MARINE PLANT COMMUNITIES OF UPWELLING AREAS WITHIN THE ARABIAN SEA

A taxonomic, ecological and biogeographic case study on the marine flora of the Socotra Archipelago (Yemen) and Masirah Island (Oman)

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MARIENE PLANTENGEMEENSCHAPPEN IN OPWELLINGSGEBIEDEN VAN DE ARABISCHE ZEE

Een taxonomische, ecologische en biogeografische casestudy naar de mariene flora van de Socotra Archipel (Jemen) en het eiland Masirah (Oman)

Tom SCHILS

Proefschrift ingediend tot het behalen van de graad van Doctor in de Wetenschappen (Biologie)

Promotor: Prof. Dr E. Coppejans

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Unrooted Tree 'Merci'

Hoewel het hier geenszins een proefschrift met een fylogenetische inslag betreft, is deze dankbetuiging (the tree 'merci') gericht aan een diverse groep van clades, allen van onmiskenbaar belang in hun specifieke bijdrage tot het volbrengen van dit proefschrift ('unrooted' dus).

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'El Sea' of 'Sweetlips', neen niet de titel van een goedkope B-film uit verjaarde videotheekrekken, maar de magistrale levensgezel die de gehele trip van kleur voorzag. Else, dank je voor de vele leuke momenten en de weelde aan goede zorgen die een apart dankwoord verdienen, op een andere plaats, onder een andere vorm. The greatest!

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Study area defined

Arabian Sea

The Arabian Sea is situated in the northwestern Indian Ocean and comprises the Gulf of Aden, the Arabian Sea *sensu stricto* (from the southern Arabian Peninsula down to the Horn of Africa and the southern tip of India), the Gulf of Oman and the Persian Gulf (Fig. 1). In this study we focus on the upwelling areas off the coasts of the southern Arabian Peninsula, using the restricted definition of the Arabian Sea *sensu* Wilson (2000): the Arabian Peninsula and the Gulf of Oman define the Arabian Sea to the north, the African continent and the Gulf of Aden to the west, South-West Asia to the east, and the southern boundary is generally considered to be the 8°N parallel. The following geographical localities are used for a clear-cut delimitation of the Arabian Sea *sensu stricto* (hereafter Arabian Sea; Wilson 2000): to the west between Ra’s Asir (11°50’N, 51°16.9’E; Somalia) and Ra’s Fartak (15°35’N, 52°13.8’E; Yemen); to the north between Ra’s Al Hadd (22°30’N, 59°48’E; Oman) and Ra’s Al Fasteh (25°04’N, 61°23’E; Iran); and from the Iran-Pakistan border (25°12’N, 61°36’E) in the east to the southern limit (8°N). In total seven nations border the Arabian Sea: Somalia, Yemen, Oman, Iran, Pakistan, India and the Maldives.

Both investigated island groups, Socotra and Masirah, are located in the Arabian Sea *s.s.* Since the Cenozoic Era (65 Ma BP-present) Arabia drifted away from Africa, giving rise to the Red Sea and the Gulf of Aden (Fig. 2). As a result, the Socotra Archipelago and Masirah Island are located on two distinct tectonic plates. Both Islands are of a unique geological composition. Mies & Printzen (1997) stressed the presence of a granite core (Haghier Mountains) on Socotra Island, which has been above sea level since the Cretaceous, and the island has been referred to as one of the most isolated landmasses since that period (Kossmat 1907). This long period of isolation is reflected in the pronounced level of endemism of the terrestrial biota on Socotra (about one third of the terrestrial plants from the archipelago is considered to be endemic, Wranik 2002) and has important biogeographic consequences (Mies 1998; Wranik 1998, 2002). Masirah, on the other hand, forms a distinct structural element within the Arabian Plate, the Masirah Ophiolite Uplift. Ophiolites provide the best exposure in the world to study the oceanic lithosphere.

