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# Deep-sea ophiuroids (Echinodermata: Ophiuroidea: Ophiurida) from the Gulf of Cadiz (NE Atlantic)

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## Abstract

The Ophiuroidea collected from mud volcanoes and adjacent bathyal environments from the Gulf of Cadiz are reviewed. Thirteen species from six families—Ophiacanthidae, Ophiactidae, Amphiuridae, Amphilepididae, Ophiuridae and Ophiolepididae—were identified. A direct relationship to the chemosynthetic assemblages has not been established as the ophiuroids found in the mud volcanoes do not appear to have novel morphological adaptations and also occur in non-reducing environments. The ophiuroid fauna from the Gulf of Cadiz differs from other cold seep regions not only by the high species richness but also because members of Amphiuridae are dominant both in number of species and abundance. One species previously unknown, *Ophiopristis gadensis* **sp. nov.**, (Ophiacanthidae) was collected from a dead cold-water coral thicket at the flank of a mud volcano and differs from its congeners in the type of disk spines which are more rugose and not smooth as in most of the other species, the presence of the thickened integument in larger specimens and the distinct separation between the oral papillae and the second oral tentacle scales.

**Key words:** mud volcanoes, reducing environments, macrofauna, biodiversity

## Introduction

The first deep-water ophiuroid was discovered more than 150 years ago in the North Atlantic at a depth of 1460 m during the sounding of Baffin Bay (Müller & Troschel 1842 in Menzies *et al*. 1973). During late 19th and early 20th centuries, ophiuroid records have significantly increased due to the collection of many specimens by several deep-water expeditions (Martynov & Litvinova 2008). However, the most important studies on ophiuroids of the Atlantic have been carried out during the past 40 years (e.g. Cherbonnier & Sibuet 1972; Gage *et al.* 1983; Paterson 1985; Bartsch 1987, 1991; Smith et al. 1995; Stöhr & Segonzac 2005) and a taxonomic and biogeographical review has been carried out recently by Martynov and Litvinova (2008). These studies have expanded the global knowledge on this group but, despite these efforts, the deep-sea ophiuroid fauna remains poorly known as many species are only reported from a single or a few individuals. Because morphological identification of ophiuroids is based almost exclusively on skeletal characters, which change greatly in number and shape during growth (Stöhr 2004, 2005), this lack of specimens is of great importance.

Ophiuroids, which have the highest abundance of all deep-sea megafauna taxa in non-reducing environments (Gage & Tyler 1991), have also been reported from several cold seeps and vents (Hecker 1985; Tyler *et al*. 1995; Sibuet & Olu 1998; Gebruk *et al*. 2003; Sahling *et al.* 2003; Van Dover *et al.* 2003; Stöhr & Segonzac 2006; Levin & Mendoza 2007). The unidentified status of several ophiuroid records suggests that the overall diversity of ophiuroids in these reducing environments remains underestimated. Seven species were reported from Blake Ridge, Gulf of Mexico and Barbados cold seeps in the Western Atlantic (Stöhr & Segonzac 2005), two from the Haakon Mosby mud volcano in the Eastern Atlantic (Gebruk *et al*. 2003) and two from the North Pacific Aleutian margin (Levin & Mendoza 2007). Presently, eight species have been reported from hydrothermal communities in the East Pacific and Mid-Atlantic Ridge (MAR) (Stöhr & Segonzac 2005, 2006). From these, only one, *Ophienigma spinil-*

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*imbatum* Stöhr & Segonzac, 2005, is considered endemic to Western Atlantic cold seeps, one, *Ophioctenella acies*, Tyler *et al*., 1995, is considered endemic to reduced environments (present at Western Atlantic cold seeps and MAR vents), and two, *Spinophiura jolliveti* Stöhr & Segonzac, 2006, and *Ophiolamina eprae* Stöhr & Segonzac, 2006, are endemic to East Pacific vents (Stöhr & Segonzac, 2006). Although some other ophiuroid species have been recorded from seeps and vents, their low abundance and rare occurrence suggest that they are not endemic to reducing habitats but possibly opportunistic species (that may reach relatively high densities) or accidental species (usually occurring at low densities) known from other habitats. For most of the ophiuroid species occurring in reducing habitats a direct relationship to the chemosynthetic assemblages has not been established and therefore they may have a broader distribution.

Information on the occurrence and distribution of ophiuroids from the Atlantic continental margins of Morocco and Iberian Peninsula was until now scarce. Marques (1980) and Bartsch (1987, 1991) recorded the distribution of *Amphipholis squamata* (Delle Chiaje, 1828), *Ophiactis lymani* Ljungman, 1872, *Ophiothrix fragilis* (Abildgaard, 1789) and *Ophiothrix indigna* Koehler, 1906 in the Southern Portuguese margin covering a bathymetric range from 500 to 820 m. In this study we report on the Ophiuroidea recovered from mud volcanoes and adjacent environments, such as carbonate chimneys and cold-water scleractinian corals, from a depth range of 200 to 4000 m in the Gulf of Cadiz. The aim of the paper is to extend the knowledge on the biodiversity and distribution of the ophiuroids in the Gulf of Cadiz, with particular emphasis on reducing habitats.

## Material and methods

**Study area.** The present work is based on samples from mud volcanoes in the Gulf of Cadiz located in the NE Atlantic, West of the Strait of Gibraltar (Fig. 1). Mud volcanoes (MV) were firstly reported on the Moroccan margin by Gardner (2001) and the first evidence of seep-related fauna in the Gulf of Cadiz was briefly mentioned by Pinheiro *et al.* (2003) from samples collected in the Moroccan, Spanish and deep Portuguese margins. A brief overview of the hydrological, geological and biogeochemical settings of the Gulf of Cadiz is given by Rodrigues *et al*. (2008). The results reported herein refer to samples collected from exposed carbonate chimney fields in submarine channels and diapiric ridges associated with erosion effects of the Mediterranean Outflow Water, and from three main areas of mud volcanoes in the Gulf of Cadiz: the shallow El Arraiche Moroccan field, the Western Moroccan field and the deep-water field.

The El Arraiche field encompasses Renard Ridge (including Pen Duick Escarpment), Vernadsky Ridge and several mud volcanoes located at depths from 200 to approximately 700 m depth. Dead cold-water scleractinian coral reefs, carbonate crusts and exposed carbonate chimneys characterise the Renard and Vernadsky Ridges. Carbonate crusts, rock blocks and clasts are often found in the craters of the shallow mud volcanoes where mild seepage activity has been recorded (Van Rensbergen *et al*. 2005). The faunal assemblages are characterised by high species richness and abundance of background fauna (mostly peracaridean crustaceans and polychaetes) and the most common chemosynthetic species are solemyid bivalves (*Petrasma* sp.) and Siboglinid polychaetes (*Siboglinum* spp.). Mercator, one of the shallowest mud volcanoes, differs significantly from the other mud volcanoes by the high chloride enrichment of its pore water. The top of the structure shows patches of disturbed sediments from which gas venting is occasionally observed (M.R. Cunha, pers. observation). Solitary corals (*Caryophyllia* sp.), accompanied by Cidaridae echinoids and Onuphidae polychaetes (*Hyalinoecia tubicola* (O. F. Müller, 1776)) are abundant at the central area of the crater.

The western Moroccan field comprises several mud volcanoes at depths between 900 and 1200 m where the occurrence of extensive *Neptunea* and *Bathymodiolus* graveyards and carbonate formations suggest that this was a very active seepage area in the past. Solemyid bivalves (*Acharax* sp.) and siboglinid polychaetes (*Siboglinum* spp.) are the most common chemosynthetic species. The Darwin mud volcano differs from the others in this area because its crater is completely covered by large carbonate slabs and crusts; the fissures among slabs and depressions with scattered crust are filled with abundant shell ash and occasionally small clumps of living *Bathymodiolus mauritanicus* Cosel, 2002 (Génio *et al*. 2008).

Meknès is the southernmost Moroccan mud volcano rising isolated among an extensive field of small coral mounds. The crater is formed by stiff, sometimes heavily disturbed, green mud breccia with scattered clasts and a striking large number of empty shells of the gastropod *Neptunea contraria* (M.R. Cunha, pers. observation). Living megafauna is rarely sighted and chemosynthetic fauna consists of *Acharax* sp and *Siboglinum* spp.

The deep-water field (1300–4000 m), mostly within the Portuguese margin, includes several mud volcanoes that are aligned along major crustal strike–slip faults associated with the African-Eurasian plate boundary (Duarte *et al*. 2005). Gas hydrates were recovered from these mud volcanoes and the methane concentrations were the highest from the Gulf of Cadiz (Vanreusel *et al*. 2009). Chemosynthetic fauna was highly diverse and include siboglinid species of the genus *Siboglinum*, *Polybrachia*, *Lamellisabella*, *Spirobrachia* and *Bobmarleyia* (Hilário & Cunha 2008; Hilário *et al.* 2010), solemyid (*Acharax* sp), thyasirid (Rodrigues *et al.* 2008) and vesycomyid bivalves. These mud volcanoes appeared to show a high degree of endemism and low penetration of background fauna in the most active areas of the crater.

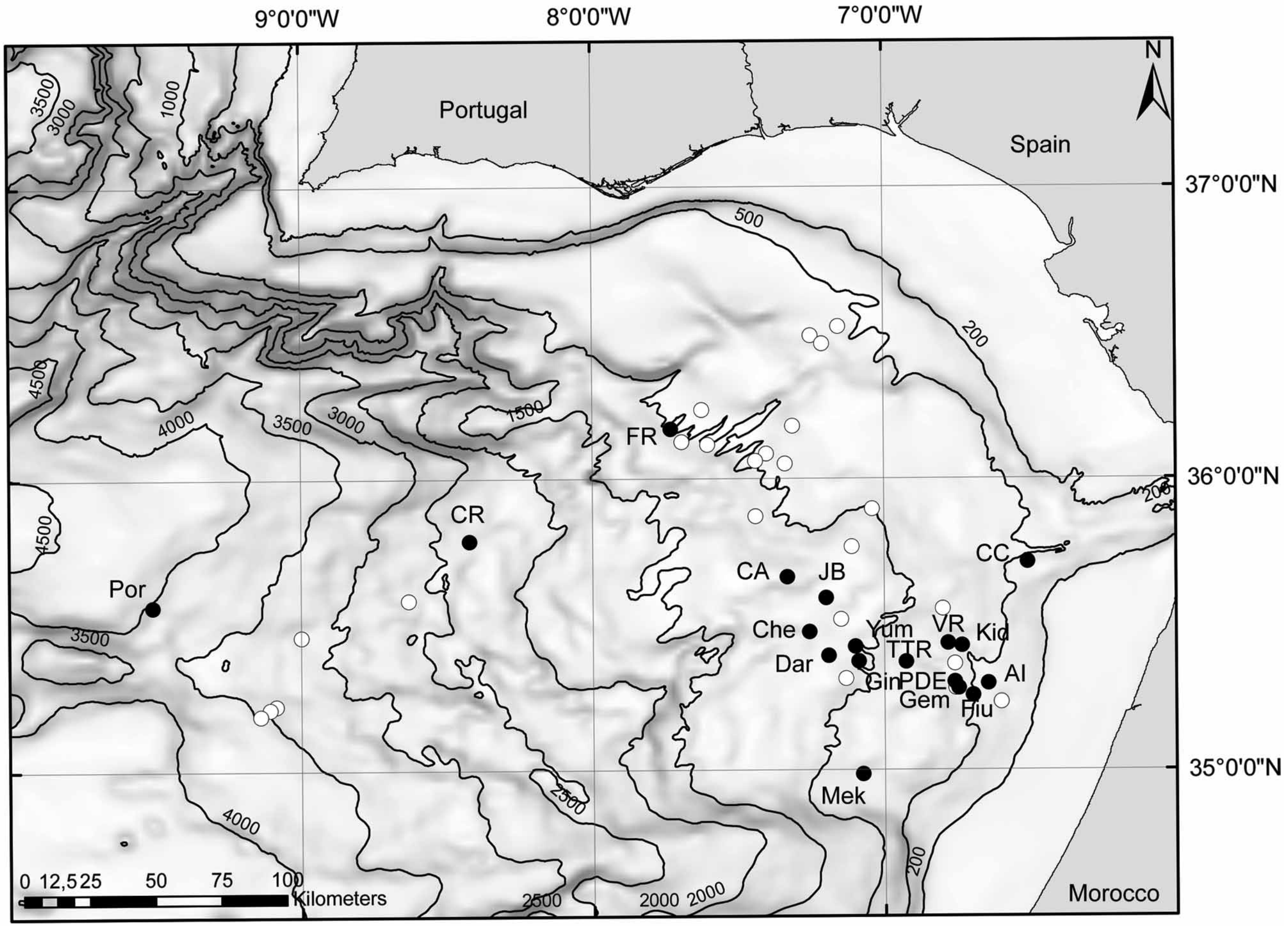


**FIGURE 1.** Map of the study area (Gulf of Cadiz) and location of sampling sites. Full circles: sampling sites with Ophiuroidea; Empty circles: other sites; AI: Al Idrisi MV; CA: Captain Arutyunov MV; CC: carbonate chimneys West of Gibraltar Strait; CR: Carlos Ribeiro MV; Che: Chechaouen MV; Dar: Darwin MV; Fiu: Fiúza MV, FR: Formosa Ridge; Gin: Ginsburg MV; JB: Jesus Baraza MV; Kid: Kidd MV; Mer: Mercator MV; Mek: Meknès MV; PDE: Pen Duick Escarpment; Por: Porto MV; TTR: TTR MV; VR: Vernadsky ridge; Yum: Yuma MV.

**Collection and preparation of specimens.** Macrofaunal samples were collected from mud volcanoes and adjacent habitats such as fields of carbonate chimneys and crusts and cold-water coral thickets (mostly dead) during several cruises carried out since 2000. Samples reported herein were taken from 19 sites during TTR11 to TTR16 cruises onboard the RV *Prof. Logachev* (IOC – MSU) and MSM01-03 cruise onboard the RV *Maria S. Merian* (IFM-GEOMAR) using mostly a TV-assisted grab or a USNEL box-corer. Occasionally faunal specimens were also recovered from Kasten-corer, multiple corer or lander samples that were carried out for different purposes. Whenever possible the specimens were sorted on board and preserved in 70 or 96% ethanol (the latter preserved for molecular analysis). Data on the stations where ophiuroids were collected are given in Table 1. Al Idrisi, Mercator, Fiuza, Kidd, and TTR mud volcanoes are included in the El Arraiche field, Meknès, Yuma, Ginsburg, Jesus Baraza, Darwin and Chechaouen in the Western Moroccan field and Captain Arutyunov, Carlos Ribeiro and Porto in the deep-water field.

