia echinata (Perrier, 1896b)	Holothuroidea	x			
Engeliella engeli Cherbonnier, 1968	Holothuroidea			x	
Enypniastes eximia Théel, 1882	Holothuroidea			x^2	
Globosita dobsoni (Bell, 1883)	Holothuroidea			x	
Hemioedema albofusca Cherbonnier, 1958e	Holothuroidea			x	
Henricia oculata (Pennant, 1777)	Asteroidea	x	x	x	
Henricia sanguinolenta (Müller, 1776)	Asteroidea		x	x	
Holothuria imperator Deichmann, 1930	Holothuroidea	x			
Holothuria suspecta Cherbonnier, 1958d	Holothuroidea			x	
Lanceophora souriei (Cherbonnier, 1949)	Holothuroidea			x	
Leptasterias danica (Levinsen, 1887)	Holothuroidea			x	
Leptosynapta marchadi Cherbonnier, 1963	Holothuroidea			x	
Mellita isometra Harold & Telford 1990	Echinoidea	x			
Mellita quinquiesperforata (Leske, 1778)	Echinoidea	x			
Ocnus cruciformis Thandar in Thandar & Mjobo, 2014	Holothuroidea			x	
Ophiacantha bidentata (Bruzelius, 1805)	Ophiuroidea		x	x	
Ophiacantha fraterna Verrill, 1885b	Ophiuroidea		x	x	
Ophioderma besnardi Tommasi, 1970a	Ophiuroidea	x			
Ophioderma holmesii (Lyman, 1860)	Ophiuroidea			x	
Oestergrenia kongoensis Heding, 1932	Holothuroidea			x	
Paramphiura punctata (Forbes, 1841)	Ophiuroidea			x	
Paracucumaria mauritanica (Hérouard, 1929)	Holothuroidea			x	
Pentacta guinensis (Heding, 1943)	Holothuroidea			x	
Pentacta hedingi Panning, 1940	Holothuroidea			x	
Protankyra panningi Heding, 1931	Holothuroidea			x	
Prototrochus meridionalis (Salvini-Plawen, 1977)	Holothuroidea			x	
Pseudocnus rhopalodiformis (Heding, 1943)	Holothuroidea			x	
Pseudocnus rugosus Cherbonnier, 1957	Holothuroidea			x	
Stereoderma monodi Cherbonnier, 1950	Holothuroidea			x	
Thyone montoucheti Tommasi, 1971	Holothuroidea	x		x	

Table S7.3. Shared Echinoderm species between areas in the North and Central Atlantic and Mediterranean Sea

	AZO	MAD	LUS	CAN	CAP	SEL	WAF	IBE	BRI	FAR	SCA	ICE	GRE	MED	CAF	ASC	STH	ANG	ART	NSC	VIR	CRL	BER	TRO	STP	TRI	BRA	TCU
AZO	64																											
MAD	34	69																										
LUS	15	16	28																									
CAN	44	48	20	85																								
CAP	27	31	14	41	76																							
SEL	12	16	4	18	14	18																						
WAF	45	50	21	62	45	12	126																					
IBE	52	55	22	65	38	14	92	153																				
BRI	38	33	14	41	23	7	60	102	141																			
FAR	19	16	8	20	14	2	33	58	83	98																		
SCA	21	20	8	25	12	3	36	69	96	87	129																	
ICE	23	15	6	19	14	2	32	50	70	69	80	89																
GRE	11	4	1	6	3	1	9	22	43	52	65	53	85															
MED	41	49	20	61	35	16	75	92	62	22	39	21	3	142														
CAF	25	38	14	51	55	11	64	49	30	15	17	14	2	46	167													
ASC	5	7	0	7	13	3	5	7	3	1	1	2	2	3	11	25												
STH	9	11	3	12	12	4	10	12	4	3	3	5	3	8	13	12	31											
ANG	12	17	6	22	22	3	30	20	10	7	7	5	1	21	59	3	9	68										
ART	3	1	1	1	1	1	1	11	29	40	58	39	59	2	1	0	1	1	66									
NSC	11	6	1	7	4	1	11	27	50	48	57	51	60	5	3	3	2	2	44	93								
VIR	14	8	5	12	6	2	14	21	34	32	31	31	32	9	7	3	3	3	20	53	85							
CRL	15	10	7	19	19	3	21	23	19	16	19	20	16	14	20	8	13	8	7	31	55	166						
BER	6	8	3	11	17	5	9	9	4	5	4	6	5	5	14	13	7	5	3	5	10	29	64					
TRO	27	15	11	28	31	5	36	34	24	15	16	20	15	22	39	20	17	15	5	26	52	154	60	483				
STP	1	3	1	2	5	1	2	2	1	1	1	1	1	1	5	5	4	3	1	1	1	7	7	10	11			
TRI	2	2	1	5	8	1	3	2	1	0	1	0	0	2	11	10	5	4	0	0	1	13	18	37	4	39		
BRA	7	8	5	10	17	4	11	8	2	1	1	2	2	7	19	9	11	11	1	3	11	50	27	113	7	24	143	
TCU	4	3	3	4	3	1	3	5	4	4	3	5	3	2	2	0	3	1	1	2	3	2	1	4	1	1	3	19

Chapter 8. Final Remarks

8.1. General discussion

Fossil Fauna of the Azores

A clear understanding of the geological evolution of Santa Maria Island, together with the litho- and bio-stratigraphy of the island's fossil outcrops have emerged since the publication of Madeira *et al*. (2011; Chapter 2, pag. 9). More recent age dating of Santa Maria Island points to a slight younger age than previous though, around 6.01 Ma (Ramalho *et al*. 2017). Moreover, not long after the Santa Maria first emergence, the island became a shallow, flat-topped seamount (or bank) similar to a guyot. The erosion of Santa Maria's volcanic edifice during this period of relative calm (5.3 and 4.1 Ma; Ramalho *et al*. 2017) between intensive volcanic activity created a unique setting in Northeast Atlantic, perfect for shallow water communities to thrive (Uchman *et al*. 2018). Later, as the volcanic activity resumed, the sedimentary sequences and biological remains became encapsulated in the volcanic edifice (Ávila *et al*. 2018a). From around 3.5 Ma to the present day, the island experienced pronounced uplift (Ramalho *et al*. 2017). This period was also characterized by a declining in the volcanic activity, which created perfect conditions, for the erosion and consequent exhumation of submarine fossiliferous sequences (Ávila *et al*. 2018a). More recent K/Ar dating have placed the older fossiliferous deposits in the Early Pliocene, with ages ranging between 4.02 ± 0.06 Ma and 3.96 ± 0.06 Ma (Sibrant *et al*. 2015), which confirm previous biostratigraphic data by Janssen *et al.* (2008). Detailed characterization of the litho- and bio-stratigraphy of the Pliocene outcrops can be found in Meireles *et al*. (2013), Ávila *et al*. (2015a, 2018a), Santos *et al.* (2015), Rebelo *et al*. (2016a, b), Uchman *et al*. (2016, 2017, 2018) and Johnson *et al*. (2017).

The earliest paleontological publication on the Pliocene echinoid fossil record of Santa Maria Island can be traced back to the late eighteenth century (*e.g.*, Mayer 1864), but published faunal lists remain unaltered since the mind 1950's. Overall, Madeira *et al*. (2011) demonstrated this subject was far from being exhausted, as it led to the inclusion of an additional five new taxa to the Early Pliocene fauna (*Echinoneus* cf. *cyclostomus*, *Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids).

Madeira *et al*. (2011) established that the Early Pliocene echinoid record is dominated by tropical shallow water taxa (*e.g*., *Eucidaris tribuloides*, see also Chapter 5, pag. 244), which agrees with recent studies in Santa Maria Island (*e.g*., Ávila *et al*. 2015a, 2016; Johnson *et al*. 2017). Moreover, since Madeira *et al.* (2011), new data on the trace fossil record of the Santa Maria Island has been published, adding new elements to its Pliocene rocky palaeoshores. Santos & Mayoral (2015 *in* Santos *et al.* 2015) described a new ichnospecies *Ericichnus bromleyi* from the 'Ichnofossil's Cave', a Pliocene outcrop in the south of Santa Maria Island (for location, see fig. 1, by these authors). These authors described bioerosive structures close to those produced by the rock boring echinoid *Echinometra lucunter* (see also Chapter 5, pag. 374). This Atlantic species as the genus to which it belongs is restricted to shallow warm water regions (Mortensen 1943), and does not occur in the extant waters of the Azores.