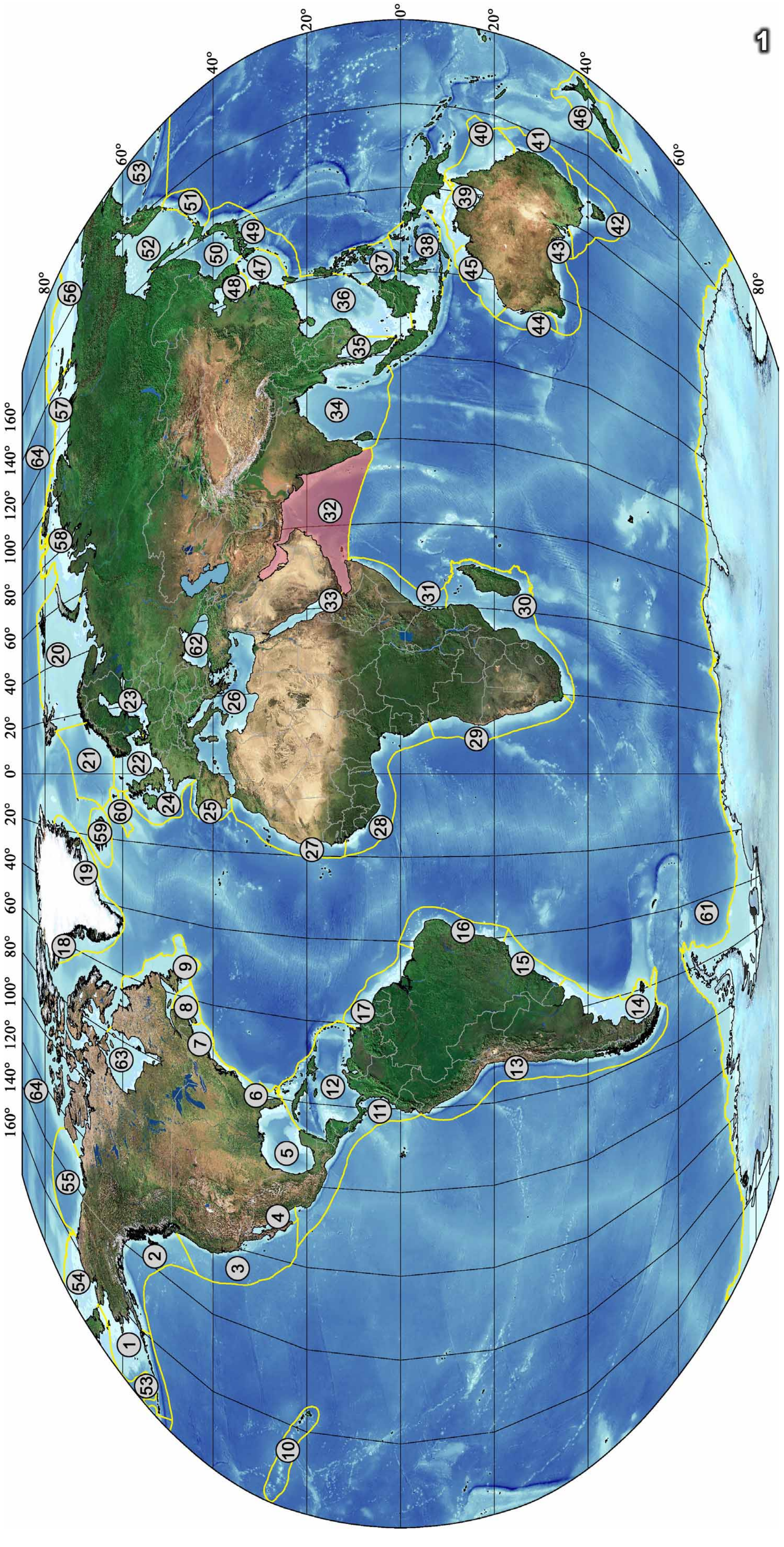
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Fig. 1. World map showing the large marine ecosystems of the world, demarcated by yellow lines and indicated with numbers. The Arabian Sea (No 32) is colored in red. Numbers correspond with: 1, East Bering Sea; 2, Gulf of Alaska; 3, California Current; 4, Gulf of California; 5, Gulf of Mexico; 6, Southeast U.S. Continental Shelf; 7, Northeast U.S. Continental Shelf; 8, Scotian Shelf; 9, Newfoundland-Labrador Shelf; 10, Insular Pacific-Hawaiian; 11, Pacific Central-American Coastal; 12, Caribbean Sea; 13, Humboldt Current; 14, Patagonian Shelf; 15, South Brazil Shelf; 16, East Brazil Shelf; 17, North Brazil Shelf; 18, West Greenland Shelf; 19, East Greenland Shelf; 20, Barents Sea; 21, Norwegian Shelf; 22, North Sea; 23, Baltic Sea; 24, Celtic-Biscay Shelf; 25, Iberian Coastal; 26, Mediterranean Sea; 27, Canary Current; 28, Guinea Current; 29, Benguela Current; 30, Agulhas Current; 31, Somali Coastal Current; 32, Arabian Sea; 33, Red Sea; 34, Bay of Bengal; 35, Gulf of Thailand; 36, South China Sea; 37, Sulu-Celebes Sea; 38, Indonesian Sea; 39, North Australian Shelf; 40, Northeast Australian Shelf/Great Barrier Reef; 41, East-Central Australian Shelf; 42, Southeast Australian Shelf; 43, Southwest Australian Shelf; 44, West-Central Australian Shelf; 45, Northwest Australian Shelf; 46, New Zealand Shelf; 47, East China Sea; 48, Yellow Sea; 49, Kuroshio Current; 50, Sea of Japan; 51, Oyashio Current; 52, Sea of Okhotsk; 53, West Bering Sea; 54, Chukchi Sea; 55, Beaufort Sea; 56, East Siberian Sea; 57, Laptev Sea; 58, Kara Sea; 59, Iceland Shelf; 60, Faroe Plateau; 61, Antarctica; 62, Black Sea; 63, Hudson Bay; 64, Arctic Ocean. After LME (2002).

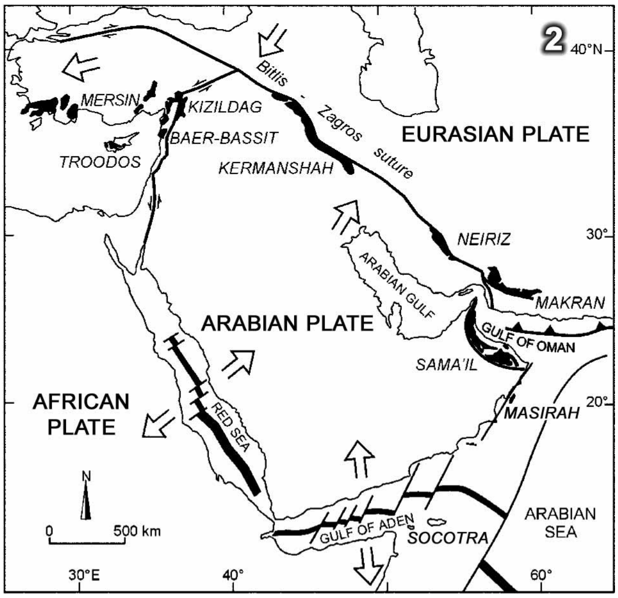

Fig. 2. Arabia detached from Africa and soon began to collide with Eurasia in mid-Tertiary time, when most ophiolite complexes emplaced at the close of the Cretaceous onto its northern margin were incorporated in the Biltis-Zagros suture zone. Only the Sama'il and Masirah ophiolite belts of southeast Arabia escaped later continental-collision events and still preserve most of their original obduction-related features. After Garzanti *et al.* (2002).