**TABLE 1.** Station data for the Gulf of Cadiz samples yielding ophiuroids. Observations from TTR12 to TTR16 and MSM01-03 cruise reports (Kenyon *et al.* 2003, 2006; Pfannkuche 2006; Akhmetzhanov *et al.* 2007, 2008). D: Dredge; G: gravity core; Gr: TV-assisted grab; UB: USNEL box core; MC: Multi core; K: Kasten core; BL: BIGO lander; FL: FLUFO lander.

| Structure | Cruise | Station | Gear | Date (dd.mm.yy) | Latitude (N) | Longitude (W) | Depth (m) | Taxa | Observations |
|---|---|---|---|---|---|---|---|---|---|
| **Mud volcanoes** | | | | | | | | | |
| Al Idrisi | TTR12 | AT412 | D | 17.07.2002 | 35°14.193' | 06°36.609' | 230 | *O. balli; A. filiformis* | Crater; limestones |
| Mercator | TTR15 | AT568 | G | 25.07.2005 | 35°17,684' | 06°39.131' | 418 | *A. squamata* | Flank; mud breccia |
| | | AT569 | Gr | 25.07.2005 | 35°17.917' | 06°38.717' | 358 | *A. chiajei; A. filiformis; A. ingolfiana; O. carnea* | Crater; mud breccia, near seep |
| | | AT575 | UB | 26.07.2005 | 35°17.903' | 06°38.715' | 355 | *A. filiformis;A. squamata; A. ingolfiana* | Crater; mud breccia; near seep |
| | | AT576 | UB | 26.07.2005 | 35°17.657' | 06°39.129' | 428 | Amphiuridae und.; *Amphiura* und; *A. chiajei; A. filiformis; A. squamata; A. hexabrachiatus; A. ingolfiana* | Flank; mud breccia |
| | | AT577 | UB | 26.07.2005 | 35°17.305' | 06°39.672' | 485 | Amphiuridae und.; *A. chiajei; A. squamata* | Off MV; hemipelagic sediments |
| | MSM01-03 | 237 | MC | 06.05.2006 | 35°17.914' | 06°38.687' | 353 | Amphiuridae und.; *A. filiformis; A. ingolfiana;* Ophiuroidea juv. | Crater; mud breccia, near seep |
| | | 241 | UB | 06.05.2006 | 35°17.918' | 06°38.717' | 353 | *Amphiura* und.; *A. filiformis; A. squamata;* Ophiuroidea und. | Crater; mud breccia, near seep; *Caryophyllia* facies |
| | | 242 | UB | 06.05.2006 | 35°17.870' | 06°38.810' | 350 | *A. filiformis; A. squamata* | Crater; mud breccia *Hyalonecia* facies |
| | | 267 | MC | 09.05.2006 | 35°17.875' | 06°38.789' | 350 | *A. filiformis;* Ophiuroidea juv. | Crater; mud breccia *Hyalonecia* facies |
| | | 287 | MC | 11.05.2006 | 35°17.890' | 06°39.059' | 379 | *A. filiformis; A. squamata;* Ophiuroidea juv. | Crater rim; mud breccia |
| Fiúza | TTR12 | AT403 | G | | | | | *A. ingolfiana* | Crater; mud breccia |
| | TTR14 | AT566 | Gr | 09.08.2004 | 35°15.510' | 06°41.702' | 414 | Amphiuridae und.; *A. filiformis; A. squamata; A. hexabrachiatus* | Crater; mud breccia, covered by marl |
| Kidd | TTR14 | AT528 | Gr | 03.08.2004 | 35°25.304' | 06°43.972' | 489 | *Amphiura* und.; *A. squamata* | Crater; mud breccia |
| | | AT559 | UB | 08.08.2004 | 35°24.777' | 06°43.782' | 552 | *A. squamata; A. hexabrachiatus; A. ingolfiana* | Off MV; hemipelagic sediments |

continued next page

**TABLE 1.** (continued)

| Structure | Cruise | Station | Gear | Date (dd.mm.yy) | Latitude (N) | Longitude (W) | Depth (m) | Taxa | Observations |
|---|---|---|---|---|---|---|---|---|---|
| | | AT560 | UB | 08.08.2004 | 35º25.306' | 06º43.976' | 498 | Amphiuridae und.; *A. chiajei; Amphiura* sp. A; *A. squamata* | Crater; mud breccia |
| | | AT561 | UB | 08.08.2004 | 35º25.602' | 06º44.099' | 526 | *A. squamata;* Ophiuroidea und. | Flank; hemipelagic sediments |
| TTR | TTR12 | AT416 | Gr | 17.07.2002 | 35º21.870' | 06º52.000' | 695 | *A. squamata* | Flank; coral framework |
| Meknès | TTR14 | AT541 | Gr | 05.08.2004 | 34º59.103' | 07º04.435' | 703 | *Amphiura* sp. A; *A. squamata* | Crater; mud breccia with strong smell of $H_2S$ |
| | TTR15 | AT581 | Gr | 28.07.2005 | 34º59.178' | 07º04.353' | 700 | *A. squamata* | Crater; mud breccia |
| | | AT585 | K | 28.07.2005 | 34º59.137' | 07º04.343' | 701 | *A. squamata* | Crater; mud breccia |
| | | AT587 | G | 28.07.2005 | 34º59.140' | 07º04.423' | 701 | *A. squamata* | Crater; mud breccia |
| | MSM01-03 | 319 | UB | 14.05.2006 | 34º59.100' | 07º04.439' | 695 | Amphiuridae und. | Crater; mud breccia |
| | | 321 | UB | 14.05.2006 | 34º58.796' | 07º04.394' | 732 | *A. squamata* | Carbonate mound; shell ash and coral debris |
| | | 335 | UB | 15.05.2006 | 34º59.035' | 07º04.552' | 703 | *A. squamata;* Ophiuroidea und. | Flank; coral debris, mud breccia |
| Yuma | TTR14 | AT524 | Gr | 02.08.2004 | 35º24.973' | 07º05.461' | 960 | *A. hexabrachiatus* | Crater; mud breccia |
| | TTR16 | AT604 | Gr | 29.05.2006 | 35º25.820' | 07º06.330' | 1030 | *Amphiura* und.; *Amphiura* sp. A; *A. squamata;* Ophiuroidea juv. | Flank; mud breccia |
| | | AT605 | Gr | 29.05.2006 | 35º25.046' | 07º05.450' | 975 | Amphiuridae und.; *A. ingolfiana* | Crater; mud breccia |
| Ginsburg | TTR16 | AT607 | Gr | 29.05.2006 | 35º22.677' | 07º04.979' | 983 | *A. squamata* | Shell ash, carbonate slabs, crusts and coral debris |
| Jesus Baraza | TTR12 | AT391 | Gr | 09.07.2002 | 35º35.439' | 07º12.264' | 1105 | *A. squamata* | |
| Darwin | TTR16 | AT608 | Gr | 30.05.2006 | 35º23.531' | 07º11.475' | 1115 | Amphiuridae und. *Amphiura* sp. A; *A. squamata; A. hexabrachiatus* | Crater; shell ash; slabs and crusts. |
| Chechaouen | TTR16 | AT610 | Gr | 30.05.2006 | 35º28.468' | 07º15.477' | 1177 | Ophiuroidea juv. | Crater; mud breccia, crusts |
| Cap. Arutyunov | TTR12 | AT399 | Gr | 13.07.2002 | 35º39.805' | 07º19.997' | 1339 | *A. squamata* | Crater rim; mud breccia |
| | TTR14 | AT546 | | 06.08.2004 | 35º39.692' | 07º20.046' | 1345 | *Amphiura* sp. A | Crater; mud breccia with gas hydrates |
| | MSM01-03 | 194 | Gr | 28.04.2006 | 35º39.282' | 07º20.012' | 1379 | *A. squamata* | Flank; hemipelagic sediments |

continued next page

**TABLE 1.** (continued)

| Structure | Cruise | Station | Gear | Date (dd.mm.yy) | Latitude (N) | Longitude (W) | Depth (m) | Taxa | Observations |
|---|---|---|---|---|---|---|---|---|---|
| | | 195 | Gr | 28.04.2006 | 35°39.274' | 07°20.013' | 1390 | *O. aristata; O. gadensis* sp. nov.; *O. abyssicola; A. hexabrachiatus* | Flank; coral thicket |
| | | 212 | BL | 30.04.2006 | 35°39.681' | 07°19.981' | 1317 | *A. squamata;* Ophiuroidea und. | Crater; mud breccia |
| | | 225 | BL | 04.05.2006 | 35°39.700' | 07°20.010' | 1320 | *A. squamata* | Crater centre; mud breccia |
| | | 274 | BL | 10.05.2006 | 35°39.738' | 07°20.001' | 1321 | *A. squamata* | Crater centre; mud breccia |
| | | 344 | FL | 16.05.2006 | 35°39.697' | 07°20.038' | 1320 | *A. squamata* | Crater; mud breccia |
| Carlos Ribeiro | MSM01-03 | 157 | UB | 23.04.2006 | 35°47.270' | 08°25.360' | 2200 | Ophiuroidea juv. | Crater; mud breccia |
| Porto | MSM01-03 | 167 | FL | 25.04.2006 | 35°33.484' | 09°30.297' | 3862 | *O. lymani* | Crater; mud breccia |
| **Carbonates and Corals** | | | | | | | | | |
| W of Gibraltar | TTR14 | AT550 | D | 07.08.2004 | 35°42.257' | 06°30.000' | 392 | *O. balli; A. squamata* | Carbonate chimneys |
| | | AT551 | D | 07.08.2004 | 35°42.769' | 06°30.305' | 393 | *Amphiura* sp. A | Carbonate chimneys |
| | | AT552 | Gr | 07.08.2004 | 35°42.816' | 06°30.234' | 428 | Amphiuridae und.; *A. filiformis; A. squamata* | Carbonate chimneys in brown marl |
| Vernadsky Ridge | TTR15 | AT574 | D | 26.07.2005 | 35°02.982' | 06°46.661' | 508 | *A. grandisquama* | Carbonate crusts and chimneys |
| Formosa Ridge | TTR12 | AT388 | Gr | 08.07.2002 | 36°10.263' | 07°43.819' | 1079 | *A. squamata* | Carbonate chimneys |
| | | AT389 | D | 08.07.2002 | 36°10.123' | 07°44.121' | 1068 | *A. squamata* | Carbonate chimneys |
| Pen Duick | TTR12 | AT406 | Gr | 15.07.2002 | 35°18.148' | 06°47.666' | 550 | *A. squamata; A. ingolfiana* | Coral framework |
| | | AT407 | Gr | 15.07.1002 | 35°17.695' | 06°47.082' | 560 | *A. filiformis* | Coral framework |
| | TTR14 | AT565 | Gr | 09.08.2004 | 35°18.180' | 06°47.656' | 544 | *A. squamata* | Coral framework, clay |
| | TTR16 | AT600 | Gr | 28.05.2006 | 35°18.779' | 06°48.453' | 610 | *A. grandisquama; Amphiura* sp. A; *A. squamata; A. hexabrachiatus* | Mud breccia covered by coral debris and carbonate crusts |
| | | AT602 | Gr | 28.05.2006 | 35°17.693' | 06°47.089' | 556 | *A. filiformis; A. squamata; A. ingolfiana* | Hemipelagic sediments, shell debris cemented by carbonate crusts |

Specimens were examined using a Leo-1455VP SEM low vacuum. Specimens were air-dried and examined uncoated.

Type specimens have been deposited at The Natural History Museum, London, and the remaining material is deposited in the Biological Research Collection of the Department of Biology, University of Aveiro.

The taxonomic classification follows the scheme suggested by Smith *et al.* (1995). Taxonomic descriptions are only provided for new taxa. Images are given for new species and new locality records.

**Abbreviations.** DBUA, Department of Biology, University of Aveiro (Biological Research Collection) (Aveiro, Portugal); IFM-GEOMAR, Institut für Meereskunde - Forschungszentrum für marine Geowissenschaften (Kiel, Germany); IOC-UNESCO, Intergovernmental Oceanographic Commission - United Nations Educational, Scientific and Cultural Organization; MAR: Mid Atlantic Ridge; MV: Mud volcano MSU: Moscow State University (Moscow; Russia); NHMUK, The Natural History Museum (London, UK); NOCS: National Oceanographic Center, Southampton (Southampton, UK); TTR, training Through Research programme.

## Systematics

### Order Ophiurida Müller & Troschel, 1840

### Suborder Ophiurina Müller & Troschel, 1840

### Family Ophiacanthidae Perrier, 1891

### Subfamily Ophiacanthinae Paterson 1985

### *Ophiacantha aristata* Koehler 1896
(Fig. 2)

**Material examined.** Captain Arutyunov MV, MSM01-03, stn 195, 1 ind. (DBUA 001063.01).

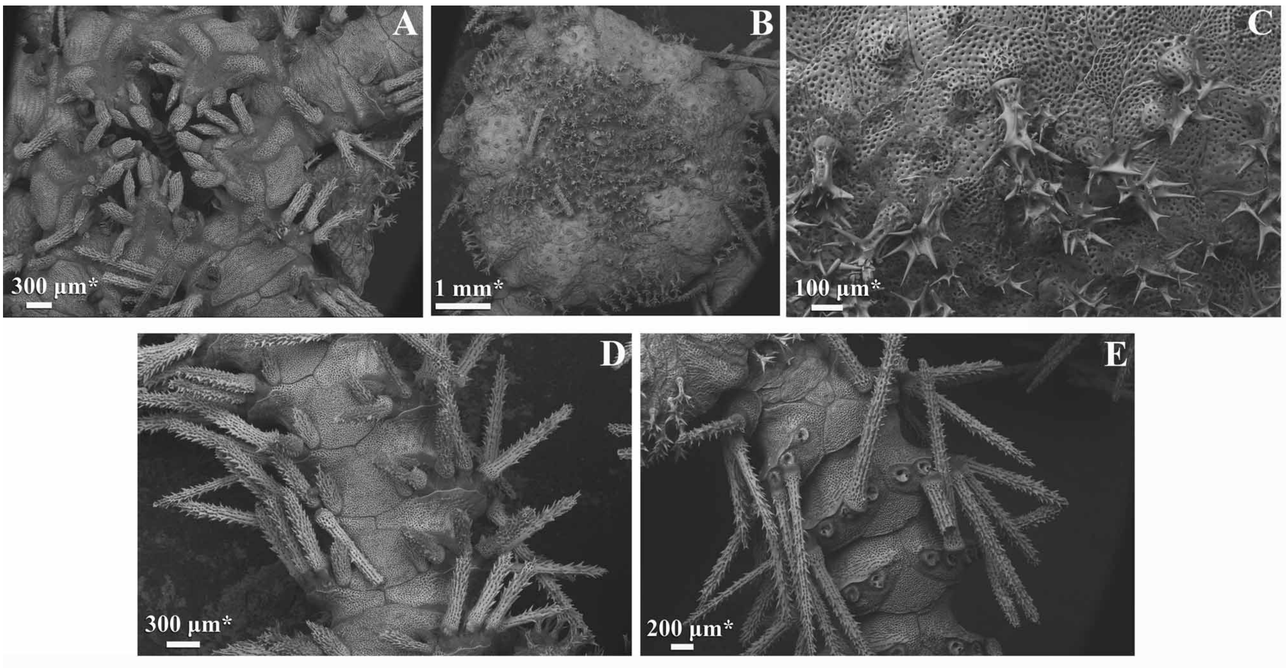


**FIGURE 2.** *Ophiacantha aristata*. A: ventral aspect; B: dorsal aspect; C: disk spinelets; D: arm ventrally; E: arm dorsally.

**Ecology and distribution.** This is a bathyal North Atlantic species (822–1700 m) known from SW Ireland south to the Canary Islands (Paterson 1985). In the Gulf of Cadiz it was collected from a coral thicket (*Dendrophylia* cf. *alternata*, mostly dead branches with a few living polyps) at a single station at the flanks of Captain Arutyunov MV (1390 m) together with *Ophiopristis gadensis* **sp. nov.**, *Ophiactis abyssicola* and *Amphioplus hexabrachiatus*.

### Subfamily Ophiotominae Paterson 1985

***Ophiopristis gadensis*** **sp. nov.**
(Figs. 3–5)

**Material examined.** *Holotype:* NE Atlantic: Gulf of Cadiz, Captain Arutyunov MV, MSM01-03, stn 195, 1 ind. (NHM 2010.352 Holotype).