In contrast with Early Pliocene, the Pleistocene (Last Interglacial) echinoid fossil record of Santa Maria Island was largely unknown. Madeira *et al*. (2011) revealed a younger fauna, more typical of warm temperate waters, in large measure identical to the Azorean vagil fauna, *i.e*., Pleistocene rocky shores of Santa Maria Island were most likely dominated by three echinoid species: *Arbacia lixula*, *Paracentrotus lividus* and *Sphaerechinus granularis*. This idea is reinforced by the presence of the ichnotaxon *Circolites* in Prainha outcrop (Ávila *et al*. 2010). These circular depressions, bored into the basalt were probably made by the rock borer *P. lividus*, and are very similar to those frequently observed in the first few meters of the present rocky shores of the Azores (for an extant example see Chapter 5, pag. 268, Fig. 5.25J).

The comparison of the Early Pliocene and the Pleistocene fossil record, reveals contrasting assemblages, *i.e*., an evolution from a tropical to a more temperate fauna, closer to the present Azorean marine fauna. This dramatic faunal change is yet another example of the Pleistocene glaciations impact on the marine shallow water community (see Ávila *et al*. 2016). Of the Pliocene taxa, identified to species level, all but one species (*Echinocyamus pusillus*) have locally disappeared. Surprisingly, this small echinoid was absent from Pleistocene faunal list presented by Madeira *et al*. (2011). All investigated Pleistocene deposits at Santa Maria Island derive from ancient rocky shores, preserving only a small part of the biodiversity that existed in the past. Thus, this absence was ruled at the time as artefact of the facies restriction and the palaeoenvironments preserved. More recently, on occasion of the annual international workshops ‘Palaeontology in Atlantic Islands’ (since 2002 onwards; University of the Azores), more material became available and specimens from the Pleistocene outcrop of Prainha were identified as *E. pusillus* (Madeira *et al*. 2017a; Annex I). This small irregular echinoid is known to presently occur in the extant waters of the Mediterranean Sea and Northeast Atlantic, from boreal waters of Scandinavia and Iceland to tropical waters of Sierra Leone, including the Azores (Schultz 2006; see also Chapter 5, pag. 305). The eurythermic nature of *E. pusillus*, reflected by its wide geographical range, provided this species with abilities to withstand different oceanographic conditions that prevail in the Azores from Early Pliocene until today, and to became one of the most pervasive faunal elements of the archipelago.

The echinoid diversity in the fossil record of Santa Maria Island is undoubtedly low, when compared with other represented animal groups, such as the Mollusca with 191 Pliocene species and 136 Pleistocene species (for complete faunal list please see Table 1, by Ávila *et al*. 2018a). The echinoid fossil record of Santa Maria is also apparently poorer, when compared with those from the nearest continental masses (*e.g.*, Pereira 2008). However, the study of Santa Maria’s fossil record made invaluable contributions to our understanding of the evolution of the shallow-water fauna through time, not only in this remote oceanic island system, but as well in the NE Atlantic.

Extant fauna of the Azores

The study of the fossils of Santa Maria Island, with its remarkably rich exposed marine fossiliferous sediments and submarine volcanic sequences (Ávila *et al*. 2018a) has reduced the knowledge gap between the marine palaeofauna and the present marine fauna inhabiting the shores of the Azores. Biogeographical interpretations on this archipelago have now a set of paleontological data that goes beyond the Pleistocene glaciations. However, the initial comparison between fossil and extant echinoid faunas of the Azores led to the detection of some inconsistences. Madeira *et al*. (2011) adverted to the unlikelihood of thermophilic *Eucidaris tribuloides* still occurring in the extant waters of the Azores (see Chapter 2, pag. 37), as was implied by recent checklists (*e.g.*, Pereira 1997; Micael *et al*. 2012). As a consequence, a more exhaustive review of the extant fauna of the Azores ensued, in order to support any future biodiversity or biogeographical studies of the archipelago’s echinoderms.

The history of zoological studies on the extant echinoderm fauna of the Azores almost mirrors that of the palaeontological research in Santa Maria Island. The first publications also date back almost 150 years, and by 1910’s, most elements living in the archipelago extant shores were known (for details, see Chapter 5, pag. 86). *Arbaciella elegans* was the last echinoid species to be added to the local shallow-water fauna by Marques (1983). This author based his record on the identification of several small arbacioid specimens collected in the Azores, now housed in the zoological collection of Museu Bocage - Museu Nacional de História Natural (Lisbon). Similarities between this material and juvenile specimens of *Arbacia lixula* from the Azores, led Kroh *et al*. (2011; Chapter 3, pag.51) to revert *A. elegans* geographical range back to the West Africa shores.

A further bibliographic review revealed other erroneous inclusions in the archipelago’s checklists, based on historical misrepresentations (*e.g.*, *Gracilechinus elegans*, pag. 373), outdated synonymy (*e.g.*, *Astropecten bipispinosus*, pag. 367) or even based on material of unknown or dubious origin (*e.g., Spatangus purpureus*, pag. 378). Moreover, examples of tropical shallow-water species being incorporated in the Azorean faunal lists solely based on young specimens were not restricted to the echinoids mentioned above, but also included the sea-cucumber *Holothuria mexicana* (pag. 330) and the brittle-star *Ophioneis reticulata* (pag. 123). Like *Eucidaris tribuloides*, both species are not seen in the archipelago waters since the publications of ‘Princessa-Alice’ and ‘Hirondelle’ reports, more than a century ago. The arrival of young stages of non-native species in the coasts of the archipelago is not unheard of (*e.g.*, Avila 2000). However, different hydrological conditions experienced in the Azores shores may render the establishment of tropical species impossible (Santos *et al*. 1995). This illustrates the dangers of misinterpreting historical data when uncritically incorporating it into faunal checklists.

Historically, both surface and deeper waters in the Azores appear to be well surveyed, through years of both local and international workshops, expeditions and oceanographic cruises (Chapter 5, pag. 86; but see Ávila 2015b). However, data is noticeable scarce on intermediate waters (50-200 m), *i.e.*, between maximum depth sampled by scuba-diving (<50 m depth) and waters normally targeted by large oceanographic cruises (>>200 m depth). Fortunately, the zoological collection of the Department of Biology (University of the Azores) houses material dredged during rare occasions in the history of marine studies of the archipelago that target precisely this depth interval (*e.g.*, the 3rd International Workshop of Malacology and Marine Biology; Martins *et al*. 2009). From its study, Madeira *et al*. (2017b; see Chapter 4, pag. 69) reported the Mediterranean *Sclerasterias richardi* for the first time in the Azores, but it soon became clear that to avoid the same trappings as those mentioned above, a more reserved stand was required. Unlike *E. tribuloides* or *O. reticulata*, *S. richardi* is not restricted to the tropics, and it is not known from waters shallower than 80 m deep (see also Chapter 5, pag. 193). Nevertheless, available material appears to be composed of small juveniles, and as is characteristic of this genus, also capable of reproduce asexually through fission (Fisher 1928). This may indicate that the animals collected in Azores are cloning representatives of a non-reproductive pseudopopulation, located in the fringes of their natural occurrence (see also Chapter 7, pag. 499).

The study of the echinoderm material housed in the above mentioned Portuguese collections, also allowed the confirmation of the presence of several species in the Azores, including some iconic species such as *Astropecten hermatophilus* (Chapter 5, pag. 202). This small sea-star was not recorded in the archipelago for over 100 years, despite the species being firstly described in the Azorean waters by Sladen (1883).