Socotra Archipelago

The Socotra Archipelago (12.47°N, 53.87°E; Fig. 2) is positioned in the southwestern part of the Arabian Sea, proximate to the Gulf of Aden. Despite being only 100 km from Somalia, Socotra politically belongs to Yemen. The archipelago comprises four islands: the main island Socotra; Abd al-Kuri; Samha and Darsa, the latter two smaller islands are also known as "The Brothers". The archipelago sits on the Carlsberg Ridge (from the archipelago, running southeast) and shallow seas connect the islands, whereas a deep trench separates the archipelago from mainland Africa. The islands have been relatively little affected by human activities due to the reduced accessibility caused by the southwest monsoon, the harsh climate, the sparse fertile grounds and stringent traveling policies. In addition to the long isolation, traditional community rules limit the exploitation to sustainable levels and make Socotra comparatively untouched.

Socotra Island is the largest Arabian island (Al-Hity 1998) and measures approximately 120 by 40 km, covering an area of about 3600 km^2. The geological composition consists of a basement complex of igneous and metamorphic rock from the Precambrian, which are overlain by sedimentary, mainly limestone and sandstone. Topographically, the island consists of three main zones: (i) the alluvial coastal plains (e.g. the Nojid Plain), (ii) a limestone plateau, with an altitude range from 300-700 m, which covers most of the island, and (iii) the Haghier mountains rising to an elevation of 1519 m. Abd al-Kuri and "The Brothers" are smaller and subject to more extreme conditions due to the absence or limited availability of fresh water, less topographical variation and fewer sheltered sites. The second largest island, Abd al-Kuri (36 by 6 km), is positioned about half way in between Socotra and Somalia. Samha and Darsa are both flat topped limestone plateaus with sheer sides, the former being inhabited by a small human population and the latter uninhabited but sustaining a large rat population (Al-Saghier & Porter 1998; Wranik 1998). Additionally, a few isolated rocky stacks, Kal Farun (literally "balls of the Farao"), Sabuniya and Hertha, occur within the archipelago, their remoteness being beneficial for certain species, e.g. breeding seabirds (Al-Saghier *et al.* 2000), and particular biotic communities that are protected from natural and anthropogenic threats: e.g. coral bleaching due to the elevated temperatures of coastal waters, fishing.

Masirah Island

Masirah Island is located in the northern part of the Arabian Sea (20.42°N, 58.79°E; Fig. 2), the island is about 65 km long and 15 km wide, covering an area of 1095 km^2. Politically, the island belongs to the Sultanate of Oman. The island has a peculiar geological history, being an excellent geological field laboratory due to the distinct obducted ophiolite sequences that were part of a Proto-Indian Ocean basin in the Late Jurassic (Marquer *et al.* 1998; Garzanti *et al.* 2002). The ophiolite covers most of Masirah Island and presumably forms the bedrock of the Masirah Channel.

The Masirah Channel separates the island from Barr al-Hikman on the Arabian Peninsula. Barr al-Hikman and Masirah Island constitute an important biotic haven on the southern Arabian shores. Together they total about 240 km^2 of exposed mudflats, which are important for the passage and wintering of water birds and for nesting and feeding of sea turtles (Gallagher *et al.* 2002). Masirah Island supports the largest loggerhead turtle (*Caretta caretta* Linnaeus) nesting grounds in the world, which mainly depend on seagrass for nourishment (Pilcher 2002). These extensive intertidal mudflats occur along the central and northern part of Masirah's west coast. Seagrass beds are especially well developed around Shaghaf Island off Masirah's west coast. This small island also harbours the only mangrove stands, *Avicennia marina* (Forsskål) Vierhapper, for Masirah island and its surrounding islets. Fringing and isolated coral communities also occur in the Masirah Channel. Off Barr al-Hikman, a remarkably large, and so-called monospecific reef (perhaps the largest monospecific coral stand known on Earth, Paulay & Meyer 2001) has developed almost exclusively made up of a cabbage coral (*Montipora* sp.). The phenomenon of coral stands that are largely dominated by one species also occurs in other parts of the world where coral development is hindered by harsh environmental conditions, e.g. large temperature variation, high sedimentation, high salinities, etc. The east coast of Masirah is exposed, consisting of sandy beaches and rocky outcrops. The terrestrial vegetation of Masirah Island is dominated by small shrubs such as *Arthrocnemum, Limonium* and *Suaeda* (Gallagher *et al.* 2002).

The mean annual rainfall is 110 mm, but is erratic and, since 1956, has varied from 0 mm to over four times the mean figure. The mean air temperature in July is 33°C and that of January is 20°C. The mean tidal variation (MHHW to MLLW) is about 1.5 m (Gallagher *et al.* 2002).