*Paratypes:* same data as holotype, 12 inds. (DBUA 001147.01); 7 inds. (NHM 2010.353-359).

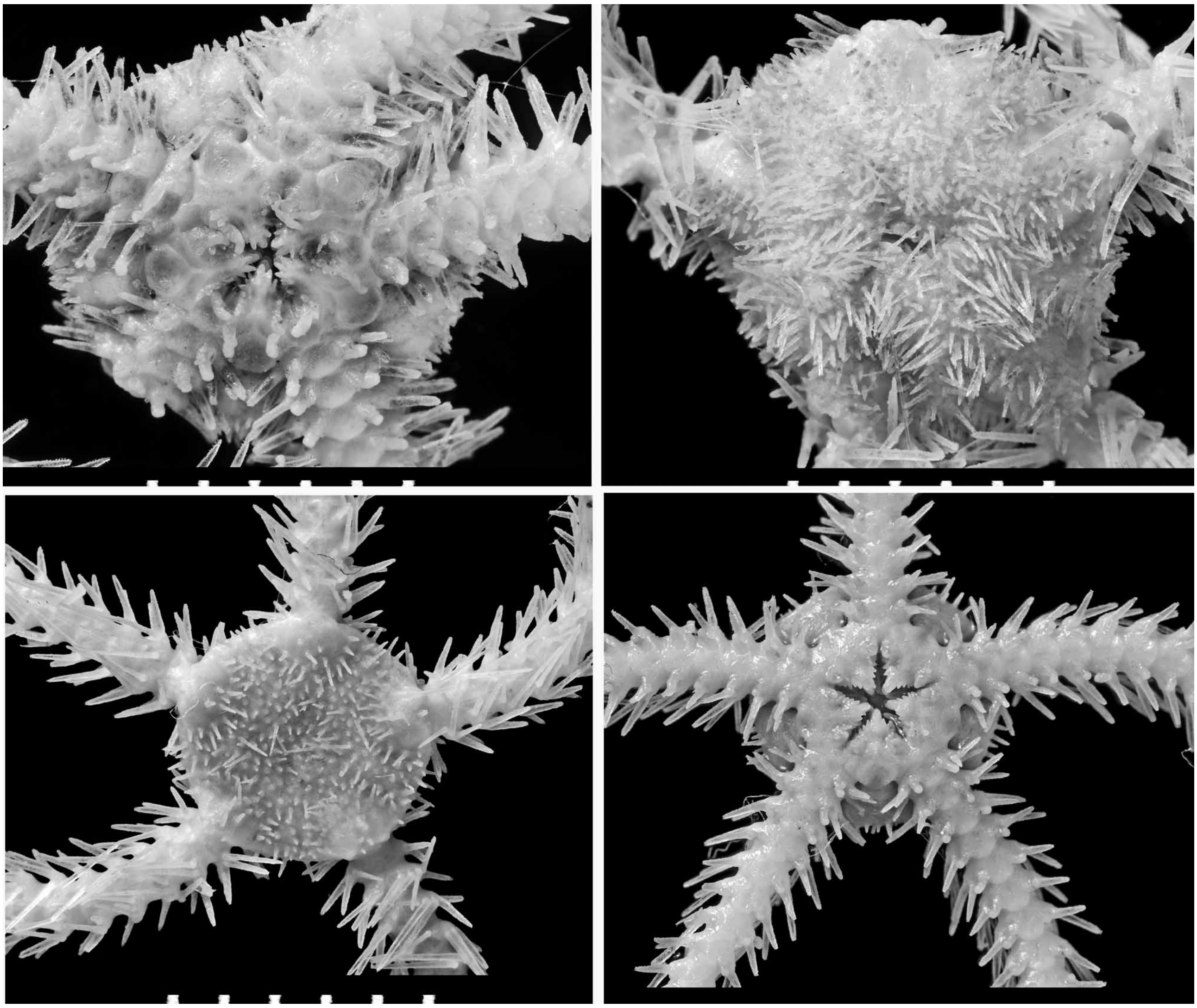

**FIGURE 3**. *Ophiopristis gadensis* **sp. nov.** A–B: Holotype, C–D: smaller specimen (paratype). A, D: ventral aspect; B, C: dorsal aspect. Scale bars = 1 cm.

**Diagnosis.** Ophiacanthid with sub-pentagonal disk; radial shields exposed, triangular in shape and less than a half disk radius in length; disk covered by thin plates; some plates bearing a spinelet; spinelets long, hollow with a smooth tip or 2–3 pointed spires.

Oral surface covered with thin opaque skin in larger individuals but skin not obvious in smaller specimens; two apical papillae with 3 to 5 pointed oral papillae; second oral tentacle pore emerges superficially onto the oral surface, 3 to 5 rounded tentacle scales associated with pore; adoral shield separating oral shield from first lateral arm plate; oral shield triangular to sub-pentagonal.

Arms distinctly noded at least 4 times disk diameter; plates become glassy on distal segments; dorsal arm plates triangular to scallop-shaped, proximally contiguous in large specimens, separated in smaller individuals; ventral arm plates rectangular with a convex distal edge; lateral arm plates with six arm spines; arm spines up to three arm segments long, dorsal arm spines finely rugose round to slightly flattened, ventral arm spines more obviously flattened with saw-like edge; proximal tentacle pores armed with two to three sub-equal tentacle scales, further out on the arm the scales reduce to two, one large leaf-like scale partially overlying a smaller scale.

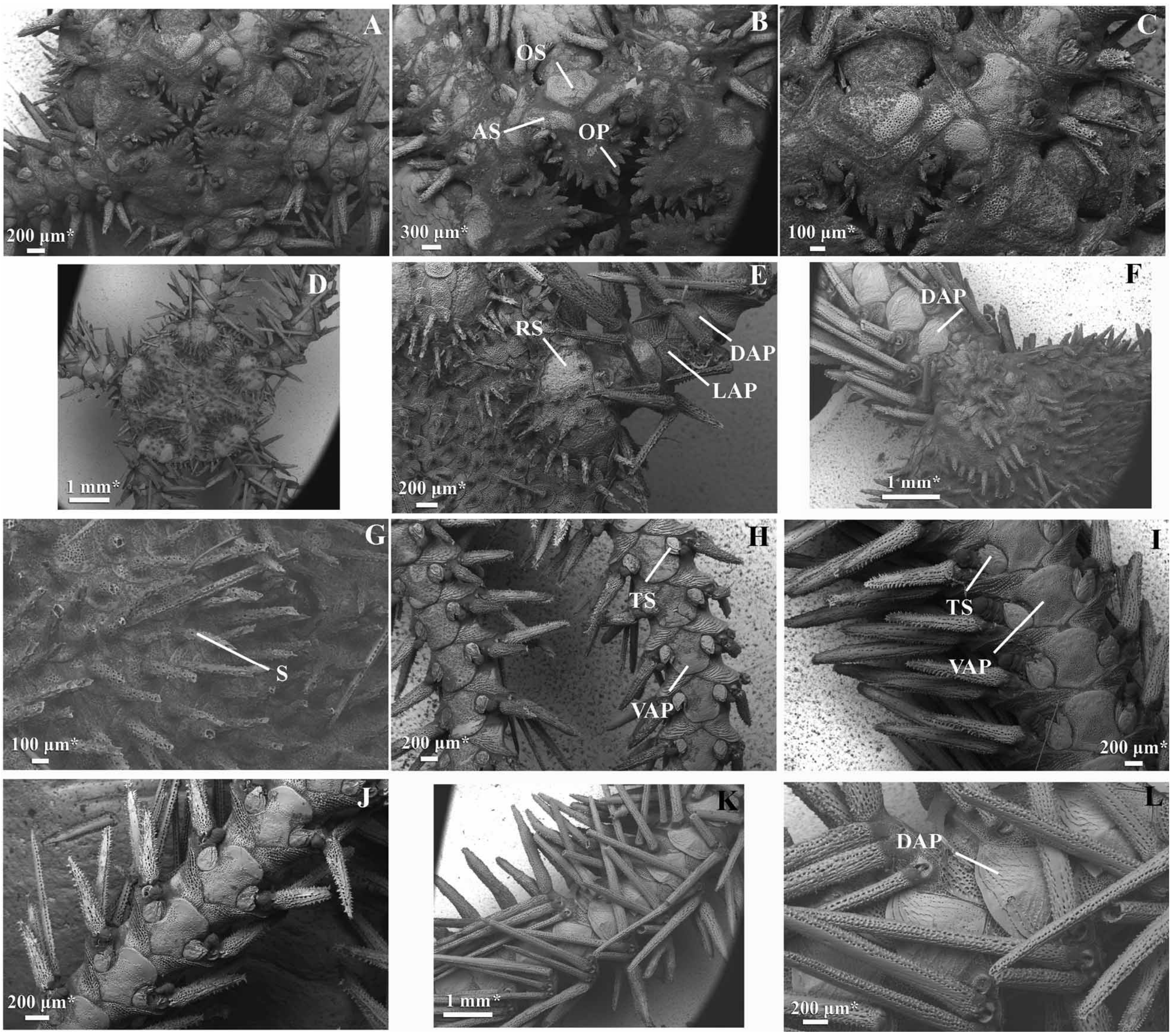


**FIGURE 4**. *Ophiopristis gadensis* **sp. nov.** (Paratype). A–B: ventral aspect, C: jaw detail, D: dorsal aspect; E–F: dorsal radial shield; G: disk spinelets; H: arm ventrally; I: arm ventrally and tentacle scale; J: outer arm ventrally; K: arm dorsally spines; L: detail of arm dorsally and spines. AS, adoral shield; DAP, dorsal arm plate; LAP, lateral arm plate; OP, oral papillae; OS, oral shield; S, spinelet; TS, tentacle scale; VAP, ventral arm plate.

**Holotype description.** disk sub-pentagonal (d.d. 8.3 mm). Arms at least four times disk diameter. Disk covered with thin scales, many carrying a spinelet. Spinelets long, hollow, rugose, with tip of spinelet produced into a smooth point, sometimes with two or three small pointed spires; spinelets in middle of disk finer than those on the periphery or in the interbrachial region. Radial shields exposed, approximately triangular in shape; each shield pair separated along whole length; length extending slightly shorter than a quarter of the disk diameter. Ventral interbrachial area covered with small scales. Spinelets present but shorter and with a lower density than aboral surface.

Oral surface covered by thin skin, partially obscuring the plate beneath. Jaws slightly longer than broad. Two apical papillae on most jaws. Up to five oral papillae along each jaw edge, papillae longer than wide with pointed tip; small pointed, distal papillae lie deeper within mouth. Second oral tentacle pore emerging superficially onto the surface of the jaw. Oral tentacle scales larger than oral papillae, four to five in number, often longer than high with a rounded free edge; tentacles scales superficial situated on oral surface and separated from oral papillae. Adoral shields large, slightly wider at their junction with the arm plates and separating oral shields from first lateral arm plate. Oral shields rounded pentagonal slightly longer than broad.

Arms long, distinctly noded in proximal segments, arm plates becoming glassy. Disk plates extending onto proximal arm segments nearly surrounding first dorsal arm plate. Dorsal arm plates triangular to scallop-shaped with convex distal edge; plates contiguous at least on proximal segments; on distal segments dorsal arm plates more triangular and just contiguous. Ventral arm plates approximately rectangular with a convex distal edge, contiguous on proximal arm segments. Tentacle pores covered, on the proximal segments oval scales, slightly pointed and often of different sizes; each pore with three scales arranged around the first two to four arm pores, decreasing to two thereafter until nearly the end of the arm; two scales comprised of a large glassy, slightly pointed, almost leaf-like scale sitting over a smaller inner scale. Lateral arm plates flared forming a ridge along the area where arm spines inserted. Arm spines six, up to three arm segments in length on proximal arm segments becoming shorter on distal ones; not quite forming a continuous row on the first free arm segment. Dorsalmost spines finely rugose, slightly flattened; ventralmost spines shorter, wider at the base of the spine, much flatter developing a saw-like edge with distinct teeth, terminating in triple-tipped spine; tip of arm spine glassy. These ventralmost spines become shorter on outer arm segments forming a row of large teeth along the ventral edge on the outer part of the arm spine.

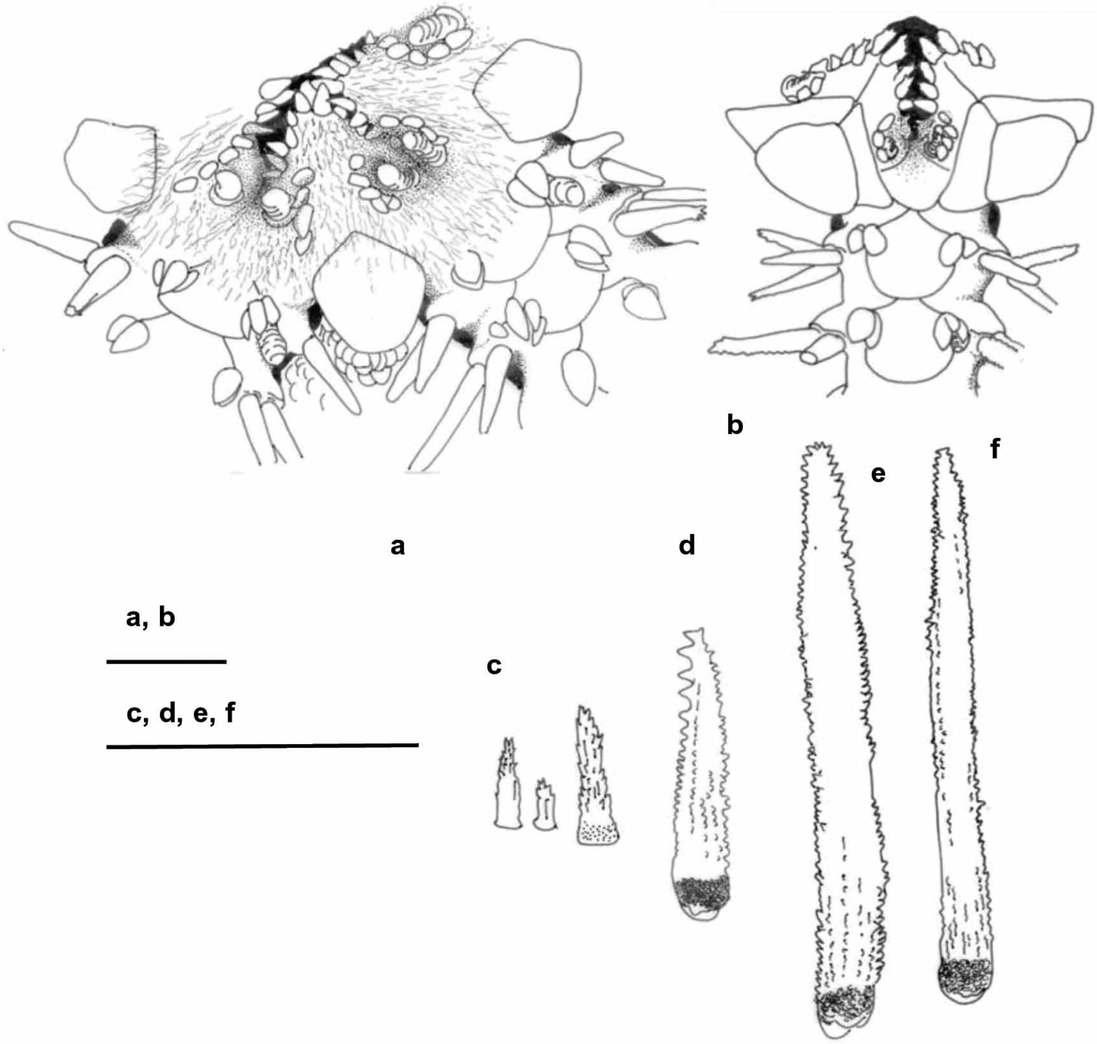


**FIGURE 5**. *Ophiopristis gadensis* **sp. nov.** A–B: ventral view of adult (disk diameter: 9.5 mm), b) oral frame of juvenile specimen (disk diameter: 3.5 mm), c) disk spinelets, d) ventralmost spine from distal arm segment, e) mid arm spine f) arm dorsally spine. Bar scales = 1 mm.