In sum, from the review of the initial 41 (Pereira 1997) to 49 species (Micael *et al*. 2012), listed as being present in the Azorean shallow-waters, Madeira *et al.* (*submitted*; Chapter 5) believed that only 29 species actually live in the archipelago at depths shallower than 50 m. The echinoderm diversity recorded in the shallow-waters of the Azores appears notably poor. Madeira *et al.* (*submitted*, Chapter 5, pag. 95) correlates this to five contributing factors: limited coastal area, low habitat diversity, absence of extended soft-bottom environments, isolation-by-distance and the recent volcanic origin of the archipelago. If deeper waters are considered (<50 m), the number of echinoderm species present in the Azores rises to 172 echinoderms (see also Annex II, pag. 599), a number comparable to the values obtained for Canaries by

Hernández *et al*. (2013). Most of these species are well distributed in the Atlantic (see Fig. 5.3, pag. 95), though the geographical range of most of the shallow-water species have the Azores as their westernmost limit. Remarkably, six out of nine endemic species (all from deep-waters) were known only form the type material, casting some doubts the validity of these species.

In Chapter 5, Madeira *et al*. (*submitted*) shows that echinoderm diversity of the Azores appears to be shaped in a number of factors, ultimately linked to the its relatively recent volcanic origin of these mid-North Atlantic islands. Unfortunately, it also appears to be shaped by the presence/absence of expertise. In general, echinoderm species are notoriously difficult to identify, relying in many instances on the observation of microstructures (*e.g.*, ossicles, pedicellariae). Nothing exemplifies this better than the Holothurians, in which the observation of gross external morphological characters is seldom sufficient (Tortonese 1965). In recent years, the researchers found in genetic tools a perfect ally (*e.g.*, Borrero-Pérez *et al*. 2009). However, as genetic protocols develop in to increasing fast and efficient tools, so thus the logistics and expertise requirements. The rapid and reliable identification of holothurians becomes increasing urgent, as both local and global markets expand to an increasingly number of exploited species (Uthicke *et al*. 2010; González-Wangüemert *et al*. 2016).

Madeira *et al* (2018; Chapter 6, pag. 451) demonstrated that a compromise can be reached, by using a somewhat old-fashion, but simple and inexpensive genetic techniques, the restriction fragment length polymorphism (RFLP), already used at the more conventional fisheries (Stefanni *et al*. 2009). Though, it was a preliminary study, restricted to two of the most common sea-cucumbers in the Azorean littoral (see Chapter 5, pags. 332, 336), Madeira *et al*. (2018) showed promising results. Furthermore, this study also demonstrated that for genetic purposes, the use of small tissue samples from tentacles or tube feet a far more effective and less destructive technique than the internal structures frequently used in genetic studies (*e.g.,* Uthicke *et al*. 2004; Borrero-Pérez *et al*. 2010; So *et al*. 2011). Combined with a non-destructive tissue sampling, this genetic tool could be also used in the identification of alive, museum, or commercially harvested specimens, without the need of taxonomical expertise or morose and expensive protocols of identification.

Biodiversity and Biogeographical patterns

On a broader biogeographical setting, the Azores position becomes even more fascinating, whether considering on an ecological timescale (*i.e.*, <100 years) or in a wider geological time frame. As in any other volcanic oceanic system, the marine shallow-water fauna in the Azores derives primarily from episodic arrival of long-distance dispersal settlers that over-time may or may not successfully establish a viable population in the islands (Ávila *et al*. 2018b). Thus, the archipelago's biotic isolation should be in large measure dictated by its geographical position and oceanographic conditions (both local and regional).

Planktonic larval stages are a common reproductive trait in benthic marine invertebrates (Pechenik 1999). Conventional wisdom dictates that planktonic feeding larvae (planktotrophic development mode) should be capable of longer dispersal than planktonic non-feeding larvae (lecithotrophic development mode), because the former can supplement the original energy allocated to the egg by feeding (Jablonski & Lutz 1983; Young *et al.* 1997; Todd 1998; McEdward & Miner 2001). Not surprisingly, most echinoderms species in Azores (as in other islands in the Atlantic) produce long-lived larval stages (*i.e.*, planktotrophic larval development), which appear to be well equipped to surmount the long stretches of inhospitable deep waters surrounding the islands.

The echinoderm fauna in the Azores is also characterized by a higher representation of species capable of asexual reproduction when compared with continental coasts at similar latitudes. The theoretical framework of Baker's law (Baker, 1955, 1966), predicts that the long-distance dispersal's demographic sieve favours colonists capable of establishing a population from a single individual after a rare chance colonization event. In simple terms, sexual reproduction further requires more or less synchronous colonization by at least two aclonal animals (Jackson, 1986). On the other hand, asexual reproduction (uniparentality) as a mechanism of density-independent reproductive assurance could play an important role in enhancing or maintaining population density by cloning individuals in remote islands or island-like habitats, or even in long-distance transportation by rafting. Sexual reproduction appears to confer advantages for survival in small isolated populations, by freezing life cycles and cloning 'best-suited' genotypes (see review by Pannel *et al*. 2015).

The Azores (as other oceanic islands and archipelagos in the Atlantic) is characterized by the prevalence of shallow-water echinoderm species with wide distributional and bathymetrical ranges. However, when considering the faunal relationships, the Azorean echinoderm fauna appeared to be shaped by a paradox, showing a close faunal proximity with the northeast Atlantic coasts, in contrast with the prevailing west driven sea-surface currents. Notwithstanding, combining the Azores with other oceanic islands and archipelagos in the Atlantic, a new picture emerges, *i.e.*, shallow-water echinoderm faunas in oceanic islands tend to be always closely related with the nearest land mass (see Fig. 7.12, pag. 490), despite the prevailing sea-surface currents. The arrival of new settlers appears to be 'episodic', by taking advantage of periodical events that reverse the main sea-surface current patterns.

Endemic species were almost absent in the studied oceanic islands and archipelagos. Low endemism rates in high-latitude oceanic islands may reflect the occurrence of past environmental alterations that caused extirpations (or even extinctions), followed by a repopulation by migrants from other areas (Briggs, 1995; Ávila *et al.*, 2008, 2019). During Pleistocene glaciations, the ice caps that repeatedly covered most of the Faroe Islands to depths well below shelf waters (Sejrup *et al.*, 2005) have in all probability extirpated the local shallow-water echinoderm fauna. Nevertheless, ice-sheet formation during glaciations is unlikely to have affected directly the southern archipelagos. Except for stenothermal species, global climatic cycles such as those of the Pleistocene were most likely of small consequence on central North Atlantic island faunas, as was shown for the marine malacofauna in the Azores (Ávila *et al.*, 2008, 2015a, 2018b). However, the glaciation cycles in the Pleistocene may have indirectly affected shallow-water species restricted to fine-sediment habitats in the islands, as the lower sea-level considerably reduced these habitats in shelf-less volcanic oceanic islands (see Ávila *et al.*, 2008b, 2015a, 2018). Mironov & Krylova (2006) attributed the general low rates of endemism in the central North Atlantic islands and seamounts to the co-operative effects of several factors: long duration of climatic and geomorphological changes, dramatic temperature changes in a recent past and a weak geomorphological separation (*e.g.*, presence of numerous seamounts between the areas).

8.2. General conclusions

The echinoderms proved to be an excellent group to study and test biogeographical models and evolutionary hypotheses, to identify factors and process, and to explore their effects in detected patterns. This animal group presents highly diverse sets of life strategies, with a remarkable amount of available information on species' distribution, habitat, development and other ecological features. The Azores, with an almost central position in the NE Atlantic, also revealed to be a perfect model area for the study of echinoderm faunas in the North Atlantic, whether at the taxonomic, ecological or biogeographical level. Unfortunately, significant deficiencies were also detected, mirroring the overall heterogeneity of available data through classes, depth and geographical areas. In Chapter 5, the review of the echinoderm fauna of the Azores shed some light of the critical flaws at a local level, but on broadening the geographical scale in Chapter 7, this pattern revealed to be far more generalised than previously acknowledged. Moreover, it was with some surprise to find other areas with a similar long tradition of marine research, such as Madeira, to have comparably more limited information on the local echinoderm faunas, mostly restricted to the first meters of the islands' extant rocky shores. Moreover, significant deficiencies on the knowledge from deeper littoral waters (between 50 and 200 m depth) were also found, particularly from unsuspected areas such as the Portuguese coasts or even the Mediterranean Sea.