Oceanography and marine ecology of the Arabian Sea

The oceanography of the Arabian Sea is driven by the alternation of two opposing monsoon winds: the southwest monsoon during summer (June–September; hereafter SW monsoon) and the northeast monsoon during winter (November–February; hereafter NE monsoon). The periodic reversals in the wind drive corresponding inversions in the currents of the upper ocean. The strong wind velocities during the SW monsoon in summer (Fig. 3), initiate the Somali Current with surface velocities of 3.7 m s^{-1} (Düing *et al.* 1980). The Somali Current has perhaps the most dramatic seasonal variation of any current in the world oceans. Its volume transport is comparable to that of the Gulf Stream but changes direction with monsoon winds: towards the poles during the SW monsoon and towards the equator during the NE monsoon (Subrahmanyam 1998). In summer, the Somali Current spins off south of Socotra and is continued along the southern Arabian shores to the mouth of the Gulf of Oman (Figs 4, 5; Currie 1992). South of Socotra, the Somali Current originates a northern eddy, the "Great Whirl" (Warren *et al.* 1966), and contiguous with the latter another anticyclonic circulation evolves east of Socotra, the "Socotra Eddy" (Bruce & Beatty 1985; Currie 1992). The Somali Current, its derived eddies and the current along the southern Arabian shores generate wind-induced upwelling of cold nutrient-rich water (Figs 4-6). The currents arise from winds that blow over the sea parallel to the coasts. Seawater, however, is not pushed directly in front of the wind, but moves at about 45° to the right of the wind's motion in the northern hemisphere (to the left in the southern hemisphere) due to the Coriolis force, an effect caused by the rotation of the earth. Further down in the water column, the direction of flow continues to be deflected rightward (or leftward), until ultimately a three-dimensional spiral is formed vertically in the water. The net transport of water, i.e. Ekman transport (Figs 6, 7), is at an angle of roughly 90° to the direction of the wind. The removal of these surface waters, to a depth of a few hundred meters, off the coast is replaced with cold and nutrient-rich waters from the deep. During the NE monsoon in winter, some areas in the eastern Arabian Sea are subject to upwelling (Fig. 4). During the SW monsoon high nutrient levels, being 3-5 times greater than those during the NE monsoon, are recorded for the upwelling waters of Oman (Barrat *et al.* 1986): 5-20 mg NO_3 m^{-3}; 1.5-2.5 mg PO_4 m^{-3}. Phytoplankton is the first to take advantage of the nutrients brought up by upwelling and initiate a quick increase in productivity, reflected by high chlorophyll a concentrations (5-20 mg m^{-3}, Savidge *et al.* 1988). In a second phase, zooplankton feeds on the abundant phytoplankton, the former falling prey to larger plankton and small fish. Whales, large fish and sea birds feed upon the smaller predators, resulting in very rich fishing grounds. The NE monsoon has received less scientific attention as it is less energetic than the SW monsoon, but the near surface circulation is still dominated by the wind system during this period (Subrahmanyam 1998). During the NE monsoon the current flows southwards along the Somali coast all the way to the equator. This southward cross-equatorial flow, however, is very shallow relative to the deep northward flow during the SW monsoon (Schott 1986). In the transition months, offshore Ekman transport is lacking, as the winds are not strong enough (Subrahmanyam 1998).

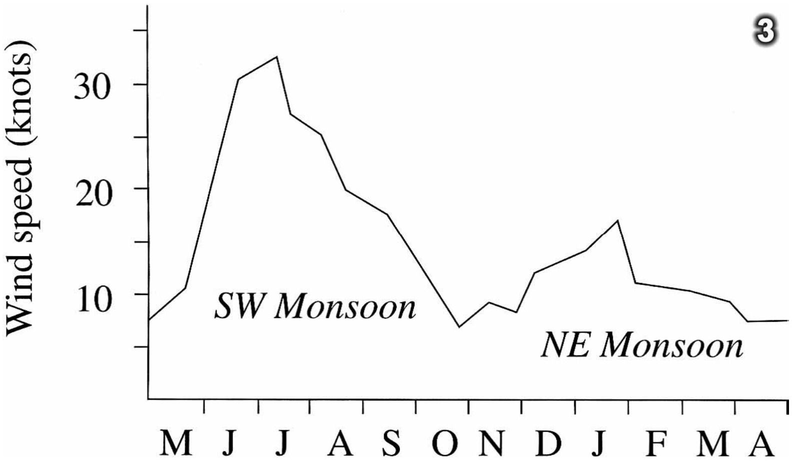

Fig. 3. Monsoonal wind speed in the northwestern Indian Ocean (15°N, 60°E). Wind speed data are monthly averages of daily measurements from 1986-1990. One knot = 0.51 m s^{-1}. From Mies & Beyhl (1998).