***Variation (Paratypes).*** Large individuals conform to the description of the holotype**.** Smaller individuals, d.d. 3.5 to 6 mm, do not have thickened skin over the oral surface so the plates are clearer. Oral shields are more rounded slightly wider than long. Jaws with three to four oral papillae which are slightly more rugose than in larger specimens. However in other characters, such as tentacle scale number and arrangement, smaller specimens resemble the larger, although the gap between the oral papillae and oral tentacle scales is more obvious. Oral shields triangular slightly more elongated and rounded. Dorsal arm plates on smaller specimens are triangular with a convex distal edge and are separated, not contiguous. Often just two tentacle scales The number of scales may be the result of a larger scale being split perhaps during development thus resulting in three scales not two.

**Distribution and ecology**. This species is only known from the type locality. It was collected from a coral thicket (*Dendrophylia* cf. *alternata*, mostly dead branches with a few living polyps) at a single station on the flanks of Captain Arutyunov MV at a depth of 1390 m, together with *Ophiactis abyssicola*, *Ophiacantha aristata* and *Amphioplus hexabrachiatus*.

**Etymology.** This species is named after the area (Gulf of Cadiz) where it was first discovered; Gades is the old Roman name for Cadiz.

**Remarks.** Placing this species within *Ophiopristis* Verrill, 1899 represents a compromise and potentially expands the definition of the genus. There are a number of characters which appear to be unique. The emergent radial shields are unusual in the Ophiotominae and in *Ophiopristis*, the arrangement of the oral papillae and second oral tentacle scales are also distinct and finally the development of thickened integument has not been reported within species of the genus. However, such variation in the degree of skin covering the disk has also been noted for other ophiacanthids, for example *Ophiolebes scorteus* Lyman, 1878, without resorting to the erection of a new genus. It is possible that this combination of characters within this species represents a new genus, however as Paterson (1985) and O'Hara and Stöhr (2006) point out, the genera within Ophiacanthidae are not well defined and so adding another would only serve to add to this problem. *Ophiopristis gadensis* **sp. nov.** share the following features with other species of the genus **-** the arm spines are slightly flattened with a rugose edge, the oral and second tentacle papillae are separated either physically or by shape and size, the tentacle scales are multiple in proximal arm segments. *Ophiopristis* can now be defined as: jaws longer than broad, flanked on each side by four or more oral papillae, second oral tentacle pore superficial opening near the surface of the jaw, armed with tentacle scales similar in size and shape to the oral papillae, sometimes confluent with oral papillae but in some separated; adoral shields long and narrow, separating the oral shield from the first lateral arm plate; disk covered with small scales carrying an elongated spinelet, often long, hollow and with pointed or furcate tips; radial shield usually concealed but maybe exposed; arm spines flattened, carrying a row of sharp points along each edge; tentacle pores armed with up to four tentacle scales on proximal first two to four pores decreasing to one to two large scales on segments thereafter.

According to Stöhr and O'Hara (2007) there are eight species of *Ophiopristis*. *O. gadensis* **sp. nov.** differs in the type of disk spines which are more rugose and not smooth as in most of the other species; the presence in larger specimens of the thickened integument and the distinct separation between the oral papillae and the second oral tentacle scales. *Ophiopristis gadensis* **sp. nov.** is similar to *O. dissidens* Koehler, 1905 in having three tentacle scales on proximal tentacle pores but differs in that the disk spinelets are not smooth, glassy and hollow. A comparison of the species is given in Table 2.

## Family Ophiactidae Matsumoto, 1915

### *Ophiactis abyssicola* (M. Sars, 1861)

(Fig. 6)

**Material examined.** Captain Arutyunov MV, MSM01-03, stn 195, 3 inds. (DBUA 001064.01).

**Ecology and distribution.** This is an Atlantic species known from a wide bathymetric range (125–4721 m) from Norway to southern Africa (Paterson 1985). In the Gulf of Cadiz it was collected from a coral thicket (*Dendrophylia* cf. *alternata*, mostly dead branches with a few living polyps) in a single station at the flanks of Captain Arutyunov MV (1390 m) together with *Ophiopristis gadensis* **sp. nov.**, *Ophiacantha aristata* and *Amphioplus hexabrachiatus*.

**TABLE 2.** Review of species of *Ophiopristis*, based on original description in the literature, unless otherwise noted. OTS- 2nd Oral Tentacle Scale; OP— Oral papillae, TS—arm tentacles scale.

| *Species* *Author* | *Disk spinelets no.* | RS exposed/hidden | *No of oral papillae* | *No of oral tentacle scales* | *Oral papillae tentacle scales size* | *Shape of oral shield* | *Tenacle scles no in proximal pores* | *Shape of TS* | *No of arm spines* | *Shape* | *Notes* | *Type locality* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *O. gadensis* sp. nov. | Rugose with pointed spire | Distal end exposed, oval | 3 | 3 | OTS=OP | Wider than long, rounded triangular to squat rounded pentagonal | 3-4-2-1 | leaf-shaped with pointed free end | 6 | Dorsally slightly flattened become distinctly flattened with serrated edge with distinct teeth | | Gulf of Cadiz, NE Atlantic, 1390 m |
| *O. dissidens* (Koehler, 1905) | Hollow, smooth with webbed pointed spire | Distal end exposed, triangular | 3-4 | 4 | OTS>OP | Wider than long, rounded proximal edge, approximately scalloped-shaped | 3-2 | leaf shaped with slightly rounded to pointed free end | 6 | Laterally compressed, edged with sharp webbed teeth | description after O'Hara & Stöhr (2006) | Indonesia, 11 m |
| *O. procera* (Koehler, 1904) | Smooth, irregularly terminated, truncated or with bifid spire | Hidden | 3 | 2 | OTS=OP | Rounded triangular | 2-1 | Oval with elongated free end | 6 | Compressed with serrated edge of fine teeth | | Off Kei Islands, Indonesia, 595 m |
| *O. luctosa* (Koehler, 1904) | Long, thin, hollow, smooth with 1 -3 sharp spires | Hidden | 3-5 | 2 | OTS>>OP | As wide as long, convex proximal edge produced distal edge | 1 | Large oval to circular | 6 | Laterally compressed, edged with sharp teeth | description after O'Hara & Stöhr (2006) | Indonesia, 216 m |

continued next page

**TABLE 2.** (continued)

| *Species Author* | *Disk spinelets no.* | RS exposed/hidden | *No of oral papillae* | *No of oral tentacle scales* | *Oral papillae tentacle scales size* | *Shape of oral shield* | *Tenacle sceles no in proximal pores* | *Shape of TS* | *No of arm spines* | *Shape* | *Notes* | *Type locality* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *O. vestita* (Koehler, 1897) | Long, smooth truncated round tip or minutely bifurcating tip | Hidden | 4 | 2 | OTS=OP | Rounded arrow-shape - Rhomboid wider than long with distal lobe | 2-1 | Elongated with rounded free tip, | 6 | Laterally compressed, edged with sharp teeth | | India, 362-390 m |
| *O. mitsuii* (Murakami, 1942) | Slender, thin with 2-3 sharp spires | hidden | 4-5 | 2 | OTS>OP | Rhombic to triangular | 3-2-1 | Leaf shaped with pointed tip | 8 | Laterally compressed with serrated edge of sharp teeth | | Kawazu, Japan, 366 m |
| *O. ensifera* Verrill, 1899 | Short, obtuse, conical | Distal end exposed, oval | 4-7 | 3-5 | OTS=OP | Squat arrow shape or rounded rhombic | 2-1 | Oval, rounded free tip | 5 | Compressed with blunt tip and serrated edge with distinct teeth | This is the type species of the genus | Havana, 201-475 m |
| *O. hirsuta* (Lyman, 1875) | Lengths from short to long and slender, with sharp spire | Distal end exposed | 5 | 2-4 | OTS=OP | Rhombic rounded but with distal lobe | 2-1 | Oval to leaf shaped with pinted free tip | 5 | Laterally compressed, edged with small sharp teeth | Description after Verrill (1899) | West Indies |
| *O. axiologus* (Clark, 1909) | Short with multiple points | Distal end exposed | 4 | 3-4 | OTS>OP | Rhombic rounded , wider than long | 3-2-1 | Leaf-shaped, long and sharply pointed | 5-6 | Smooth arm spines | Clark (1909) does not give any further description of the arm spines and the diagram shows smooth spines | Australia 99-108 m |

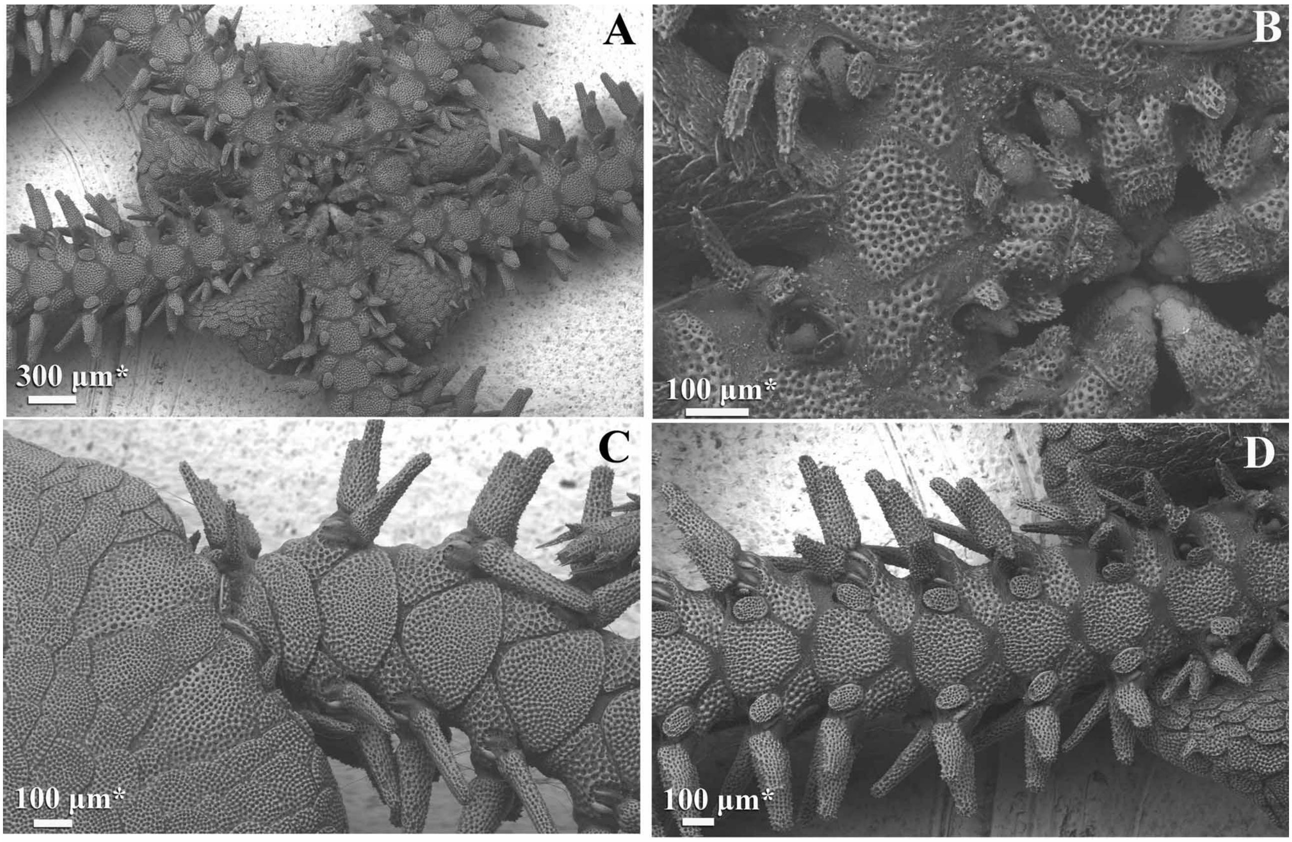


**FIGURE 6**: *Ophiactis abyssicola*. A: ventral aspect; B: oral plates with papillae detail; C: arm dorsally; D: arm ventrally.

### *Ophiactis balli* (Thompson, 1840)

**Material examined.** Al Idrisi MV, TTR12, stn AT412, 2 ind. (DBUA 001065.01); West of Gibraltar Strait, TTR14, stn AT550, 1 ind. (DBUA 001066.01).

**Ecology and distribution.** This is an Eastern Atlantic species known from depths of 60–400 m (Paterson 1985), generally found in crevices or amongst sessile invertebrates with the body concealed and the arms extended out into the water. It is characteristic of exposed or moderately exposed rocky situations especially on limestone (Picton & Morrow 2007). In the Gulf of Cadiz it was collected within its known bathymetric range from limestones at the crater of Al Idrisi MV and from carbonate chimneys in an exposed site (high bottom currents) West of Gibraltar Strait.

## Family Amphiuridae Ljungman, 1867

### *Amphiura grandisquama* Lyman, 1869

**Material examined.** Vernadsky Ridge, TTR15, stn AT574, 1 ind. (DBUA 001067.01); Pen Duick Escarpment, TTR16, stn AT600, 4 inds. (DBUA 001068.01).

**Ecology and distribution.** In the Eastern Atlantic *A. grandisquama* has been recorded from Iceland south to the Azores and Cape Verde Islands at depths of 861–1635 m (Paterson 1985). In the Gulf of Cadiz it was collected from carbonate chimneys and crusts at shallower depths (508–610 m) (Fig. 7A).

### *Amphiura chiajei* Forbes, 1843

**Material examined.** Mercator MV, TTR15, stn AT569, 1 ind. (DBUA 001069.01), stn AT576, 15 inds. (DBUA 001069.02), stn AT577, 2 inds. (DBUA 001069.03); Kidd MV, TTR14, stn AT560, 1 ind. (DBUA 001070.01).

**Ecology and distribution.** *Amphiura chiajei* has been recorded from the Eastern Atlantic and Mediterranean, and from West Africa; it is usually a shelf species but has been recorded from a depth of 1200 m (Paterson 1985). This species is reported as living buried in muddy sand, extending its arms above the surface of the sediments to feed on deposited material. In the Gulf of Cadiz it was collected from soft mud breccia in the crater of Mercator and Kidd mud volcanoes within its known bathymetric range (Fig. 7A).