In a true oceanic system such as the Azores, reducing the local echinoderm diversity to a static number underestimates the true richness of the archipelago's fauna. In other words, before adding or subtracting a species to an oceanic faunal landscape, a researcher has to measure the true weight of that addition (*e.g.,* invasive species) or subtraction (*e.g.,* local disappearance), whether constructing a biodiversity model or designing conservation and management policies. The presence of the Mediterranean *Sclerasterias richardi* in the Azores illustrates this dilemma perfectly (Chapter 4). This recent record may or may not mirror the restrict knowledge on the Azorean fauna living deeper than 50 m, particularly considering the species' cryptic nature. What is certain is that this species is well equipped for dispersal and colonization of remote areas such as the Azores (by means of a long larval development), and to withstand long stretches of time in isolation, whether in a traveling raft or in a remote area such as the Azorean coasts (*i.e.* asexual development). Despite the doubtful status in the Azorean faunal list, the presence alone of this sea star in São Miguel Island typifies the main features that characterize the archipelago´s fauna.

In sum, oceanic islands are a promising setting, a 'natural laboratory' to study biodiversity and biogeographical models. However, these 'discrete microcosms' and 'time-coded' entities are also notorious for conservation issues, after all it is already part of the common imaginarium that minor anthropogenic changes in islands (or island-like habitats) can result in rapid catastrophic ecological changes. Nonetheless, considering the technological advances seen in the recent years, it is expected a better understanding of both shallow and deep echinoderms faunas in the Atlantic and in the near future, that could not only further substantiate key findings in the present work, but to extend its main premises to the deep-water realm of the Azores and in the Atlantic.

8.3. References

Ávila, S.P. (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago*, Supplement 2(A), 99–131.

Ávila, S.P., Madeira, P., Mendes, N., Rebelo, A., Medeiros, A., Gomes, C., García-Talavera, F., Da Silva, C.M., Cachão, M., Hillaire-Marcel, C. & Martins, A.M.F. (2008) Mass extinctions in the Azores during the last glaciation: fact or myth? *Journal of Biogeography*, 35, 509–518.

Ávila, S.P., Ramalho, R.S., Habermann, J.M., Quartau, R., Kroh, A., Berning, B., Johnson, M., Kirby, M.X., Zanon, V., Titschack, J. & Goss, A. (2015a) Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores). *Palaeogeography, Palaeoclimatology, Palaeoecology, 430, 57*–73.

Ávila, S.P., P. Madeira, A.C. Rebelo, C. Melo, A. Hipólito, J. Pombo, A.Z. Botelho & Cordeiro, R. (2015b) *Phorcus sauciatus* (Koch, 1845) (Mollusca: Gastropoda) in the Archipelago of the Azores (NE Atlantic Ocean): the onset of a biological invasion. *Journal of Molluscan Studies*, 81: 516-521. doi:10.1093/mollus/eyv012

Ávila, S. P., Melo, C., Berning, B., Cordeiro, R., Landau, B., & da Silva, C.M. (2016) *Persististrombus coronatus* (Mollusca: Strombidae) in the lower Pliocene of Santa Maria Island (Azores, NE Atlantic): paleoecology, paleoclimatology and paleobiogeographic implications.*Palaeogeography, Palaeoclimatology, Palaeoecology*, 441, 912-923.

Ávila, S. P., Ramalho, R. S., Habermann, J.M., & Titschack, J. (2018a). The marine fossil record at Santa Maria Island (Azores). *In*: Kueppers U. & Beier C. (Eds.). *Volcanoes of the Azores*, Springer, Berlin, Heidelberg, pp. 155-196.

Ávila, S. P., Cordeiro, R., Madeira, P., Silva, L., Medeiros, A., Rebelo, A. C., Melo, C., Neto, A.I., Haroun, R., Monteiro, A., Rijsdijk, K. & Johnson, M. (2018b). Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands. *Marine pollution bulletin*, 126, 101-112.

Ávila, S.P., Melo, C., Sá, N., Quartau, R., Rijsdijk, K., Ramalho, R.S., Berning, B., Cordeiro, R., Sá, N.C. de, Pimentel, A., Baptista, L., Medeiros, A., Gil, A., Johnson, M.E. (2019) Towards a “Sea-Level Sensitive Marine Island Biogeography” model: the impact of glacio-eustatic oscillations in global marine island biogeographic patterns. *Biological Reviews*. DOI: 10.1111/brv.12492.

Baker, A.N., Clark, H.E.S. & McKnight, D.G. (2001) New species of the brittlestar genus *Astrogymnotes* H.L. Clark, 1914, from New Zealand and Japan (Echinodermata: Ophiuroidea). *Journal of the Royal Society of New Zealand*, 31(2), 299–306.

Baker, H.G. (1955) Self-compatibility and establishment after'long-distance'dispersal. *Evolution*, 9(3), 347–349.

Borrero-Pérez, G.H., Pérez-Ruzafa, A., Marcos, C. & González-Wangüemert, M. (2009) The taxonomic status of some Atlanto-Mediterranean species in the subgenus *Holothuria* (Echinodermata: Holothuroidea: Holothuriidae) based on molecular evidence. *Zoological Journal of the Linnean Society*, 157, 51–69.

Borrero-Pérez, G.H., Gómez-Zurita, J., González-Wangüemert, M., Marcos, C. & Pérez-Ruzafa, A. (2010) Molecular systematics of the genus *Holothuria* in the Mediterranean and Northeastern Atlantic and a molecular clock for the diversification of the Holothuriidae (Echinodermata: Holothuroidea). *Molecular Phylogenetics and Evolution*, 57, 899–906.

Briggs, J.C. (1995) *Global biogeography*. Elsevier, Amsterdam, xvii+452 pp.

Fisher, W.K. (1928) Asteroidea of the North Pacific and adjacent waters. Part 2: Forcipulata. *Bulletin of the United States National Museumi*, 76, 1–245.

González-Wangüemert, M., Valente, S., Henriques, F., Domínguez-Godino, J.A. & Serrão, E.A. (2016) Setting preliminary biometric baselines for new target sea cucumbers species of the NE Atlantic and Mediterranean fisheries. *Fisheries Research*, 179, 57–66.

Hernández J.C., Clemente S., Tuya F., Pérez-Ruzafa, A., Sangil, C., Moro-Abad, L. & Bacallado-Aránega J.J (2013) Echinoderms of the Canary Islands, Spain. *In*: Alvarado J.J., Solis-Marin F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*. Springer Berlin Heidelberg, pp. 471–510.

Jablonski, D. & Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.*, 58, 21–89.

Jackson, J.B.C. (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species’ distributions and genetic structure of local populations. *Bulletin of Marine Science*, 39(2), 588–606.

Johnson, M. E., Uchman, A., Costa, P.J., Ramalho, R. S., & Ávila, S.P. (2017) Intense hurricane transports sand onshore: Example from the Pliocene Malbusca section on Santa Maria Island (Azores, Portugal). *Marine Geology,* 385, 244–249.

Kroh, A., Madeira, P. & Haring, E. (2011) Species distribution: virtual or real – the case of *Arbaciella elegans* (Echinoidea: Arbaciidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 99–105.

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61(3), 243–264.

Madeira, P., Kroh, A., Melo, C., Cordeiro & Ávila, S.P. (2017a) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic). *In*: Ávila, S.P. & Melo, C. (Eds.). RCANS *2017 - 6th Regional Committee on Neogene Atlantic Stratigraphy, Ponta Delgada, São Miguel Island, Azores, July, 10-13, University of the Azores (Abstract Book)*, p. 44.

Madeira, P., Frias Martins, A.M. & Ávila, S.P. (2017b) First record of the Mediterranean asteroid *Sclerasterias richardi* (Perrier, *in* Milne-Edwards, 1882) in the Azores Archipelago (NE Atlantic Ocean). *Arquipelago*. *Life and Marine Sciences*, 35, 11–18.

Marques, V.M. (1984) Peuplements benthiques de Açores, 1 — echinoderms. *Arquivo do Museu Bocage*, AII (I), 1–7.

Martins, A.M.F. (Ed.) (2009) The Marine Fauna and Flora of the Azores: Proceedings of the Third International Workshop of Malacology and Marine Biology, São Miguel, Azores, July 17–28 2006. *Açoreana*, supplement 6, 225 pp.