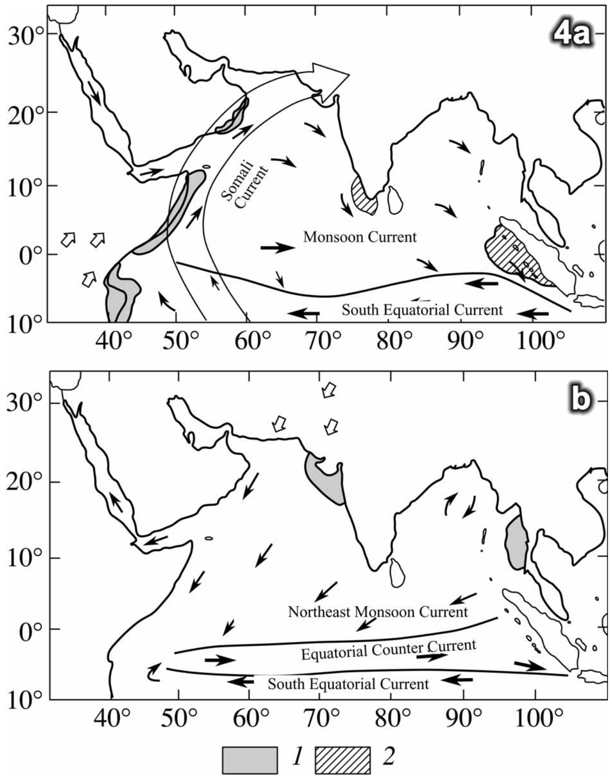

Fig. 4. Surface water circulation in the northern part of the Indian Ocean **(a)** in July (maximum of the SW monsoon) and **(b)** in February (maximum of the NE monsoon). Open arrows show the direction of monsoons; filled arrows show the direction of surface currents. *1*, the zones of seasonal upwelling; *2*, the zones of episodic upwelling. The major open arrow represents the direction of the latent heat transfer from the southern subtropical Indian Ocean maximum to the Asian continent with the Findlater jet flow. From Ivanova (2002).

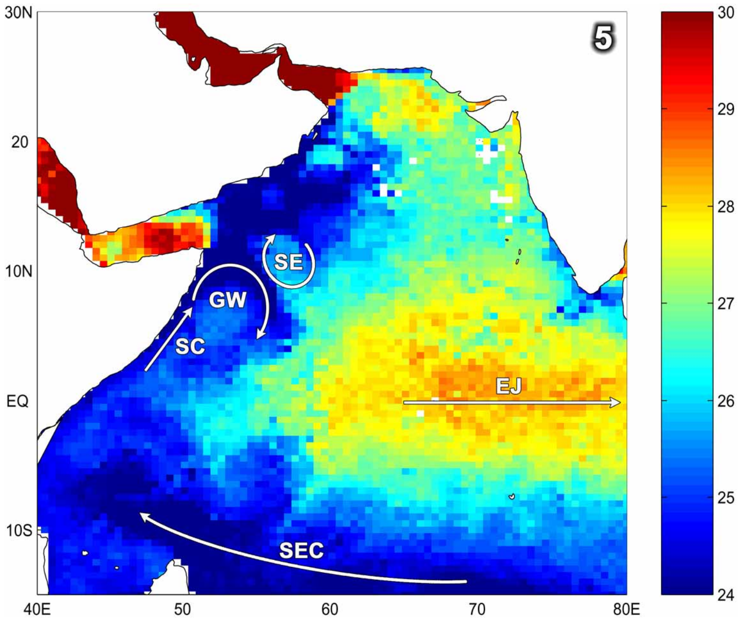

Fig. 5. Sea surface temperatures (°C) of Arabian Sea waters in August 1993 (SW monsoon). The Equatorial Jet (EJ), Great Whirl (GW), Somali Current (SC), Socotra Eddy (SE) and the South Equatorial Current (SEC) are indicated. After Subrahmanyam (1998) and Kantha *et al.* (2002).

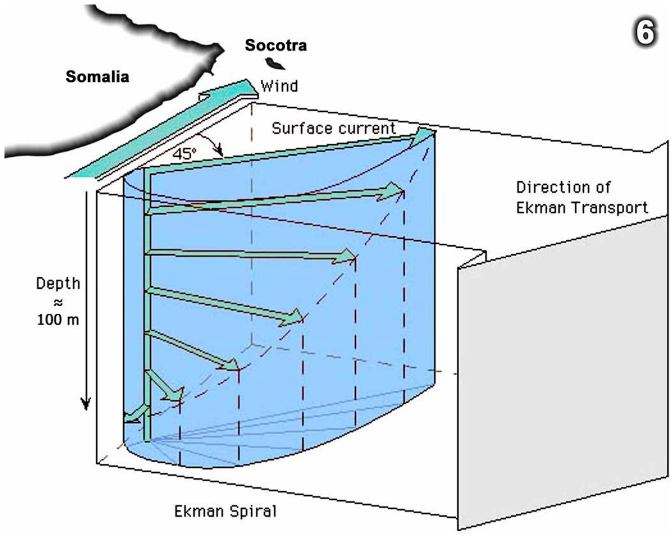

Fig. 6. Wind blowing parallel to the shore in the northern hemisphere during the SW monsoon, inducing a surface current (Somali Current) and upwelling by means of surface water transport through the Ekman spiral. After Thurman (1996).