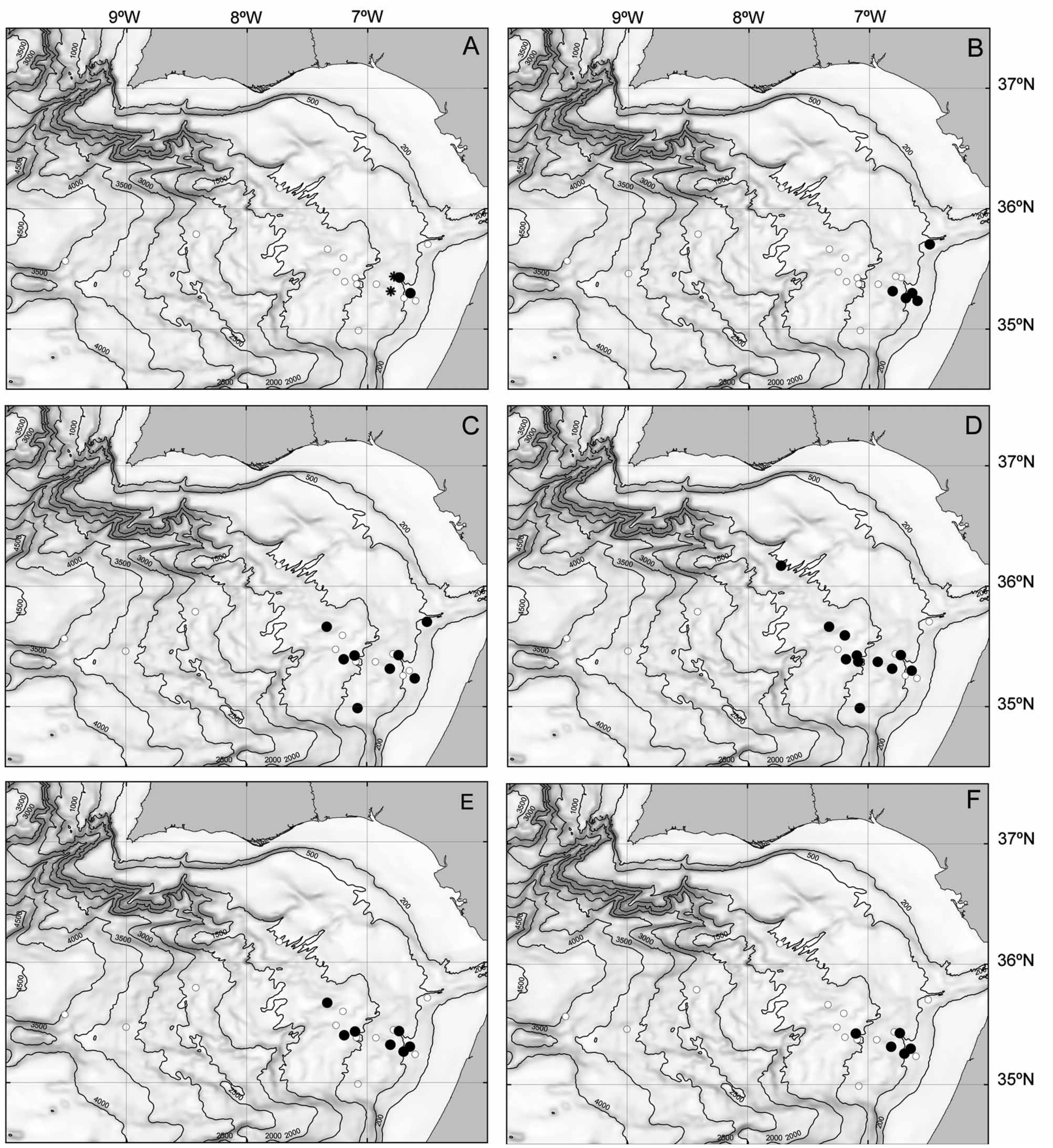


**FIGURE 7.** Distribution of Amphiuridae species in the Gulf of Cadiz. A: *Amphiura grandisquama* (full circles) and *Amphiura chiajei* (asterisks); B: *Amphiura filiformis*; C: *Amphiura* sp. A; D: *Amphipholis squamata*; E: *Amphioplus hexabrachiatus*; F: *Amphilepis ingolfiana.*

### *Amphiura filiformis* (O.F. Müller, 1776)

**Material examined.** Al Idrisi MV, TTR12, stn AT412, 2 ind. (DBUA 001071.01); Mercator MV, TTR15, stn AT569, 10 inds. (DBUA 001072.01); stn AT575, 18 inds. (DBUA 001072.02); stn AT576, 17 inds. (DBUA 001072.03); MSM01-03, stn 237, 2 inds. (DBUA 001073.01); stn 241, 37 inds. (DBUA 001073.02); stn 242, 24 inds. (DBUA 001073.03); stn 267, 2 inds. (DBUA 001073.04); stn 287, 3 inds. (DBUA 001073.05); Fiuza MV, TTR14, stn AT566, 5 inds.; West of Gibraltar Strait, TTR14, stn AT552, 1 ind. (DBUA 001074.02); Pen Duick Escarpment, TTR12, stn AT407, 1 ind. (DBUA 001071.02); TTR16, stn AT602, 1 ind. (DBUA 001075.01).

**Ecology and distribution.** *Amphiura filiformis* is a common, predominantly shallow-water species of the north-Eastern Atlantic. It is known to occur from Norway to West Africa and also in the Mediterranean Sea at depths up to 1665 m (Paterson 1985). This species is often found sympatric with *A. chiajei*. Both species live buried in fine muddy sand but, unlike its congener, *A. filiformis* feeds in the water current extending its arms vertically 3–4 cm above the sediment surface (Vopel *et al*. 2003). In the Gulf of Cadiz *A. filiformis* co-occurred with *A. chiajei* in Mercator MV (Fig. 7B). The highest density of *A. filiformis* (72–144 ind.m$^{-2}$) occurs in the crater where only one specimen of *A. chiajei* was collected; the latter reaches densities of 60 ind.m$^{-2}$ on the flank where the density of *A. filiformis* drops to 68 ind.m$^{-2}$. *Amphiura filiformis* has also a much wider distribution and has been recorded in two other mud volcanoes (Al Idrisi and Fíuza) and in association with carbonate chimneys and crusts at two other sites (West of Gibraltar and Pen Duick Escarpment) at depths between 230 and 556 m.

### *Amphiura* sp. A Stöhr and Segonzac, 2005

*Amphiura* sp. Stöhr and Segonzac 2005: 396–397, figure 8

**Material examined.** Kidd MV, TTR14, stn AT528, 6 inds. (DBUA 001077.01); stn AT560, 3 ind. (DBUA 001077.02); Meknès MV, TTR14 stn AT541, 9 inds. (DBUA 001077.03); Yuma MV, TTR16, stn AT604, 1 ind. (DBUA 001078.01); Darwin MV, TTR16, stn AT608, 1 ind. (DBUA 001078.02); Captain Arutyunov MV, TTR14, stn AT546, 3 inds. (DBUA 001077.04); West of Gibraltar Strait, TTR14, stn AT551, 1 ind. (DBUA 001077.05); Pen Duick Escarpment, TTR16, stn AT600, 1 ind. (DBUA 001078.03).

**Remarks.** This species, herein designated as *Amphiura sp. A*, closely resembles the description given by Stöhr and Segonzac (2005) from West Atlantic cold seeps. The species is characterised by, having two tentacle scales on each arm tentacle pore and a scale-like distal oral scale, ten with a more spike-like scale situated on the adoral shields and just three arm spines, a character shared with other *Amphiura* species, the middle arm spine of the three is swollen**.**

We have not formally classified this species because *Amphiura* species with three arm spines are common within the family (approximately 28 species). To formally name this species would require a major taxonomic review which is beyond the scope of the present work.

**Ecology and distribution.** *Amphiura* sp. A as described by Stöhr & Segonzac was previously known from mud sediments among chemosynthetic fauna (*Bathymodiolus boomerang*, *Escarpia* sp.) of the Orinoco cold seeps, West Atlantic, at 1947 m. In the Gulf of Cadiz it has a wide distribution in the shallow and western areas of the Moroccan margin (carbonate provinces) predominantly associated to the presence of carbonate crusts and covering a bathymetric range of 489–1345 m (Fig. 7C). It was recorded from five mud volcanoes and two other sites with carbonate chimneys or crusts, often co-occurring with *Amphipholis squamata* and occasionally with other Amphiuridae (*Amphioplus hexabrachiatus*, *Amphiura filiformis* and *Amphiura grandisquama*).

### *Amphipholis squamata* (Delle Chiaje, 1828)
(Fig. 8)

**Material examined.** Mercator MV, TTR15, stn AT568, 1 ind. (DBUA 001080.07); stn AT575, 10 inds (DBUA 001080.01), stn AT576, 5 inds. (DBUA 001080.02), stn AT577, 2 inds. (DBUA 001080.03); MSM01-03, stn 241, 18 inds. (DBUA 001081.01), stn 242, 9 inds. (DBUA 001081.02), stn 287, 1 ind.; Fiuza MV, TTR14, stn AT566, 2 inds. (DBUA 001079.01); Kidd MV, TTR14, stn AT528, 2 inds.; stn AT559, 2 ind. (DBUA 001079.02), stn AT560, 9 inds. (DBUA 001079.03), stn AT561, 3 inds. (DBUA 001079.04); TTR MV, TTR12, stn AT416, 16 inds. (DBUA 001082.01); Meknès MV, TTR14, stn AT541, 1 ind.; TTR15, stn AT581, 1 ind. (DBUA 001080.04), stn AT585, 1 ind. (DBUA 001080.05), stn AT587, 1 ind. (DBUA 001080.06); MSM01-03, stn 321, 7 inds. (DBUA 001081.03), stn 335, 15 inds. (DBUA 001081.04); Yuma MV, TTR16, stn AT604, 4 inds. (DBUA 001083.01); Ginsburg MV, TTR16, stn AT607, 3 inds. (DBUA 001083.02); Jesus Baraza MV, TTR12, stn AT391, 1 ind. (DBUA 001082.02); Darwin MV, TTR16, stn AT608, 8 inds. (DBUA 001083.03); Captain Arutyunov MV, TTR12, stn AT399, 2 ind. (DBUA 001082.03); MSM01-03, stn 212, 1 ind. (DBUA 001081.05), stn194, 2 inds. (DBUA 001081.06), stn 225, 4 inds. (DBUA 001081.07), stn 274, 4 inds. (DBUA 001081.08), stn 344, 2 ind. (DBUA 001081.09); Formosa Ridge, TTR12, stn AT388, 2 ind. (DBUA 001082.04), stn AT389, 5 inds. (DBUA 001082.05); West of Gilbratar Strait, TTR14, stn AT550, 3 inds. (DBUA 001079.05), stn AT552, 24 inds. (DBUA 001079.06); Pen Duick Escarpment, TTR12, stn AT406, 18 inds. (DBUA 001082.06); TTR14, stn AT565, 1 ind. (DBUA 001079.07); TTR16, stn AT600, 8 inds. (DBUA 001083.04), stn AT602, 4 inds. (DBUA 001083.05).

**Ecology and distribution.** *Amphipholis squamata* is known from several substrata (under stones, amongst algal and bryozoan turfs, rockpool weeds and occasionally on sandy bottoms) from the intertidal to 1200 m. Current distribution records suggests that it is abundant in the Eastern Atlantic from Iceland along the European margin, Mediterranean Sea, West coast of Africa, West and East coast of South Africa and Madagascar (Alva & Vadon 1989). The taxonomy of this species is currently being investigated (S. Stöhr, per comm.). It is likely that this presumed cosmopolitan species will turn out to be a complex of cryptic species and that there will need to be a revision of its geographic distribution.

This species can switch from deposit feeding by collecting particles within its tube feet to suspension feeding via trapping detritus in mucus. In the Gulf of Cadiz it was the most common ophiuroid, recorded from 10 mud volcanoes and at three other sites in association to carbonate chimneys and crusts as well as cold-water corals (Fig. 7D). Young, intermediate and adult stages were found together at the same localities. This species was found at depths from 350 to 1379 m which is its deepest known record.

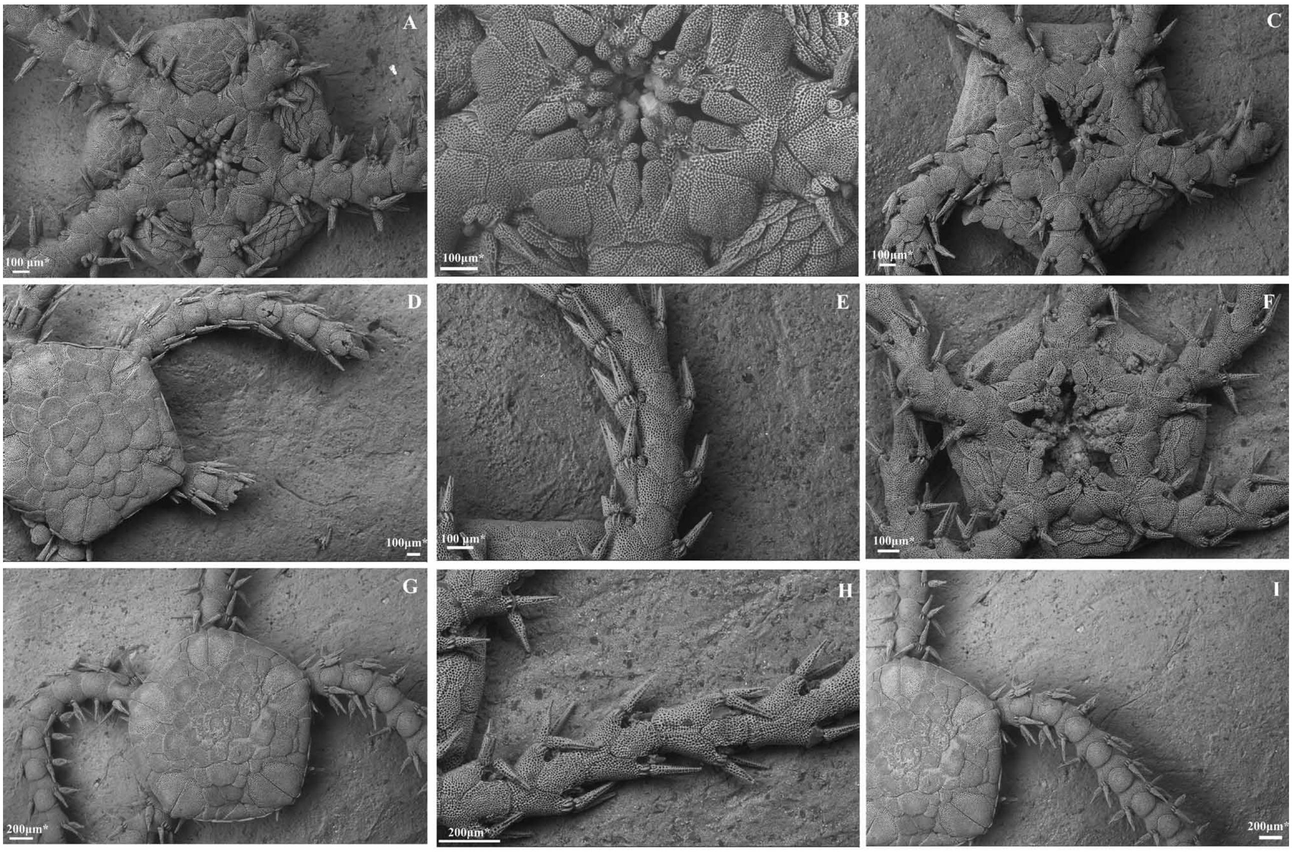


**FIGURE 8**. *Amphipholis squamata*. A, B, C, F: ventral aspect; D, I: dorsal aspect; E, H: arm ventrally; I: arm dorsally. A, B: specimen 1; C, D, E: specimen 2; F, G, H, I: specimen 3. All specimens were collected at the same location (TTR mud volcano).