Mayer, K. (1864) SystematischesVerzeichniss der fossilen reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. *In*: G. Hartung, *Geologische Beschreibung der Inseln Madeira und Porto Santo*. W. Engelmann, Leipzig, pp. 183–298.

McEdward, L.R. & Miner, B.G. (2001) Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology*, 79, 1125–1170.

Micael, J., Alves, M.J., Jones, M.B. & Costa, A.C. (2012) Diversity of shallow-water asteroids (Echinodermata) in the Azorean Archipelago. *Marine Biodiversity Records*, 5 (e49), 1–5, doi: 10.1017/S1755267211000534.

Mironov, A.N. & Krylova, E.M. (2006) Origin of the fauna of the Meteor Seamounts, north-eastern Atlantic. *In*: Mironov, A.N., A.V. Gebruk & A.J. Southward (Eds.) *Biogeography of the North Atlantic Seamounts*, pp. 22–57.

Mortensen, T. (1943b) *A monograph of the echinoidea. III.3 Camarodonta II*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 446 pp.

Pannell, J.R., Auld, J.R., Brandvain, Y., Burd, M., Busch, J.W., Cheptou, P.O., Conner, J.K., Goldberg, E.E., Grant, A.-G., Grossenbacher, D.L., Hovick, S.M., Igic, B., Kalisz, S., Petanidou, T., Randle, A.M., de Casas, R.R., Pauw, A., Vamosi, J.C. & Winn, A.A. (2015) The scope of Baker’s law. *New Phytologist*, 208, 656–667.

Pechenik, J.A. (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, 177,269–297.

Pereira, M.O.R. (1997) Checklist of the littoral echinoderms of the Azores. *Açoreana*, 8, 331–337.

Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Thomas, C., Quartau, R., Hipólito, A., Rovere, A., Hearty, P.J. & Ávila, S.P. (2017) The emergence and evolution of Santa Maria Island (Azores) – the conundrum of uplifting islands revisited. *Geological Society of America Bulletin*. doi:10.1130/B31538.1.

Santos, A., Mayoral, E., Dumont, C.P., da Silva, C.M., Ávila, S.P., Baarli, B.G., .Cachão, M., .Johnson, M.E. & Ramalho, R.S. (2015). Role of environmental change in rock-boring echinoid trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 432, 1-14.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M. & Isidro, E.J. (1995) Marine research and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5, 311–354.

Schultz, H. (2006) *Sea Urchins. A guide to worldwide shallow water shallow water species*. Heinke & Peter Schultz Partner Scientific Publications, 3rd edition, 484 pp.

Sejrup, H.P, Hjelstuen, B.O., Dahlgren, K.I.T., Haflidason, H., Kuijpers, A., Nygård, A., Praeg, D., Stoker, M.S. & Vorren, T.O. (2005) Pleistocene glacial history of the NW European continental margin. *Marine and Petroleum Geology*, 22, 1111–1129.

Sibrant, A.L.R., Hildenbrand, A., Marques, F.O., & Costa, A.C.G. (2015) Volcano-tectonic evolution of the Santa Maria Island (Azores): Implications for paleostress evolution at the western Eurasia–Nubia plate boundary. *Journal of Volcanology and Geothermal Research*, 291, 49–62.

Sladen, W.P. (1883) The Asteroidea of H.M.S. Challenger Expedition. Part II, Astropectinidae. *Journal of the Linnean Society. Zoology*, 17, 214–269.

So, J.J., Uthicke, S., Hamel, J.-F. & Mercier, A (2011) Genetic population structure in a commercial marine invertebrate with long–lived lecithotrophic larvae: *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Marine Biology*, 158, 859–870.

Todd, C.D. (1998) Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, 376, 1–21.

Tortonese, E. (1965) *Fauna D'Italia – Echinodermata*. Edizioni Calderini, Bologna, 422 pp.

Janssen, A.W., Kroh, A. & Ávila, S.P. (2008) Early Pliocene heteropods and pteropods (Mollusca, Gastropoda) from Santa Maria (Azores, Portugal): systematics and biostratigraphic implications. *Acta Geologica Polonica*, 58, 355–369.

Meireles, R.P., Quartau, R., Ramalho, R. S., Rebelo, A. C., Madeira, J., Zanon, V. & Ávila, S.P. (2013). Depositional processes on oceanic island shelves–Evidence from storm-generated Neogene deposits from the mid-North Atlantic. *Sedimentology*, 60(7), 1769-1785.

Pereira, P. (2008). *Echinoids from the Neogene of Portugal mainland: Systematics, Palaeoecology, Palaeobiogeography*. Ph. D. thesis, University of Lisbon, 200 pp.

Rebelo, A. C., Rasser, M. W., Kroh, A., Johnson, M. E., Ramalho, R. S., Melo, C., Uchman, A., Berning, B., Silva, L., Zanon, V., Neto, A.I., Cachão, M., Ávila, S.P. (2016a) Rocking around a volcanic island shelf: Pliocene Rhodolith beds from Malbusca, Santa Maria Island (Azores, NE Atlantic). *Facies*, *62*(3), 1–31.

Rebelo, A.C., Meireles, R.P., Barbin, V., Neto, A.I., Melo, C. Ávila, S.P. (2016b) Diagenetic history of lower Pliocene rhodoliths of the Azores archipelago (NE Atlantic): application of cathodoluminescence techniques. *Micron*, 80, 112–121.Uchman, A., Johnson, M., Rebelo, A.C., Melo, C., Cordeiro, R., Ramalho, R.S., Ávila, S.P. (2016) Vertically-oriented trace fossil *Macaronichnus segregatis* from Neogene of Santa Maria Island (Azores; NE Atlantic) records vertical fluctuations of the coastal groundwater mixing zone on a small oceanic island. *Geobios*, 49, 229–241.

Uchman, A., Johnson, M., Rebelo, A. C., Melo, C., Cordeiro, R., Ramalho, R. S. & Ávila, S.P.. (2016) Vertically-oriented trace fossil *Macaronichnus segregatis* from Neogene of Santa Maria Island (Azores; NE Atlantic) records vertical fluctuations of the coastal groundwater mixing zone on a small oceanic island. *Geobios*, 49, 229–241.

Uchman, A., Quintino, V., Rodrigues, A.M., Johnson, M.E., Melo, C., Cordeiro, R., Ramalho, R.S., Ávila, S.P. (2017) The trace fossil *Diopatrichnus santamariaensis* isp. nov. – a shell armoured tube from Pliocene sediments of Santa Maria Island, Azores (NE Atlantic Ocean). *Geobios*, 50, 459–469.

Uchman, A., Torres, P., Johnson, M. E., Berning, B., Ramalho, R. S., Rebelo, A. C., Melo, C., Baptista, L., Madeira, P., Cordeiro, R. & Ávila, S.P. (2018) Feeding traces of recent ray fish and occurrences of the trace fossil *Piscichnus waitemata* from the pliocene of Santa Maria Island, Azores (Northeast Atlantic). *Palaios*, 33(8), 361–375.

Uthicke, S., Byrne, M. & Conand, C. (2010) Genetic barcoding of commercial Bêche-de-mer species (Echinodermata: Holothuroidea). *Molecular ecology resources*, 10(4), 634–646.

Young, C.M., Sewell, M.A., Tyler, P.A., Metaxas, A. (1997) Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiversity and Conservation*, 6, 1507–1522.

Annex I

Echinocyamus pusillus (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic)

Madeira, P., Kroh, A., Melo, C., Cordeiro, R. & Ávila, S.P. (2017) *Echinocyamus pusillus* (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic). *In*: Ávila, S.P. & Melo, C. (Eds.). RCANS *2017 - 6th Regional Committee on Neogene Atlantic Stratigraphy, Ponta Delgada, São Miguel Island, Azores, July, 10-13, University of the Azores (Abstract Book)*, p. 44.