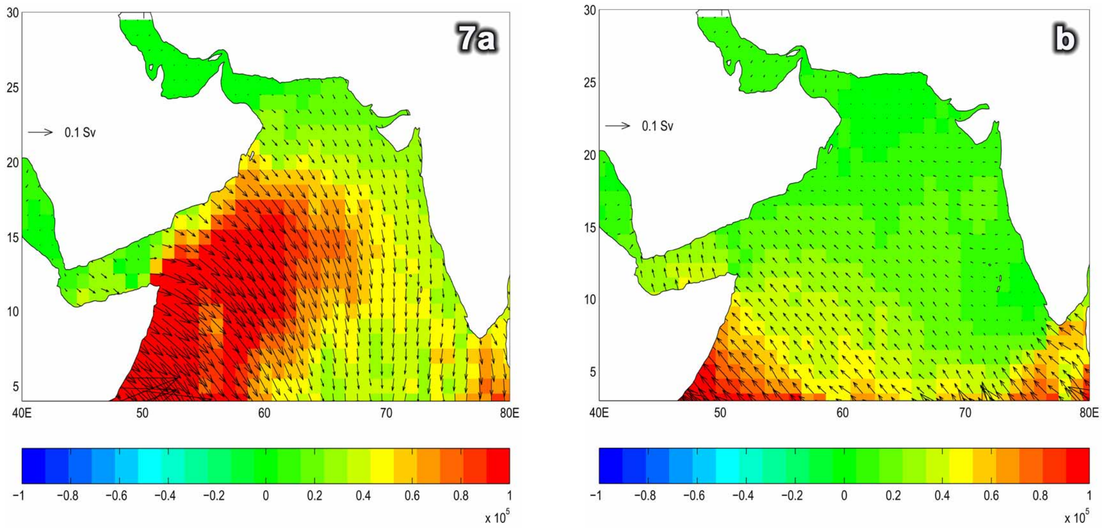

Fig. 7. Ekman transport (Sv) in the Arabian Sea during **(a)** the peak SW monsoon (July 1993) and **(b)** the peak NE monsoon (January 1993). From Subrahmanyam (1998).

The upwelling phenomenon creates extreme marine conditions in the Arabian Sea. Coastal sea surface temperatures (SST) vary by an average of 10°C (Wilson 2000). Savidge *et al.* (1990) even recorded a minimum SST of 15.9°C during the SW monsoon of 1989 in the Arabian Sea, whereas Salm (1993) reports on a maximum SST of 39°C in 1990 for the Gulf of Oman. The deeper waters of the Arabian Sea, below 100 m deep, are also extreme in having critically low levels of dissolved oxygen. Arabian Sea water is higher in salinity than the surrounding Indian Ocean due to surface evaporation and intensified by intrusions of higher salinity water from the Persian Gulf at 300 m deep and from the Red Sea at 800 m deep (Wyrtki 1973). Vertical mixing of these layers results in a thick layer of high salinity water, which extends to depths of 2000 m. The isolation of this water together with a high pelagic productivity creates a large mass of water with a very low oxygen concentration from 200 to 2000 m deep. The O_2 values of this layer in the Arabian Sea (0.2-1 ml l^{-1}) are 2-4 times lower in comparison to other Indian Ocean waters at this depth (Sheppard *et al.* 1992). Following upwelling this suboxic layer reaches the surface with widespread mortality among fish as a result. The effects were perceived during the field trip to Masirah Island (November 1999, the aftermath of the SW monsoon), where great numbers of triggerfish (Balistidae), apparently particularly prone to low oxygen concentrations, washed ashore.

The investigated islands, Socotra and Masirah, are both subjected to intense upwelling during the SW monsoon. Both harbour a similar diversity in marine habitats, but differ in their geographical position within the Arabian Sea and the corresponding upwelling areas.

Socotra Archipelago

The upwelling at the Socotra Archipelago results from the Somali Current, which flows northwards in summer and initiates the “Great Whirl” and the “Socotra Eddy” (Fig. 5; Currie 1992; Bruce & Beatty 1985). The Great Whirl mainly affects the southern coasts of the Socotra Archipelago and the Socotra Eddy influences the east coast of the main island. At the end of the SW monsoon (October) the Great Whirl decays into a series of complex current patterns around the archipelago.

Masirah Island

Masirah Island is located in the upwelling area off the southern Arabian Peninsula. The southwestern winds blow parallel to the shores, initiating strong upwelling along the coasts of Hadramout (Yemen) and Dhofar (Oman) to Ra’s al Hadd (Oman). The east coast of Masirah is the exposed shore subjected to upwelling. The west coast, from Masirah Channel to Barr al-Hikman, is on the leeward side of the strong surface currents during the SW monsoon. As a result this protected channel shows monsoonal currents of less than half a knot (Gallagher *et al.* 2002).

Biogeography and paleoceanography of the Arabian Sea

The biota associated with the lower water temperatures during upwelling periods, generally occur in the temperate waters at higher latitudes, a phenomenon that has been termed the “pseudo-high latitude effect” (Sheppard *et al.* 1992; Kemp 1998b). The Arabian Sea is characterized by a seasonal peak in productivity and a patchy distribution of different biocoenoses consisting of scarce coral reefs, scattered coral communities and macroalgal dominated subtidal communities. The Arabian Sea is generally regarded as part of the larger Arabian region, being a biogeographic sub-region of the Indian Ocean and comprising the Red Sea, Gulf of Aden, Arabian Sea, Gulf of Oman and Persian Gulf (Sheppard *et al.* 1992). These authors note that a subdivision in sub-provinces might be useful for certain groups of fish, but they concluded that it cannot be justified for the marine plants. Sheppard *et al.* (1992), however, largely based their opinion on restricted information, i.e. the seagrasses, mangroves and some seaweeds of the Red Sea.