## *Amphioplus hexabrachiatus* Stöhr, 2003

(Figs. 9–10)

**Material examined.** Mercator MV, TTR15, stn AT576, 4 inds. (DBUA 001084.01); Fiuza MV, TTR14, stn AT566, 2 inds. (DBUA 001085.01); Kidd MV, TTR14, stn AT559, 2 inds. (DBUA 001085.02); Yuma MV, TTR14, stn AT524, 1 ind. (DBUA 001085.03); Darwin MV, TTR16, stn AT608, 1 ind. (DBUA 001086.01); Captain Arutyunov MV, MSM01-03, stn 195, 1 ind. (DBUA 0010.87.01); Pen Duick Escarpment, TTR16, stn AT600, 1 ind..

**Remarks.** This species is hexamerous, reproduces asexually by division, and reaches a maximum size of about 2.5 mm disk diameter. This is the first six-armed species of *Amphioplus* and the third species of the genus known from the deep North Atlantic. The specimens from the Gulf of Cadiz closely resemble the description and images given by Stöhr (2003). This is obviously a morphologically variable species; in the range of body sizes observed in this study, key features such as the arrangement of the oral papillae and buccal scale are often not developed. It is only in the larger specimens (disk diameter > 2 mm) where the tentacle scales develop and are conspicuous. On the dorsal surface the development of the radial shields changes from small plates only separated at the inner edge to more elongated, larger plates separated nearly the full length of the plate only contiguous at the outer end. Smaller specimens show distinct evidence of fissiparity with one side of the disk being less well developed and smaller.

**Ecology and distribution.** This species was described from southwest of Iceland at depths of 1000–1500 m, collected by the Benthic Invertebrates of Icelandic Waters (BIOICE) programme (Stöhr 2003). In the Gulf of Cadiz (Fig. 7E) it was collected from the Pen Duick Escarpment and mud volcanoes of the Moroccan margin usually in areas with carbonate crusts or coral framework at depths between 414 and 1390 m extending the upper bathyal limit from 1000 to 414 m. The records from Cadiz also extend considerably the known geographical range of this species.

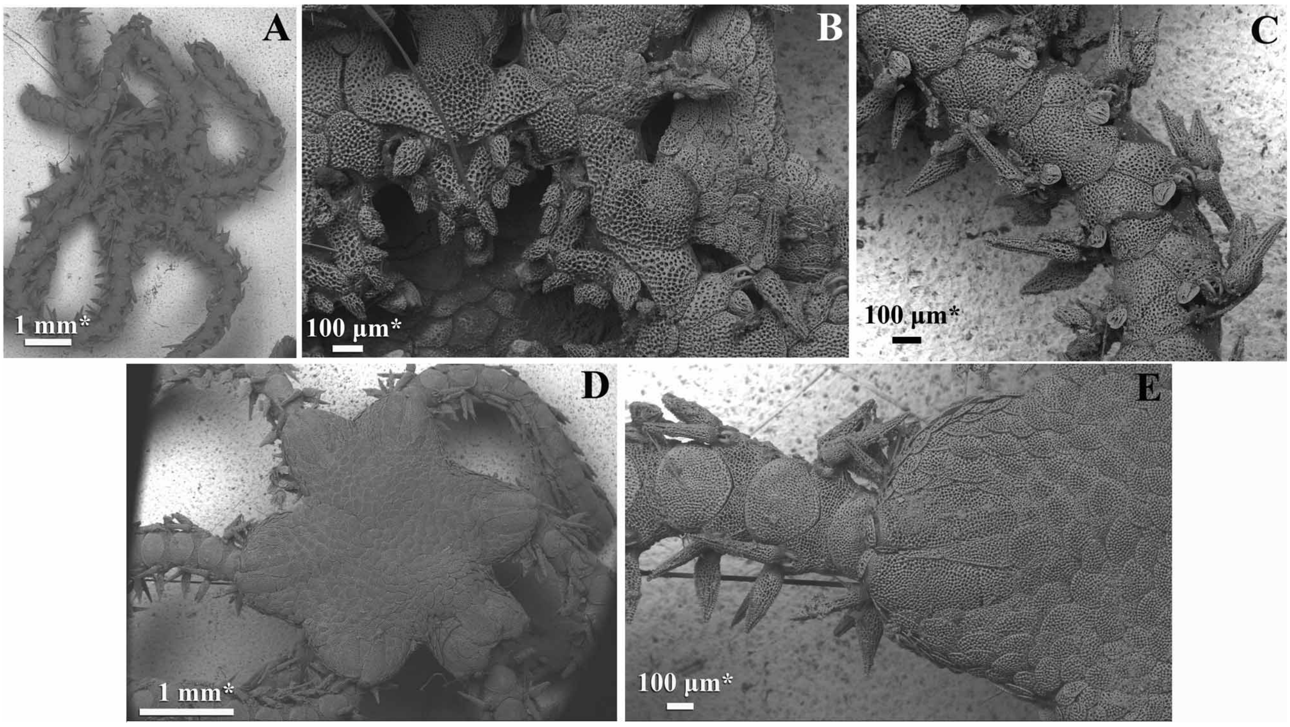


**FIGURE 9.** *Amphioplus hexabrachiatus*. A: ventral aspect; B: oral plates with papillae detail; C: arm ventrally; D: dorsal aspect; E: arm dorsally.

## Family Amphilepididae Matsumoto, 1915

### *Amphilepis ingolfiana* Mortensen, 1933

**Material examined.** Mercator MV, TTR15, stn AT569, 1 ind. (DBUA 001088.01), stn AT575, 4 inds. (DBUA 001088.02), stn AT576, 5 inds. (DBUA 001088.03); MSM01-03, stn 237, 1 ind. (DBUA 001089.01); Fiuza MV, TTR12, stn AT403, 1 inds.; Kidd MV, TTR14, stn AT559, 2 inds. (DBUA 001091.01); Yuma MV, TTR16, stn AT605, 1 ind. (DBUA 001092.01); Pen Duick Escarpment, TTR12, stn AT406, 1 ind. (DBUA 001090.01); TTR16, stn AT602, 1 ind. (DBUA 001092.02).

**Ecology and distribution.** *Amphilepis ingolfiana* is a deep-sea species (957–4829 m) known to occur in the NE Atlantic from the Rockall Trough south to off North Africa (Paterson 1985). In the Gulf of Cadiz it was collected at the Moroccan margin in four mud volcanoes and in the Pen Duick Escarpment, often associated with carbonate crusts and at shallower depths (353–975 m) than previously reported (Fig. 7F).

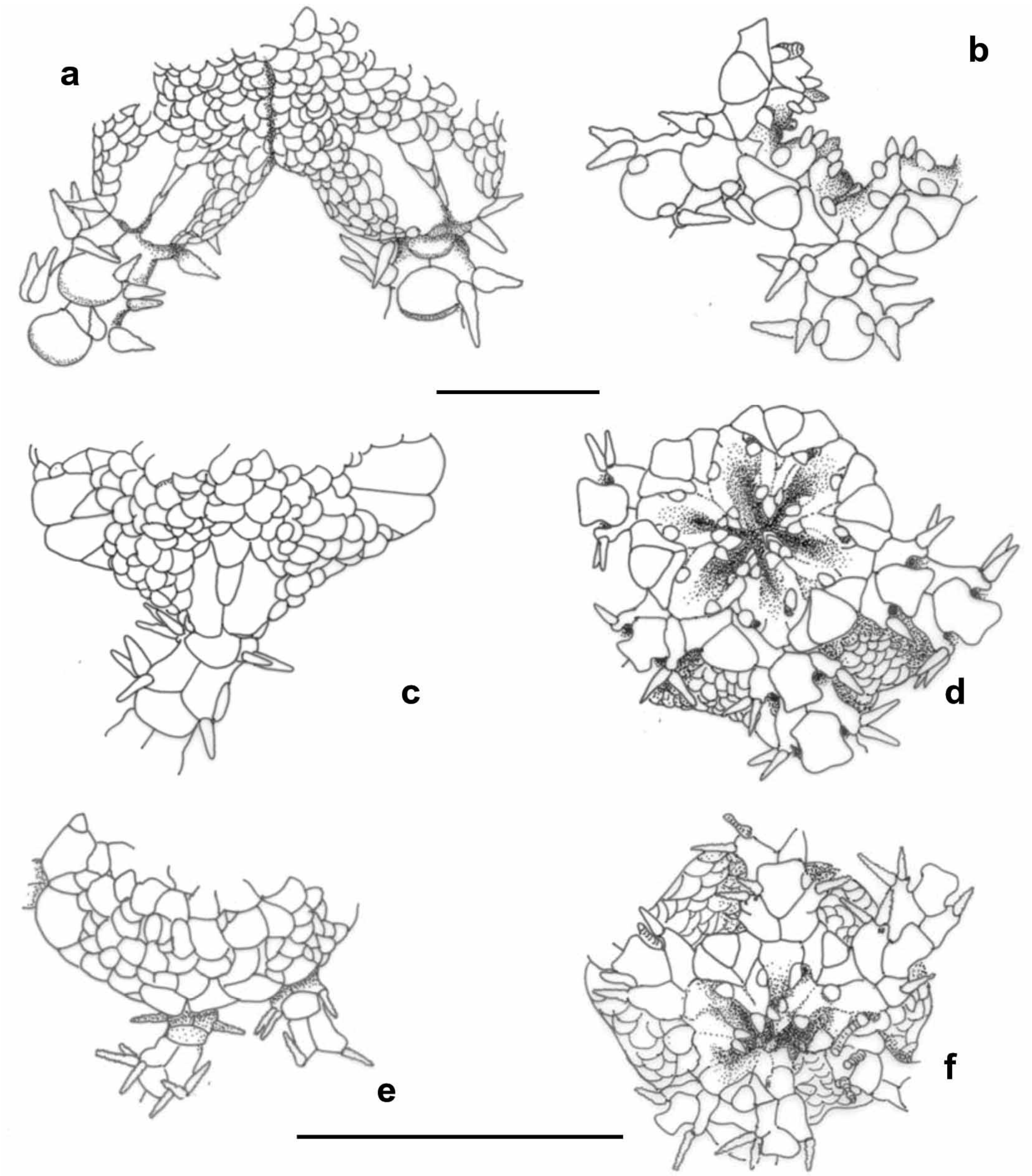


**FIGURE 10**. *Amphioplus hexabrachiatus*. Three specimens showing variation in both ventral and dorsal structures. a) and b) represent the largest diameter specimens with indented disk and well defined arrangement of oral papillae. c) and d) mid sized specimen. e) and f) small specimen showing distinct signs of fissiparity. Bar scales = 1mm.

## Family Ophiuridae Lyman, 1865

### Subfamily Ophiurinae Lyman, 1865

### *Ophiura (Dictenophiura) carnea* Lütken, 1858

**Material examined.** Mercator MV, TTR15, stn AT569, 1 ind. (DBUA 001093.01).

**Ecology and distribution.** *Ophiura carnea* is reported from the Mediterranean Sea and in the Atlantic from Norway south to the Cape Verde Islands at depths ranging 40 to 2857 m (Paterson 1985; Tyler & Fenaux, 1994). In the Gulf of Cadiz it was recorded at a single station located near an active seepage area in the crater of Mercator MV co-occurring with *Amphiura chiajei*, *Amphiura filiformis* and *Amphilepis ingolfiana*.

### Family Ophiolepididae Ljungman, 1867

### *Ophiomusium lymani* Wyville Thomson, 1873

**Material examined.** Porto MV, MSM01-03, stn 167, 1 ind. (DBUA 001094.01).

**Ecology and distribution.** *Ophiomusium lymani* is a bathyal and abyssal species with a wide distribution in the Atlantic and Indo-Pacific oceans (Alva & Vadon 1989). In the Atlantic it has been reported from SE Iceland south to Cap Blanc at depths ranging from 651 to 4829 m (Paterson 1985). The single record from the Gulf of Cadiz is within its known bathymetric range. Only one specimen was collected from Porto MV among the frenulate (Polychaeta: Siboglinidae) fields that cover the crater.

## Discussion

The Gulf of Cadiz is presently the most extensive cold seepage area known from European margins, spreading between 200 and 4000 m depths and including over 40 mud volcanoes with a variable seepage activity. To date, processed biological samples are available from 18 mud volcanoes, ophiuroids were recorded from 15 (Table 1). In addition ophiuroids have also been found at four sites from other bathyal environments such as cold-water coral thickets and fields of carbonate chimneys and crusts (Table 1).

From a total of 476 individuals from 60 samples thirteen different species were recorded, one of which, *Ophiopristis gadensis* **sp. nov.**, previously unknown. The mud volcano Mercator had the highest abundance (up to 256 ind.$m^{-2}$) and species richness; a total of six species, with five co-occurring in a single box-core sample (area=0.25$m^2$). Most samples yielded one to three ophiuroid species and, in general, the shallower sites (<1400 m), which were also the best sampled, showed the highest species richness and abundance (Fig. 11). Globally, low abundance of ophiuroids has been reported from cold seeps (Stöhr & Segonzac 2005) but numbers per sample or area sampled are usually not available. The deeper mud volcanoes in the Gulf of Cadiz are also the most active and the low number of species recorded at these sites may be following a putative global pattern of low ophiuroid diversity at cold seeps. However, rather abundant, large-sized ophiuroids were often recorded during deep-towed TV observations in Porto (3800 m—TTR16, TTR17, MSM01-03), Bonjardim (3100 m—MSM01-03, TTR17), Olenin (2610 m—TTR15) and Carlos Ribeiro mud volcanoes (2200 m—TTR11, TTR16, MSM01-03) (M.R. Cunha, pers. observation). The low abundance estimates in the present study may be a consequence of undersampling—only a few samples were collected at the deeper mud volcanoes—or a result of the type of sampling gear. Large ophiuroids tend to be dispersed, thus corers with limited sampling area are not a good collecting gear for these animals.

The ophiuroids from Gulf of Cadiz were recorded from the shallowest (Al Idrisi, 230 m) to the deepest (Porto, 3862 m) mud volcanoes in this region and extend the known bathymetric ranges of *Amphilepis ingolfiana*, *Amphiura* sp. A, *Amphiura grandisquama* and *Amphioplus hexabrachiatus*, to shallower depths and of *Amphipholis squamata* to greater depths (Figs. 7, 12).

Previous records on deep-sea ophiuroids from reducing environments compiled from the available literature (Table 3) referred to four families, of which three, Ophiacanthidae, Ophiuridae and Amphiuridae are represented at cold seeps. These three families are also found in the Gulf of Cadiz, but we can now add the occurrence of Ophiactidae, formerly recorded only at hydrothermal vents.