RCANS 2017 - 6th Regional Committee on Neogene Atlantic
Stratigraphy, Ponta Delgada, São Miguel Island, Azores
July, 10-13, University of the Azores

Echinocyamus pusillus (Echinodermata; Echinoidea): a new record from the Pleistocene of Santa Maria Island (Azores, NE Atlantic)

Santa Maria, in the easternmost of the Azores, is the only island of the archipelago with fossiliferous sediments exposed on the surface. Pleistocene (MIS5e) deposits investigated so far all derive from ancient rocky shores, preserving only a small part of the biodiversity that existed in the past. A recent review of the fossil echinoid fauna of this island, revealed three species from the Pleistocene fossil record (MIS5e): *Arbacia lixula*, *Sphaerechinus granularis* and *Paracentrotus lividus*. All species are regarded as the most conspicuous elements of the extant rocky shores of the Azores. We present a fourth new species, *Echinocyamus pusillus* (O.F. Müller, 1776), an echinoid known to occur in the extant waters of the Mediterranean Sea and Northeast Atlantic, from boreal waters of Scandinavia and Iceland to tropical waters of Cabo Verde and Sierra Leone. This species is a common element in today's Azorean coasts. However, unlike the previous identified Pleistocene species, this soft bottom inhabitant is also known from the Pliocene fossil record of Santa Maria. The presence of *E. pusillus* among hard substrata inhabitants was not entirely surprising given the resilience of *Echinocyamus* tests to survive transportation and the fact that modern *E. pusillus* occurs in a wide range of habitats, including small patches of sand or gravel in hard-bottom settings. In the Azores, extant *Echinocyamus* specimens are frequently found among the debris in beaches and occasional are also found trapped among algae mats. Additionally, the rather broad geographical distribution in the extant waters of the Northeast Atlantic may be the key to understand the constant presence of this species throughout the history of the archipelago, from Pliocene to present times. In sum, this new record further reinforces the close faunal affinities with the NE Atlantic continental shores, found both in the fossil and extant Azorean coasts.

Key words: Pleistocene; MIS 5e; Echinoidea; *Echinocyamus pusillus*; Azores; NE Atlantic.

Annex II

Extant echinoderm fauna of the Azores – Species list

- Phylum Echinodermata Bruguière, 1791
- Class Crinoidea Miller, 1821
    - Order Comatulida Clark, 1908
        - Family Antedonidae Norman, 1865
            - Genus *Antedon* de Fréminville, 1811
                - *Antedon bifida moroccana* (Clark, 1914)
        - Family Pentametrocrinidae Clark, 1908
            - Genus *Pentametrocrinus* Clark, 1908
                - *Pentametrocrinus atlanticus* (Perrier, 1883a)
        - Family Bourgueticrinidae Loriol, 1882
            - Genus *Democrinus* Perrier, 1883b
                - *Democrinus parfaiti* Perrier, 1883b
        - Family Bathycrinidae Bather, 1899
            - Genus *Bathycrinus* Thomson, 1872a
                - *Bathycrinus gracilis* Thomson, 1872a
    - Order Cyrtocrinida Sieverts-Doreck, *in* Moore *et al*., 1952)
        - Family Holopodidae Zittel, 1879
            - Genus *Cyathidium* Steenstrup, 1847
                - *Cyathidium foresti* Cherbonnier & Guille, 1972
    - Order Hyocrinida Rasmussen, 1978
        - Family Hyocrinidae Carpenter, 1884
            - Genus *Anachalypsicrinus* Clark, 1973
                - *Anachalypsicrinus nefertiti* Clark, 1973
- Class Ophiuroidea Gray, 1840
    - Order Amphilepidida O'Hara *et al*. 2017
        - Family Amphiuridae Ljungman, 1867
            - Genus Amphipholis Ljungman, 1866
                - *Amphipholis squamata* (Delle Chiaje, 1828)
            - Genus Amphiura Forbes, 1843
                - *Amphiura otteri* Ljungman, 1872
                - *Amphiura richardi* Koehler, 1896b
                - *Amphiura sarsi* Ljungman, 1872
                - *Amphiura* (*Amphiura*) *grandisquama* Lyman, 1869
        - Family Ophiactidae Matsumoto, 1915
            - Genus *Ophiactis* Lütken, 1856
                - *Ophiactis abyssicola* (Sars, 1861)
                - *Ophiactis canotia* Lyman, 1879
                - *Ophiactis tyleri* Stöhr & Segonzac, 2005
                - *Ophiactis virens* (Sars, 1859)
        - Family Ophiolepididae Ljungman, 1867
            - Genus *Ophiotypa* Koehler, 1897a
                - *Ophiotypa simplex* Koehler, 1897a
        - Family Ophionereididae Ljungman, 1867
            - Genus *Ophiochiton* Lyman, 1878
                - *Ophiochiton ternispinus* Lyman, 1883
        - Family Ophiothamnidae O'Hara *et al*. 2018
            - Genus *Histampica* Clark, 1970
                - *Histampica duplicata* (Lyman, 1875)
        - Family Ophiotrichidae Ljungman, 1867
            - Genus *Ophiothrix* Müller & Troschel, 1840a
                - *Ophiothrix fragilis* (Abildgaard, *in* Müller, 1789)
                - *Ophiothrix luetkeni* Thomson, 1873
    - Order Euryalida Lamarck, 1816
        - Family Asteronychidae Verrill, 1899
            - Genus *Astrodia* Verrill, 1899
                - *Astrodia tenuispina* (Verrill, 1884)

- Family Euryalidae Gray, 1840
    - Genus Asteroschema Oerstedt & Lütken, 1856
    - *Asteroschema inornatum* Koehler, 1906a
- Order Ophiacanthida O'Hara *et al*., 2017
  - Family Ophiacanthidae Ljungman, 1867
    - Genus *Ophiacantha* Müller & Troschel, 1842
    - *Ophiacantha abyssicola* Sars, 1872
    - *Ophiacantha aculeata* Verrill, 1885a
    - *Ophiacantha aristata* Koehler, 1895c
    - *Ophiacantha crassidens* Verrill, 1885a
    - *Ophiacantha lineata* Koehler, 1896b
    - *Ophiacantha mesembria* Clark, 1915
    - *Ophiacantha notata* Koehler, 1906a
    - *Ophiacantha setosa* (Bruzelius, 1805)
    - *Ophiacantha simulans* Koehler, 1895c
    - *Ophiacantha smitti* Ljungman, 1872
    - *Ophiacantha veterna* Koehler, 1907a
    - Genus *Ophiochondrus* Lyman, 1869
    - *Ophiochondrus armatus* (Koehler, 1907a)
    - Genus *Ophiomitrella* Verrill, 1899
    - *Ophiomitrella cordifera* Koehler, 1896b
  - Family Ophiomyxidae Ljungman, 1867
    - Genus *Ophioconis* Lütken, 1869
    - *Ophioconis forbesi* (Heller, 1863)
    - Genus *Ophiomyxa* Müller & Troschel, 1840
    - *Ophiomyxa serpentaria* Lyman, 1883
  - Family Ophiotomidae Paterson, 1985
    - Genus *Ophiocomina* Koehler, 1922
    - *Ophiocomina nigra* (Abildgaard, *in* Müller, 1789)
    - Genus *Ophiotoma* Verrill, 1899
    - *Ophiotoma alberti* (Koehler, 1896b)
    - Genus Ophiotreta Verrill, 1899
    - *Ophiotreta valenciennesi* (Lyman, 1879)
- Order Ophioleucida O'Hara *et al*. 2017
  - Family Ophiernidae O'Hara *et al*. 2017
    - Genus *Ophiernus* Lyman, 1878
    - *Ophiernus vallincola* Lyman, 1878
- Order Ophioscolecida O'Hara *et al*., 2017
  - Family Ophiohelidae Perrier, 1893
    - Genus Ophiomyces Lyman, 1869
    - *Ophiomyces frutectosus* Lyman, 1869
  - Family Ophioscolecidae Lütken, 1869
    - Genus *Ophiophrura* Clark, 1911b
    - *Ophiophrura tripapillata* (Stöhr & Segonzac, 2005)
- Order Ophiurida Müller & Troschel, 1840a *sensu* O'Hara *et al*., 2017
  - Family Astrophiuridae Sladen, 1879
    - Genus *Ophiophycis* Koehler, 1901
    - *Ophiophycis mirabilis* Koehler, 1901
  - Family Ophiopyrgidae Perrier, 1893
    - Genus *Amphiophiura* Matsumoto, 1915
    - *Amphiophiura convexa* (Lyman, 1878)
    - Genus Ophiopleura Duncan, 1878
    - *Ophiopleura inermis* (Lyman, 1878)
    - Genus *Ophioplinthus* Lyman, 1878
    - *Ophioplinthus inornata* (Lyman, 1878)