The biodiversity within the upwelling areas of the Arabian Sea has gradually been revealed over the past two decades. The location of these upwelling areas between the Red Sea, the Persian Gulf and the "parent" Indian Ocean (Sheppard *et al.* 1992) makes the Arabian Sea an area of sympatry for biota from these water bodies (Kemp 1998b). During the Late Pleistocene Glaciation (17 Ka BP, the peak of the last glaciation) sea level was about 130 m below present (Hopley 1982), which dried out the Persian Gulf and potentially the Red Sea, or turning the latter hypersaline. About 15 Ka BP global surface temperatures increased markedly, resulting in the Holocene transgression during which macroscopic marine life recruited both seas via the northern Indian Ocean. During the early part of the transgression and about 3-4 Ka years thereafter, the intensity of the monsoons and the Arabian Sea upwelling were considerably reduced. On the contrary, 9±2 Ka BP upwelling was considerably stronger than today and from that time on the upwelling intensity gradually declined to its present, moderate state. So, the recruitment of biota into the Red Sea and the Persian Gulf most likely happened in the late Pleistocene-early Holocene. In the mid Holocene, the intensified upwelling and its larger geographical extent probably caused a barrier to tropical biota, resulting in vicariance speciation in the pockets of (sub)tropical waters. During this time favorable habitats for temperate marine biota expanded, e.g. luxuriant algal communities (Sheppard *et al.* 1992).

Dependent on the author and the investigated group of organisms, the region is said to comprise a large number of widespread species and few endemics (Wilson 2002), whereas others characterize the Hadramout (Yemen) and Dhofar (Oman) coasts of the Arabian Peninsula as centers of endemism (Randall & Hoover 1995; Randall 1996). In this context, Paulay (1999) notes that the coral communities of the Arabian Sea are isolated from reefs in the surrounding seas by unfavourable habitats, i.e. intense upwelling toward the west and soft bottoms and major river discharge (Indus) toward the east. This isolation is conducive to allopatric speciation. Furthermore, the coral reefs of Oman are located at the entrance to the ancient European Tethys, and because of their isolation could conceivably be home to relict taxa from the ancient tethyan biota. This factor may contribute toward the occurrence of relic endemics. Detailed taxonomic work on other Arabian Sea biota has also lead to new insights as the extension of known distribution ranges of organisms (e.g. Kemp 1998b); the occurrence of disjunctly distributed species (e.g. the coral and algal species from Oman that also occur in Hawaii and Japan, respectively; Coles 1995; Wynne 2000); the discovery of new (endemic) species (e.g. Wynne 1999a); the significant increase of the regional marine biodiversity (e.g. the rich fauna of decapod Crustaceae, Apel 2000; the high diversity and high degree of endemism of echinoderms for the Arabian Sea, Price 1982); and taxonomic updates (e.g. the intensely observed, so-called "*Montipora foliosa*" reefs seem to represent a new endemic species, Paulay & Meyer 2001).

Sample sites defined: marine habitats

“Marine plant communities of upwelling areas within the Arabian Sea” implies that the studied flora grows in marine influenced habitats. Adlittoral and intertidal habitats were generally devoid of algal communities because of the limited splash zone during the NE monsoon, the high evaporation rate, the solar irradiation and wind stress that limit algal growth severely. Due to the relatively low tidal range of the area, intertidal biotopes were largely limited to areas with a gentle slope. The few extensive intertidal habitats include the upper zone of mudflats and certain seagrass beds, composed of macroalgal assemblages, seagrasses and rarely mangroves. Besides these biotopes of fine sediment, sample efforts were focused on hard substrata, i.e. rocks and coral deposits (sometimes covered by a layer of fine sediment), as most benthic organisms (algae) grow best on these surfaces. The subtidal habitats harbour the most luxuriant biotic life and different biotopes can readily be discerned: coral reefs, coral communities, seagrass beds, macroalgal communities and soft sediment biotopes. An additional semi-marine biotope includes the blue holes, i.e. terrestrial pits that are interconnected with the sea by means of caves, characterized by a layer of fresh water on top of the saline water mass. They contain a specialized flora (e.g. *Ruppia maritima* Linnaeus), restricted to the photic top layer, which can cope with salinity fluctuations according to the specific zonation belt. A characteristic macroalgal zonation pattern of intertidal and exposed rocky shores of the Arabian Sea is presented in Fig. 8. Besides intertidal pools, the intertidal of less exposed shores is relatively barren with few macroalgae (e.g. *Codium arabicum* Kützing).

Socotra Archipelago

Whereas the south coast of Socotra Island is greatly affected by the upwelling phenomenon, the northern shores are more protected, especially certain embayments near the center of the north coast. Dunes and sandy beaches characterize the north coast, and well-developed coral communities thrive well at certain sheltered sites. Due to their small size, the outer islands, Abd al-Kuri and The Brothers, are less protected from the extreme upwelling conditions. F. Leliaert (Ghent University) was the first phycologist to participate in a marine survey in the framework of the United Nations Development Programme and Global Environment Facility (hereafter UNDP/GEF) project entitled “Conservation and sustainable use of biodiversity of Socotra Archipelago”. He collected 463 algal samples from 63 sites in the period from 13 January-20 February 1999 (Leliaert 2000). These specimens were very helpful to acquire an insight in the macroalgal flora of the main island. Since complete lists of the investigated sites and quantitative (relevé) data could not be assessed due to time restrictions, the ecological analysis of this thesis was confined to the material collected during the two subsequent studies. The second field trip to the Socotra Archipelago took place from 26 March-7 May 2000. A map of sample sites where detailed species inventories were recorded is presented in Fig. 1c of *chapter 7*.