**TABLE 3.** Compilation of ophiuroid records from reducing environments. CS: cold seeps; V: hydrothermal vents; O: non-reducing environments. +: presence; (+): presence only in probably inactive adjacent habitats (e.g. cold water corals and carbonates in the vicinity of seeps).

| Species | O | | V | | CS | |
|---|---|---|---|---|---|---|
| Ophiacanthidae | | | | | | |
| *Ophiacantha aristata* Koehler 1896 | + | a) | | | (+) | b) |
| *Ophiacantha longispina* Stöhr & Segonzac, 2005 | | | | | (+) | c) |
| *Ophienigma spinilimbatum* Stöhr & Segonzac, 2005 | | | | | + | c) |
| *Ophiolamina eprae* Stöhr & Segonzac, 2006 | | | + | d) | | |
| *Ophiomitra spinea* Verrill, 1885 | + | c) | + | c) | | |
| *Ophioplinthaca chelys* (WyvilleThomson, 1877) | + | a) | | | + | c) |
| *Ophiopristis gadensis* **sp. nov.** | | | | | (+) | b) |
| *Ophiotreta valenciennesi* Koehler, 1896 | + | c) | + | c) | (+) | c) |
| Ophiactidae | | | | | | |
| *Ophiactis abyssicola* (M. Sars,1861) | + | a) | | | (+) | b) |
| *Ophiactis balli* (Thompson, 1840) | + | a) | | | + | b) |
| *Ophiactis tyleri* Stöhr & Segonzac, 2005 | + | c) | + | c) | | |
| Amphiuridae | | | | | | |
| *Amphioplus* sp | | | | | + | c) |
| *Amphioplus hexabrachiatus* Stöhr, 2003 | + | e) | | | + | b) |
| *Amphipholis squamata* (Delle Chiaje, 1828) | + | f) | | | + | b) |
| *Amphiura* sp. | | | | | + | g) |
| *Amphiura* sp. sensu Stöhr & Segonzac 2005 | | | | | + | b) c) |
| *Amphiura chiajei* Forbes, 1843 | + | a) | | | + | b) |
| *Amphiura filiformis* (O.F. Müller, 1776) | + | a) | | | + | b) |
| *Amphiura grandisquama* Lyman, 1869 | + | a) | | | (+) | b) |
| Amphilepididae | | | | | | |
| *Amphilepis ingolfiana* Mortensen, 1933 | + | a) | | | + | b) |
| Ophiuridae | | | | | | |
| *Ophiura carnea* Lütken, 1858 | + | a) | | | + | b) |
| *Ophiura clemens* (Koehler, 1904) | + | | + | c) | | |
| *Ophioctenella acies* Tyler et al., 1995 | | | + | c) | + | c) |
| *Ophiocten centobi* Paterson, Tyler & Gage, 1982 | + | c) | + | c) | | |
| *Ophiocten gracilis* (G.O. Sars, 1871) | + | | | | + | h) |
| *Ophiomusium anaelisae* Tommasi & Abreu, 1974 | | | | | (+) | i) |
| *Ophiomusium lymani* W. Thomson 1873 | + | a) f) | | | + | b) |
| *Ophiopleura borealis* Danielssen & Koren, 1877 | + | | | | + | h) |
| *Spinophiura jolliveti* Stöhr & Segonzac 2006 | | | + | d) | | |

a) Paterson 1985; b) this study; c) Stöhr & Segonzac 2005; d) Stöhr & Segonzac 2006; e) Stöhr 2003; f) Alva & Vadon 1989; g) Levin & Mendoza 2007; h) Gebruk *et al.* 2003; i) Sumida *et al.* 2004.

Only two species of the family Ophiacanthidae were found in the Gulf of Cadiz: the new species *Ophiopristis gadensis* **sp. nov.** and *Ophiacantha aristata*, both from a single record in dead scleractinean corals, at the flank of a mud volcano. Within the species of Ophiacantidae recorded from reducing environments, only *Ophienigma spinilimbatum*, found in association with tubeworms and mussels in four locations from Barbados and Gulf of Mexico (1947 to 3300 m), is probably endemic to cold seeps (Stöhr & Segonzac 2005); while *Ophiolamina eprae*, is endemic to vents in the East Pacific. A small number of individuals of *Ophiacantha longispina* Stöhr & Segonzac, 2005 have been collected from the type locality at a Barbados cold seep, and this species does not show a particular association with reduced environments (Stöhr & Segonzac 2005), *Ophiotreta valenciennesi rufescens* Koehler, 1896 was collected from scleractinean corals in the vicinity of a cold seep, and this is the only species known to occur at vent, non-vent and cold seep sites (Stöhr & Segonzac 2005). Three other bathyal species of this family are known to occur in reduced environments: *Ophiomitra spinea* Verrill, 1885, collected from vent and non vent sites on the MAR, and *Ophioplinthaca chelys* (Wyville Thomson, 1877) from the Barbados cold seeps (Stöhr & Segonzac 2005, 2006).

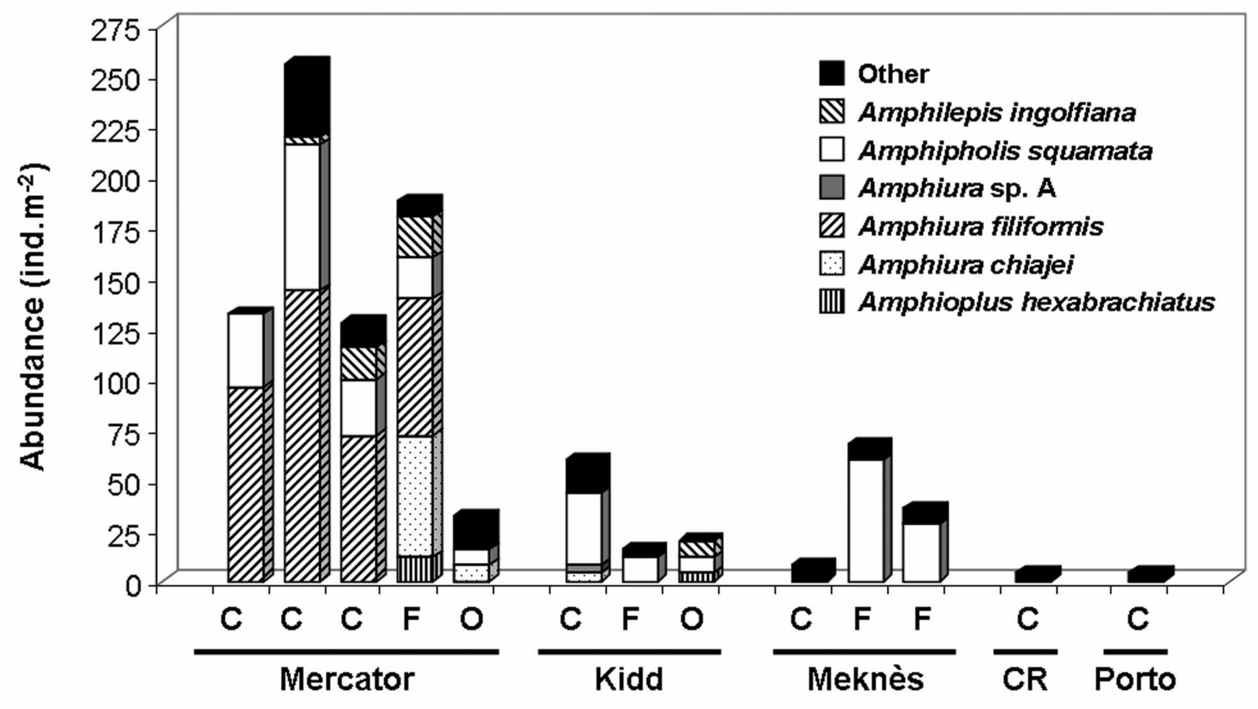


**FIGURE 11.** Abundance of Amphiuridae and other species estimated from box cores (A: 0.25m$^{-2}$) collected in Gulf of Cadiz mud volcanoes (shallowest at left to deepest at right). C: crater samples; F: flank samples; O: samples collected off the mud volcano; CR: Carlos Ribeiro MV.

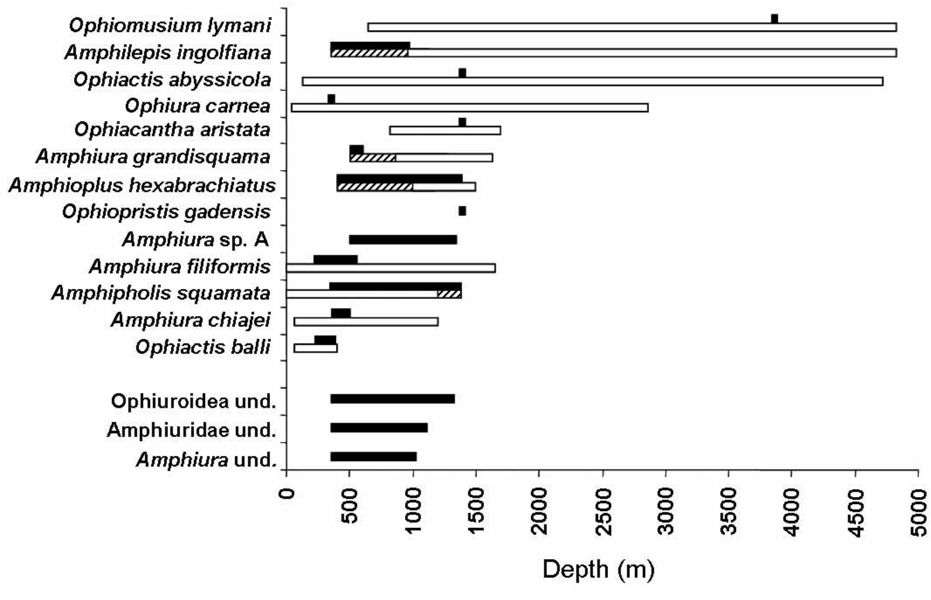


**FIGURE 12.** Bathymetric ranges of the ophiuroid species collected in the Gulf of Cadiz. Undetermined specimens (Ophiuroidea und., Amphiuridae und. and *Amphiura* und.) were mostly juveniles or damaged specimens. Black bars: depth ranges in the Gulf of Cadiz from the present study; White bars: previously known depth range; Striped bars: extended depth range by the records of the present study.

The family Ophiactidae was represented in the Gulf of Cadiz by only a few records of two *Ophiactis* species, *O. abyssicola* found in dead scleractinean corals and *O. balli* associated with carbonates and sandstones. *Ophiactis abyssicola* and *Ophiactis tyleri* Stöhr and Segonzac, 2005 were reported from non vent MAR sites with the latter also occurring at vents (Stöhr & Segonzac 2005).

Amphiuridae was the best represented family in the Gulf of Cadiz with six species (Fig. 7), of which four belong to the genus *Amphiura*. *Amphiura* sp. A occurred mostly in the craters of mud volcanoes, but it was also found associated with carbonate chimneys and crusts in areas with no evidence of present seepage activity. *Amphiura filiformis* has a wide distribution in the Gulf of Cadiz and was also found at mud volcanoes and in carbonate areas but never in co-occurrence with *Amphiura* sp. A. *Amphiura chiajei* and *A. grandisquama* were less common but also showed segregated distributions with the former associated only with soft sediments and the latter with hard substrates (carbonates and dead scleractinean corals) always off the crater. *Amphipholis squamata* was the most abundant and widespread ophiuroid in the Gulf of Cadiz, occurring in 70% of the samples and in all types of substrata. *Amphioplus hexabrachiatus* was also found on all types of substrata. At present, there are no records of Amphiuridae from vent habitats and the records from other cold seeps are restricted to the findings of an undetermined *Amphioplus* sp. from the Gulf of Mexico (Stöhr & Segonzac 2005) and *Amphiura* spp. from Barbados (Stöhr & Segonzac 2005) and Alaska (Levin & Mendoza 2007).

The distribution of *Amphiura* sp. A, known to occur both at Barbados (Stöhr & Segonzac 2005) and in the Gulf of Cadiz (this study) raises once more the question of population connectivity in cold seep species. Trans-Atlantic larval dispersal along the equatorial belt region has been suggested to explain the occurrence of genetically related *Bathymodiolus* populations at West Africa and the Barbados cold seeps (Cordes *et al.* 2007; Olu-LeRoy *et al.* 2007; Génio *et al*. 2008). In the case of ophiuroids only known from reducing environments but with wide Atlantic distributions, such as *Ophioctenella acies* (Stöhr & Segonzac 2005) and now *Amphiura* sp. A, further analyses, particularly using molecular techniques would provide useful data on whether these distributions are a single species or examples of cryptic speciation.

The families Ophiuridae and Ophiolepididae were poorly represented in the samples taken from Gulf of Cadiz. Only one species of each family (*Ophiura carnea* and *Ophiomusium lymani*, respectively*)* were collected although Ophiuridae appeared to be the dominant background megafauna, recorded during video observations at the deeper mud volcanoes (M.R. Cunha, pers. observation). Sumida *et al*. (2004) reported abundant specimens of *Ophiomusium anaelisae* Tommasi & Abreu, 1974, accounting for 72% of the fauna collected by dredging coral rubble and sediments from pockmarks in Santos Basin off SE Brazil, but the authors did not provide strong evidence of active seepage. Two other Ophiuridae species, *Ophiocten gracilis* (G.O. Sars, 1871) and *Ophiopleura borealis* Danielssen & Koren, 1877, dominated the background community at the Haakon Mosby MV (Gebruk *et al*. 2003). The same applies, for instance, to Carlos Ribeiro MV where ophiurids were abundant at the flanks and base of the mud volcano although they appeared more scattered in the crater (M.R. Cunha, pers. observation). Specimens in photographs taken with the ROV ISIS (NOCS) from this mud volcano were identified as large individuals of *Ophiomusium lymani.* Stöhr and Segonzac (2005, 2006) reported one Ophiuridae species from East Pacific vents, *Spinophiura jolliveti*, possibly endemic; from MAR three species have been reported: *Ophiura clemens* (Koehler, 1904) and *Ophiocten centobi* Paterson, Tyler and Gage, 1982, both found at vent and non- vent sites, and *Ophioctenella acies*. The distribution of *O. acies* ranges from 1626 to 3500 m depth and encompasses several vents from the MAR and cold seeps in the Western Atlantic; this species is considered by Stöhr and Segonzac (2005) as restricted to reducing environments.

## Conclusions

Compared to other known cold seep areas, the Gulf of Cadiz shows a highly diverse ophiuroid fauna which may be related to the high habitat heterogeneity (e.g. Cordes *et al*. 2010) and wide bathymetric range of the studied sites. A direct relationship to the chemosynthetic assemblages has not been established as the ophiuroids found in the mud volcanoes do not appear to have novel morphological adaptations and also occur in non-reducing environments. The data on deep-sea ophiuroids from reducing environments compiled from the available literature showed very different faunal compositions in hydrothermal vents and cold seeps. The Gulf of Cadiz ophiuroid fauna is especially distinct by the dominance of the family Amphiuridae (both in number of species and abundance) contrasting with the absence of records of this family from hydrothermal vents.

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## References

Akhmetzhanov, A.M., Ivanov, M.K., Kenyon, N.H. & Mazzini, A. (Eds) (2007) Deep water cold seeps, sedimentary environments and ecosystems of the Black and Tyrrhenian Seas and the Gulf of Cadiz. Preliminary results of investigations during the TTR-15 cruise of RV Professor Logachev, June–August, 2005. *IOC Technical Series*, 72, 99 pp + annexes

Akhmetzhanov, A.M., Kenyon, N.H., Ivanov, M.K., Westbrook, G. & Mazzini, A. (Eds) (2008) Deep water depositional systems and cold seeps of the Western Mediterranean, Gulf of Cadiz and Norwegian continental margins. Preliminary results of investigations during the TTR-16 cruise of RV Professor Logachev, June-August, 2005. *IOC Technical Series*, 76, 58 pp + annexes

Abildgaard, P.C. (1789) pp 66–67, pl 119, figs 1–4. In Müller, O.F. ed. Zoologica Danica seu analaium Daniae et Norvegiae. Haviniae 3.

Alva, V. & Vadon, C. (1989) Ophiuroids from the western coast of Africa (Namibia and Guinea-Bissau). *Scientia Marina*, 53 (4), 827–845.