Ophioplinthus pseudotessellata Martynov & Litvinova, 2008
Ophioplinthus tessellata (Verrill, 1894)
Family Ophiosphalmidae O'Hara *et al*. 2018
Genus *Ophiomusium* Lyman, 1869
Ophiomusium lymani Thomson, 1873
Genus *Ophiosphalma* Clark, 1941
Ophiosphalma armigerum (Lyman, 1878)
Family Ophiuridae Müller & Troschel, 1840a
Genus *Ophiocten* Lütken, 1855
Ophiocten centobi Paterson *et al*., 1982
Ophiocten hastatum Lyman, 1878
Genus *Ophioctenella* Tyler *et al*., 1995
Ophioctenella acies Tyler *et al*., 1995
Genus *Ophiura* Lamarck, 1801
Ophiura albida Forbes, 1839
Ophiura imprudens (Koehler, 1906a)
Ophiura ljungmani (Lyman, 1878)
Ophiura saurura (Verrill, 1894)
Ophiura (*Dictenophiura*) *carnea carnea* Lütken, 1858
Ophiura (*Ophiura*) *mundata* (Koehler, 1906a)
Ophiura (*Ophiuroglypha*) *concreta* (Koehler, 1901)
Class Asteroidea de Blainville, 1830
Order Velatida Perrier, 1884
Family Myxasteridae Perrier, 1885b
Genus *Pythonaster* Sladen, *in* Thomson & Murray, 1885
Pythonaster atlantidis Clark, 1948
Family Pterasteridae Perrier, 1875
Genus *Calyptraster* Sladen, 1882
Calyptraster personatus (Perrier, 1885c)
Genus *Hymenaster* Thomson, 1873
Hymenaster anomalus Sladen, 1882
Hymenaster giboryi Perrier, 1894
Hymenaster pellucidus Thomson, 1873
Hymenaster roseus Koehler, 1907a
Hymenaster tenuispinus Sibuet, 1976
Genus Pteraster Müller & Troschel, 1842
Pteraster personatus Sladen, 1891
Superorder Forcipulatacea Blake, 1987
Order Brisingida Fisher, 1928
Family Brisingidae Sars, 1875
Genus *Hymenodiscus* Perrier, 1884
Hymenodiscus coronata (Sars, 1872)
Family Freyellidae Downey, 1986
Genus *Freyastera* Downey, 1986
Freyastera sexradiata (Perrier, 1885c)
Genus *Freyella* Perrier, 1885d
Freyella elegans (Verrill, 1884)
Order Forcipulatida Perrier, 1884
Family Asteriidae Gray, 1840
Genus *Coscinasterias* Verrill, 1870
Coscinasterias tenuispina (Lamarck, 1816)
Genus Marthasterias Jullien, 1878
Marthasterias glacialis (Linnaeus, 1758)
Family Pedicellasteridae Perrier, 1884

- Genus *Hydrasterias* Sladen, 1889
  - *Hydrasterias sexradiata* (Perrier, *in* Milne-Edwards, 1882)
- Family Stichasteridae Perrier, 1885b
  - Genus *Neomorphaster* Sladen, 1889
    - *Neomorphaster margaritaceus* (Perrier, *in* Milne-Edwards, 1882)
- Family Zoroasteridae Sladen, 1889
  - Genus *Zoroaster* Thomson, 1873
    - *Zoroaster fulgens* Thomson, 1873

Superorder Valvatacea Blake, 1987

Order Notomyotida Ludwig, 1910

- Family Benthopectinidae Verrill, 1899
  - Genus *Cheiraster* Studer, 1883
    - *Cheiraster* (Cheiraster) sepitus (Verrill, 1885a)
  - Genus Pectinaster Perrier, 1885c
    - *Pectinaster filholi* Perrier, 1885c

Order Paxillosida Perrier, 1884

- Family Astropectinidae Gray, 1840
  - Genus Astropecten Gray, 1840
    - *Astropecten hermatophilus* Sladen, 1883
  - Genus *Dytaster* Sladen, 1889
    - *Dytaster grandis grandis* (Verrill, 1884)
    - *Dytaster insignis* (Perrier, 1884)
    - *Dytaster intermedius* Perrier, 1891
    - *Dytaster mollis* (Perrier, 1885c)
  - Genus *Persephonaster* Wood-Mason & Alcock, 1891
    - *Persephonaster patagiatus* (Sladen, 1889)
    - *Persephonaster sphenoplax* (Bell, 1892)
  - Genus *Plutonaster* Sladen, 1889
    - *Plutonaster agassizi notatus* Sladen, 1889
- Family Luidiidae Sladen, 1889
  - Genus *Luidia* Forbes, 1839
    - *Luidia ciliaris* (Philippi, 1837)
    - *Luidia sarsii sarsii* Düben & Koren, *in* Düben, 1845
- Family Porcellanasteridae Sladen, 1883
  - Genus Hyphalaster Sladen, 1883
    - *Hyphalaster inermis* Sladen, 1883
  - Genus *Porcellanaster* Wyville Thomson, 1877
    - *Porcellanaster ceruleus* Thomson, 1877
  - Genus *Styracaster* Sladen, 1883
    - *Styracaster armatus* Sladen, 1883
    - *Styracaster elongatus* Koehler, 1907a
- Family Pseudarchasteridae Sladen, 1889
  - Genus *Paragonaster* Sladen, *in* Thomson & Murray, 1885
    - *Paragonaster subtilis* (Perrier, 1881)
  - Genus *Pseudarchaster* Sladen, 1889
    - *Pseudarchaster gracilis gracilis* (Sladen, 1889)
    - *Pseudarchaster parelii* (Düben & Koren, 1846)

Superorder Valvatacea Blake, 1987

Order Valvatida Perrier, 1884

- Family Asterinidae Gray, 1840
  - Genus *Asterina* Nardo, 1834
    - *Asterina gibbosa* (Pennant, 1777)
- Family Chaetasteridae Sladen, 1889
  - Genus *Chaetaster* Müller & Troschel, 1840
    - *Chaetaster longipes* (Bruzelius, 1805)

Family Goniasteridae Forbes, 1841
Genus *Ceramaster* Verrill, 1899
Ceramaster granularis granularis (Retzius, 1783)
Ceramaster grenadensis grenadensis (Perrier, 1881)
Genus *Plinthaster* Verrill, 1899
Plinthaster dentatus (Perrier, 1884)
Genus *Sphaeriodiscus* Fisher, 1910
Sphaeriodiscus bourgeti (Perrier, 1885c)
Family Odontasteridae Verrill, 1899
Genus *Hoplaster* Perrier, *in* Milne-Edwards, 1882
Hoplaster spinosus Perrier, *in* Milne-Edwards, 1882
Family Ophidiasteridae Verrill, 1870
Genus *Hacelia* Gray, 1840
Hacelia attenuata Gray, 1840
Genus *Ophidiaster* Agassiz, 1836
Ophidiaster ophidianus (Lamarck, 1816)
Ophidiaster reyssi Sibuet, 1977
Subphylum Echinozoa Haeckel, 1896
Class Echinoidea Leske, 1778
Subclass Cidaroidea Smith, 1984
Order Cidaroida Claus, 1880
Family Cidaridae Gray, 1825
Genus *Cidaris* Leske, 1778
Cidaris cidaris (Linnaeus, 1758)
Subclass Euechinoidea Bronn, 1860
Infraclass Acroechinoidea Smith, 1981
Order Diadematoida Duncan, 1889
Family Diadematidae Gray, 1855a
Genus *Centrostephanus* Peters, 1855
Centrostephanus longispinus (Philippi, 1845)
Order Pedinoida Mortensen, 1939
Family Pedinidae Pomel, 1883
Genus *Caenopedina* Agassiz, 1869
Caenopedina cubensis Agassiz, 1869
Infraclass Carinacea Kroh & Smith, 2010
Superorder Calycina Gregory, 1900
Order Salenioida Delage & Hérouard, 1903
Family Saleniidae Agassiz, 1838
Genus *Salenocidaris* Agassiz, 1869
Salenocidaris hastigera (Agassiz, 1879)
Salenocidaris varispina Agassiz, 1869
Superorder Echinacea Claus, 1876
Order Arbacioida Gregory, 1900
Family Arbaciidae Gray, 1855
Genus *Arbacia* Gray, 1835
Arbacia lixula (Linnaeus, 1758)
Order Camarodonta Jackson, 1912
Infraorder Echinidea Kroh & Smith, 2010
Family Echinidae Gray, 1825
Genus *Echinus* Linnaeus, 1758
Echinus melo Lamarck, 1816
Genus Gracilechinus Fell & Pawson, *in* Moore, 1966
Gracilechinus affinis (Mortensen, 1903)
Gracilechinus alexandri (Danielssen & Koren, 1883)
Family Parechinidae Mortensen, 1903
Genus Paracentrotus Mortensen, 1903
Paracentrotus lividus (Lamarck, 1816)