Bartsch, I. (1987) Notes on Ophiuroidea (Echinodermata) from the northeastern Atlantic Ocean. I. Ophicanthidae. *Spixiana*, 14 (1), 95–112.

Bartsch, I. (1991) Schlangenterne (Ophiuroidea) in NO-Atlantik, im der ibero-marokkanish-mauretanischen Region. *Spixiana*, 10 (2), 115–130.

Cherbonnier, G. & Sibuet, M. (1972) Résultats scientifiques de la campagne Noratlante: Astérides et Ophiurides. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Serie 3. Zoologie*, 76 (102), 1333–1394.

Clark, H.L. (1909) Scientific results of the trawling expedition of H.M.C.S. Thetis. Echinodermata. *Memoirs of the Australian Museum*, 4, 519–564.

Cordes, E.E., Carney, S.L., Hourdez, S., Carney, R.S., Brooks, J.M. & Fisher, C.R. (2007) Cold seeps of the deep Gulf of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. *Deep-Sea Research I*, 54, 637–653.

Cordes, E., Cunha, M.R., Galeron, J., Mora, C., Olu-Le-Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A. & Levin, L. (2010) The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. *Marine Ecology*, 31(1), 51–65.

Cosel, R. Von (2002) A new species of bathymodioline mussel (Mollusca, Bivalvia, Mytilidae) from Mauritania (West Africa), with comment.s on the genus *Bathymodiolus* Kenk & Wilson, 1985. *Zoosystema*, 24 (2), 259–271.

Danielssen, D.C. & Koren, K. (1877) Fra den norske Nordhavsexpedition: Echinoderms. *Nyt Magazin for Naturvidenskaberne*, 23 (3), 45–83.

Delle Chiaje, S. (1828) Memoire sulla storia e notomia degli animali senza vertebre del regno di Napoli. *Napoli: Societa Tipographica*, 3, 1–232.

Forbes, E. (1843) On the Radiata of the eastern Mediterranean. Part 1. Ophiuridae. *Transactions of the Linnean Society of London*, 19, 143–153.

Gage, J.D. & Tyler, P.A. (1991) *Deep-Sea Biology. A Natural History of Organisms at the Deep-Sea Floor.* Cambridge University Press. 504 pp.

Gage, J.D., Pearson, M., Clark, A.M., Paterson, C.L.J. & Tyler, P.A. (1983) Echinoderms of the Rockall Through and adjacent areas. *Bulletin of the British Museum (Natural History) Zoology*, 45 (5), 263–308.

Gardner, J.M. (2001) Mud volcanoes revealed and sampled on the western Morrocan continental margin. *Geophysical Research Letters*, 28 (2), 339–342.

Gebruk, A.V., Krylova, E.M., Lein, A.Y., Vinogradov, G.M., Anderson, E., Pimenov, N.V., Cherkashev, G.A. & Crane, K. (2003) Methane seep community of the Hakon Mosby mud volcano (the Norwegian Sea): composition and trophic aspects. *Sarsia*, 88, 394–403.

Génio, L., Johnson, S.B., Vrijenhoek, R.C., Cunha, M.R., Tyler, P.A., Kiel, S. & Little, CT.S. (2008) New record of "*Bathymo-*

*diolus" mauritanicus* Cosel 2002 from the Gulf of cadiz (NE Atlantic) mud volcanoes. Journal of Shellfish Research, 27 (1), 53–61.

Hecker, B. (1985) Fauna from a cold sulfur-seep in the Gulf of Mexico: Comparison with hydrothermal vent communities and evolutionary implications. *Bulletin of the Biological Society of Washington*, 6, 465–473.

Hilário, A. & Cunha, M.R. (2008) On some frenulate species (Annelida: Polychaeta: Siboglinidae) from mud volcanoes in the Gulf of Cadiz (NE Atlantic). *Scientia Marina*, 72 (2), 361–371.

Hilário, A., Johnson S.B., Cunha, M.R. & Vrijenhoek R. (2010) High diversity of frenulates (Polychaeta: Siboglinidae) in the Gulf of Cadiz mud volcanoes: A DNA taxonomy analysis. *Deep-Sea Research I*, 57, 143–150.

Kenyon, NH, Ivanov, M.K., Akhmetzhanov, A.M. & Akhmanov, G.G. (Eds) (2003) Interdisciplinary Geoscience Research on the North East Atlantic Margin, Mediterranean Sea and Mid-Atlantic Ridge. Preliminary results of investigations during the TTR-12 cruise of RV Professor Logachev, June-August, 2002. *IOC Technical Series*, 67, 112 + Annexes.

Kenyon, N.H., Ivanov, M.K., Akhmetzhanov, A.M. & Kozlova, E.V. (Eds) (2006) Interdisciplinary Geoscience Studies of the Gulf of Cadiz and Western Mediterranean basins. Preliminary results of investigations during the TTR-14 cruise of RV Professor Logachev, July–September, 2004. *IOC Technical Series*, 70, 115 + Annexes.

Koehler, R. (1896) Resultats scientifiques de la compagne du Caudan dans le Golfe de Gascogne. Echinodermes. *Annales de l'Universite de Lyon*, 26, 33–122.

Koehler, R. (1897) Échinodermes recuellis par l'Investigator dans l'Océan Indien.I. Les ophiures des mers profonde Annales des Science naturelles, *Zoologie*, 8, 277–372.

Koehler, R. (1904) Ophiures de l'expedition du Siboga. 1e. Partie: Ophiures de mer profonde. *Siboga-Expeditie Monograph*, 45 (a), 1–167.

Koehler, R. (1905) Ophiures de l'expedition du Siboga. 2e. Partie: Ophiures littorales. *Siboga Expeditie Monograph*, 45 (b), 1–142.

Koehler, R. (1906) Description des Ophiures nouvelle recuillies par le Travailleur et Talisman pendant les compagnes 1880, 1881, 1882 et 1883. *Memoires de la Societe Zoologique de France*, 19, 5–34.

Levin, L.A. & Mendoza, G.F. (2007) Community structure and nutrition of deep methane-seep macrobenthos from the North Pacific (Aleutian) Margin and the Gulf of Mexico (Florida Escarpment). *Marine Ecology*, 28, 131–151.

Ljungman, A.V. (1867) Om nagra arter of Ophiurider. *Ofversigt of Kongl. Vetenskaps-Akademiens Förhandlinger* Stockholm, 1866, 153–166.

Ljungman, A.V. (1872) For teckning ovfer uti vestindien af Dr A. Goës samt under Korvetten Josephinas Expedition I Atlantiska Oceanen samlade Ophiurider. *Ofversigt of Kongl, Vetenskaps-Akademiens Förhandlinger* Stockholm, 1871, 615–658.

Lütken, C.F. (1858) Systematisk oversight over Gronlands echinodemer. *Videnskabelige Meddelelser fra Dansk Naturhistorik Forening I Kjobenhavn*, 1857 (1–7), 1–109.

Lyman, T. (1865) Ophiuroidea and Astrophytidae. *Illustrated catalogue of the Museum of Comparative Zoology*, 23 (2), 1–200.

Lyman, T. (1869) A preliminary report on the Ophiuroidea and Astrophytidae dredged in deep water between Cuba and Florida Reef. *Bulletin of the Museum of Comparative Zoology*, 1, 309–354.

Lyman, T. (1875) Zoological results of the Hassler expedition. 2. Ophiuridae and Astrophytidae. *Illustratd Catalogue of the Museum of Comparative Zoology*, Harvard university 8, 1–34.

Lyman, T. (1878) Ophiuroidea and Astrophytidae of the exploring voyage of the HMS Challenger I. *Bulletin of the Museum of Comparative Zoology*, 5 (7), 65–168.

Marques, V.M. (1980) Echinodermes recueillis pendant la mission "Hespérides 76" du N/O Jean Charcot. *Arquivos do Museu Bocage*, 7 (7), 95–l08.

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, 76–111.

Matsumoto, H. (1915) A new classification of the Ophiuroidea. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 67, 43–92.

Menzies, R.J., George, R.Y. & Rowe, G.T. (1973) Abyssal Environment and Ecology of the World Ocean. New York: John Wiley Intersience. 590pp.

Mortensen, T. (1933) Ophiuroidea. *Danish Ingolf Expedition*, 4 (8), 121 pp.

Müller, J. & Troschel, F.H. (1840) Ueber die Gattungen der Ophiuren. Arch Naturgesch, 6 (1), 327–330.

Müller, O.F. (1776) *Zoologiae danicae prodromus*. Havniae. 282 pp.

Murakami, S. (1942) Ophiurans of Izu, Japan. Journal of the Department of Agriculture, *Kyûshû Imperial University* 7, 1–36.

O'Hara, T.D. & Stöhr, S. (2006) Deep water Ophiuroidea (Echinodermata) of New Caledonia: Ophiacanthidae and Hemieuryalidae. In Richer de Forge, B & Justine, J.-L. (eds), *Tropical Deep Sea Benthos*, 24, 33–141.

Olu-Le Roy, K., Cosel, R.V., Hourdez, S., Carney, S.L. & Jolivet, D. (2007) Amphi-Atlantic cold seep Bathymodiolus species complexes across the equatorial belt. *Deep Sea Research I*, 54, 1890–1911.

Paterson, G.L.J. (1985) The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History) Zoology*, 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.

Pfannkuche, O. (2006) RV Maria S. Merian Cruise Nº1 Leg 3 - PreliminaryReport. IFM-Geomar, Liebniz Instituteof Marine

Sciences, Kiel, Germany. 19 pp.
Perrier, E. (1891) *Traite de Zoologie* pp.854–861. Librarie F. Savy, F. I. Paris.
Picton, B.E. & Morrow, C.C. (2007) *Encyclopedia of Marine Life of Britain and Ireland*. Available from: http://www.habitas.org.uk/marinelife/species.asp?item=ZB2680 (20/11/2008)
Pinheiro, L.M., Ivanov, M.K., Sautkin, A., Akhmanov, G., Magalhães, V.H., Volonskaya, A., Monteiro, J.H., Somoza, L., Gardner, J., Hamouni, N. & Cunha, M.R. (2003) Mud volcanism in the Gulf of Cadiz: results from the TTR-10 cruise. *Marine Geology*, 195, 131–151.
Rodrigues, C.F, Oliver, P.G. & Cunha, M.R. (2008) Thyasiroidea (Mollusca: Bivalvia) from the mud volcanoes of the Gulf of Cadiz (NE Atlantic). *Zootaxa*, 1752, 41–56.
Sahling, H., Galkin, S.V., Salyuk, A., Greinert, J., Foerstel, H., Piepenburg, D. & Suess, E. (2003) Depth-related structure and ecological significance of cold-seep communities – a case study from the Sea of Okhotsk. *Deep-sea Research I*, 50, 1391–1409.
Sars, G.O. (1871) Nye Echinodermer fra den norske kyst. *Förhandlinger I Videnskabssel skabet I Kristiania*, 1871, 1–31.
Sars, M. (1861) *Oversigt of Norges Echinoderm*. Christiania. 160 pp.
Sibuet, M. & Olu, K. (1998) Biogeographic, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research II - Topical studies in Oceanography*, 45, 517–567.
Smith, A.B., Paterson, G.L.J. & Lafay, B. (1995) Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. *Zoological Journal of the Linnean Society*, 114, 213–243.
Stöhr, S. (2003) A new fissiparous amphiurid brittlestar (Echinodermata: Ophiuroidea) from southwest of Iceland. *Sarsia*, 88, 373–378.
Stöhr, S. (2004) *Ophiuraster patersoni* Litvinova, 1998 is the postlarva of *Ophiomyxa serpentaria* Lyman, 1883 (Echinodermata, Ophiuroidea). *Zoosystema*, 26 (1), 95–105.
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. & Segonzac, M. (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*, 85, 383–402.
Stöhr, S. & Segonzac, M, (2006) Two new genera and species of Ophiuroid (Echinodermata) from hydrothermal vents in the East Pacific. *Species Diversity*, 11, 7–32.
Stöhr, S. & O´Hara, T. (2007) *World Ophiuroidea database*. Available from http://www.marinespecies.org/ophiuroidea. (10/12/2008)
Sumida, P.Y.G., Yoshinaga, M.Y., Madureira, L.A.S.-P. & Hovland, M. (2004) Seabed pockmarks associated with deepwater corals off SE Brazilian continental slope, Santos Basin. *Marine Geology*, 207, 159–167.
Thompson, C. Wyville (1873) *The Depths of the Sea*. Macmillan & Co. London, 527 pp.
Thomson, C. Wyville (1877) *The voyage of the Challenger. The Atlantic*. A preliminary account of the general results of the exploring voyage of H.M.S. Challenger, 1, 424 pp.
Thompson, W. (1840) Contributions towards a knowledge of the Mollusca Nudibranchia and Mollusca Tunicata of Ireland with a description of some apparently new species of invertebrates. *Annals and Magazine of Natural History*, 5, 84–102.
Tommasi, L.R. & Abreu, J. (1974) Equinodermes do Brasil. IV. Sobre seis espécies novas de Ophiuroidea da região ao largo da Ilha Grande (RJ). *Boletim do Instituto Oceanográfico*, São Paulo, 23, 17–32.
Tyler, P.A. & Fenaux, L. (1994) Cherchez la femme – is the upper bathyal ophiuroid *Ophiura carnea* the adult of *Ophoipluteus compressus.* Sarsia, 79, 45–52.
Tyler, P.A., Paterson, G.L.J., Sibuet, M., Guille, A., Murton, 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, U.K.* 75, 977–986.
Van Dover, C.L., Aharon, P., Bernhard, J.M., Caylor, E., Doerries, M., Flickinger, W., Gilhoolym, W., Goffredi, S.K., Knick, K.E., Macko, S.A., Rapoport. S., Raulfs, E.C., Ruppel, C., Salerno, J.L., Seitz, R.D., Sen Gupta, B.K., Shank, T., Turnipseed, M. & Vrijenhoek, R. (2003) Blake Ridge methane seeps: characterization of a soft sediment, chemosynthetically based ecosystem. *Deep Sea Research I*, 50, 281–300.
Van Rensbergen, P., Depreiter, D., Pannemans, B., Moerkerke, G., Van Rooij, D., Marsset, B., Akhmanov, G., Blinova, V., Ivanov, M., Rachidi, M., Magalhaes, V.H, Pinheiro. L., Cunha, M. & Henriet, J.P. (2005) The El Arraiche mud volcano field at the Moroccan Atlantic slope, Gulf of Cadiz. *Marine Geology*, 219, 1–17.
Vanreusel, A., Andersen, A.C., Boetius, A., Connelly, D., Cunha, M.R., Decker, C., Hilario, A., Kormas, K.A. Maignien, L., Olu, K., Pachiadaki, M., Ritt, B., Rodrigues, C., Sarrazin, J., Tyler, P., Van Gaever, S. & Vanneste, H.(2009) Biodiversity of cold seep ecosystems along the European margins. *Oceanography*, 22, 110–127.
Verrill, A.E. (1885) Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England Nº11. *American Journal of Science*, 29, 149–157.
Verrill, A.E. (1899) Report on the Ophiuroidea collected by the Bahama expedition in 1893. *American Journal of Science*, 28, 213–220.
Vopel, K., Thistle, D. & Rosenberg, R. (2003) Effect of the Brittle Star Amphiura filiformis (Amphiuridae, Echinodermata) on Oxygen Flux into the Sediment. *Limnology and Oceanography*, 48(5), 2034–2045.