Superfamily Odontophora Kroh & Smith, 2010
Family Toxopneustidae Troschel, 1872
Genus *Sphaerechinus* Desor, 1856
Sphaerechinus granularis (Lamarck, 1816)
Infraorder Temnopleuridea Kroh & Smith, 2010
Family Trigonocidaridae Mortensen, 1903
Genus *Trigonocidaris* Agassiz, 1869
Trigonocidaris albida Agassiz, 1869
Genus *Genocidaris* Agassiz, 1869
Genocidaris maculata Agassiz, 1869
Order Echinothurioida Claus, 1880
Family Echinothuriidae Thomson, 1872b
Genus *Araeosoma* Mortensen, 1903b
Araeosoma fenestratum (Thomson, 1872b)
Genus *Calveriosoma* Mortensen, 1934
Calveriosoma hystrix (Thomson, 1872b)
Genus *Hygrosoma* Mortensen, 1903b
Hygrosoma petersii (Agassiz, 1880)
Genus *Sperosoma* Koehler, 1897b
Sperosoma grimaldii Koehler, 1897b
Genus *Tromikosoma* Mortensen, 1903
Tromikosoma koehleri Mortensen, 1903
Family Phormosomatidae Mortensen, 1934
Genus *Phormosoma* Thomson, 1872b
Phormosoma placenta placenta Thomson, 1872b
Infraclass Irregularia Latreille, 1825
Superorder Atelostomata von Zittel, 1879
Order Spatangoida Agassiz, 1840
Suborder Brissidina Stockley *et al*., 2005
Family Brissidae Gray, 1855
Genus *Brissopsis* Agassiz 1840
Brissopsis lyrifera lyrifera (Forbes, 1841)
Genus *Brissus* Gray, 1825
Brissus unicolor (Leske, 1778)
Family Palaeotropidae Lambert, 1896
Genus *Palaeotropus* Lovén, 1874
Palaeotropus josephinae Lovén, 1871
Superfamily Spatangidea Fischer, 1966
Family Loveniidae Lambert, 1905
Genus *Araeolampas* Serafy, 1974
Araeolampas atlantica Serafy, 1974
Subfamily Echinocardiinae Cooke, 1942
Genus *Echinocardium* Gray, 1825
Echinocardium cordatum (Pennant, 1777)
Echinocardium flavescens (Müller, 1776)
Suborder Paleopneustina Markov & Solovjev, 2001
Family Paleopneustidae Agassiz, 1904
Genus *Peripatagus* Koehler, 1895b
Peripatagus cinctus Koehler, 1895b
Family Schizasteridae Lambert, 1905
Genus Aceste Thomson, 1877
Aceste bellidifera Thomson, 1877
Superorder Neognathostomata Smith, 1981
Order Clypeasteroida Agassiz, 1872
Suborder Scutellina Haeckel, 1896
Infraorder Laganiformes Desor, 1847
Family Echinocyamidae Lambert & Thiéry, 1914
Genus *Echinocyamus* van Phelsum, 1774

- *Echinocyamus grandiporus* Mortensen, 1907
- *Echinocyamus pusillus* (Müller, 1776)
- *Echinocyamus scaber macrostomus* Mortensen, 1907

Class Holothuroidea de Blainville, 1834
- Order Apodida Brandt, 1835
  - Family Chiridotidae Östergren, 1898
    - Genus *Chiridota* Eschscholtz, 1829
      - *Chiridota abyssicola* Marenzeller, 1892
  - Family Synaptidae Burmeister, 1837
    - Genus *Leptosynapta* Verrill, 1867
      - *Leptosynapta inhaerens* (Müller, 1776)
- Order Dendrochirotida Grube, 1840
  - Family Cucumariidae Ludwig, 1894
    - Genus *Abyssocucumis* Heding, 1942
      - *Abyssocucumis abyssorum* (Théel, 1886a)
- Order Elasipodida Théel, 1882
  - Family Deimatidae Théel, 1882
    - Genus *Deima* Théel, 1879
      - *Deima validum validum* Théel, 1879
    - Genus *Oneirophanta* Théel, 1879
      - *Oneirophanta mutabilis mutabilis* Théel, 1879
  - Family Elpidiidae Théel, 1882
    - Genus *Amperima* Pawson, 1965
      - *Amperima furcata* (Hérouard, 1899)
    - Genus *Ellipinion* Hérouard, 1923
      - *Ellipinion delagei* (Hérouard, 1896)
    - Genus *Peniagone* Théel, 1882
      - *Peniagone azorica* Marenzeller von, 1892
      - *Peniagone diaphana* (Théel, 1882)
      - *Peniagone longipapillata* Gebruk, 2008
      - *Peniagone marecoi* Gebruk, 2008
    - Genus *Penilpidia* Gebruk, 1988
      - *Penilpidia midatlantica* Gebruk, 2008
  - Family Laetmogonidae Ekman, 1926
    - Genus *Benthogone* Koehler, 1895c
      - *Benthogone rosea* Koehler, 1896c
    - Genus *Laetmogone* Théel, 1879
      - *Laetmogone violacea* Théel, 1879
  - Family Psychropotidae Théel, 1882
    - Genus *Benthodytes* Théel, 1882
      - *Benthodytes gosarsi* Gebruk, 2008
      - *Benthodytes janthina* Marenzeller, 1892
      - *Benthodytes lingua* Perrier1896
      - *Benthodytes sanguinolenta* Théel, 1882
      - *Benthodytes typica* Théel, 1882
      - *Benthodytes valdiviae* Hansen, 1975
    - Genus *Psychropotes* Théel, 1882
      - *Psychropotes depressa* (Théel, 1882)
      - *Psychropotes longicauda* Théel, 1882
      - *Psychropotes semperiana* Théel, 1882
- Order Holothuriida Miller *et al.*, 2017
  - Family Holothuriidae Burmeister, 1837
    - Genus *Holothuria* Linnaeus, 1767
      - *Holothuria* (*Holothuria*) *mammata* Grube, 1840

Holothuria (*Panningothuria*) *forskali* Delle Chiaje, 1823
Holothuria (*Platyperona*) *sanctori* Delle Chiaje, 1823
Holothuria (*Vaneyothuria*) *lentiginosa lentiginosa* Marenzeller, 1892
Family Mesothuriidae Smirnov, 2012
Genus *Mesothuria* Ludwig, 1894
Mesothuria maroccana Perrier1898
Mesothuria milleri Gebruk & Solís-Marín, *in* Gebruk *et al*., 2012
Mesothuria murrayi Théel, 1886a
Mesothuria rugosa Hérouard, 1912
Genus *Zygothuria* Perrier, 1898
Zygothuria lactea (Théel, 1886a)
Order Persiculida Miller *et al*., 2017
Genus *Benthothuria* Perrier, 1898
Benthothuria funebris Perrier, 1898
Family Pseudostichopodidae Miller *et al*., 2017
Genus *Pseudostichopus* Théel, 1882
Pseudostichopus peripatus (Sluiter, 1901)
Order Synallactida Miller *et al*., 2017
Family Stichopodidae Haeckel, 1896
Genus *Parastichopus* Clark, 1922
Parastichopus regalis (Cuvier, 1817)
Family Synallactidae Ludwig, 1894
Genus *Paelopatides* Théel, 1886
Paelopatides atlantica Hérouard, 1902