Masirah Island

In 1999, the Ardoukoba Association (France) organized the scientific campaign “Oman 99” to Masirah Island. Eleven marine scientists (zoologists, botanists and biochemists) participated in a joint effort to characterize the biocoenoses of the different ecosystems and to search for bioactive molecules. The base camp was installed at the southern tip of the island where the upwelling coasts border the upwelling sheltered shores, being an excellent location to sample the contrasting biotopes by small boats. The impact of the upwelling phenomenon in the area was striking in many ways: suspension feeders were extremely abundant, the population density of most invertebrates was very high, corals displayed extensive bioerosion, and consequently reef construction was extremely limited (Paulay 1999). Sampling of macroalgae was undertaken between 2-30 November 1999. Fig. 1b (*chapter 7*) shows a map of sample sites with detailed species inventories.

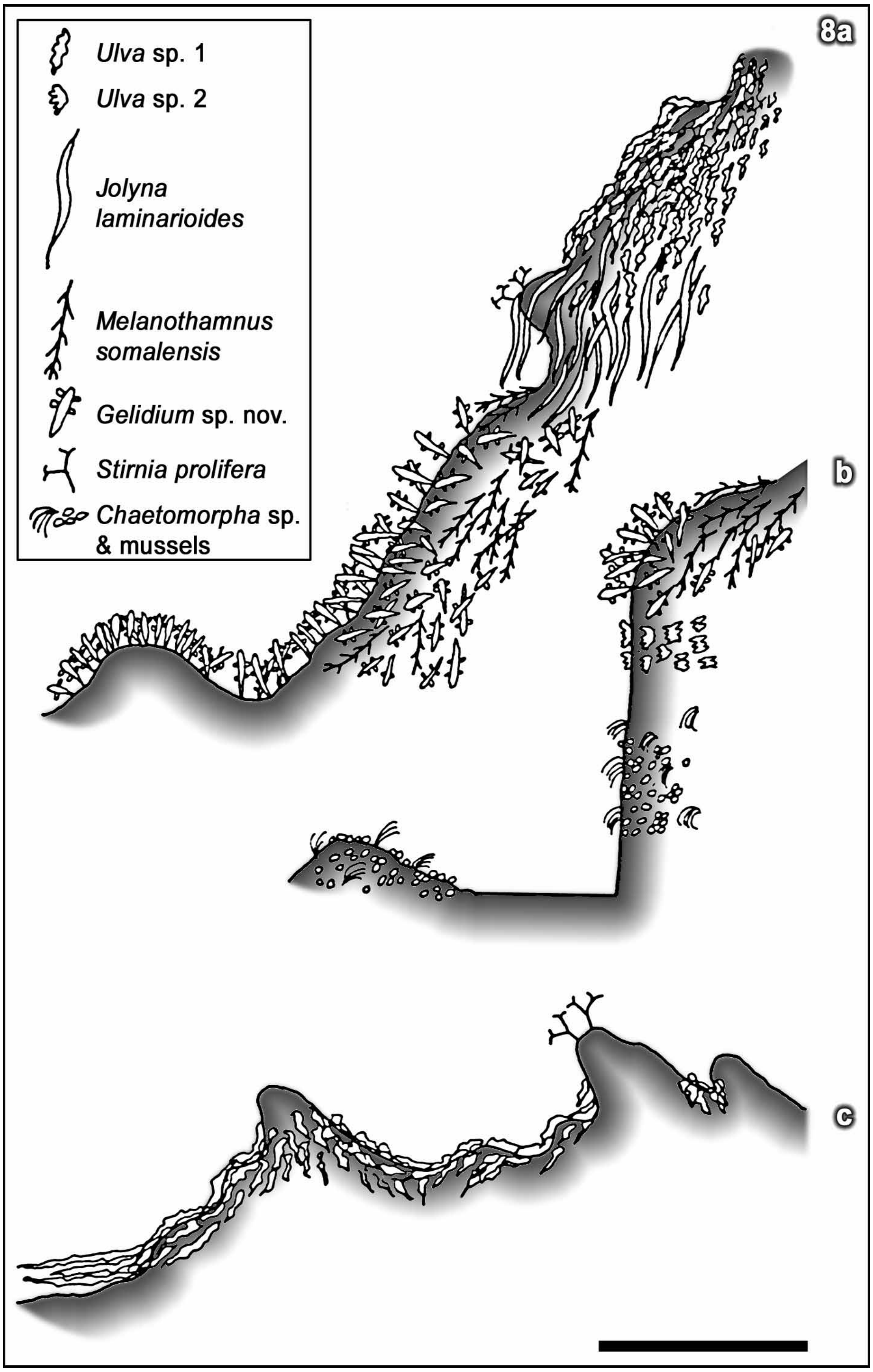

Fig. 8. A diagrammatic representation of the dominant species in the intertidal on the exposed rocky shores of southern Oman. **(a)** General, steeply sloping rock of the type found at Mughsayl, Raysut and Sadha. **(b)** Vertical rock face at Mughsayl. **(c)** Semi-exposed broken rock at Mirbat. Scale bar = approx. 1 m. After Barratt *et al.* (1984).

Ecological and biogeographic units: macroalgal and seagrass species

In analyzing the biodiversity, the similarities and the biogeography of the sampling sites from the different marine plant communities, there was a need for a basic unit. In broad ecological studies, the commonly used entity, and arguably the only biologically meaningful level (Sheppard *et al.* 1992), is the basic taxonomic unit "species". More refined identifications of different growth forms from a specific species (ecological or regional variants: varieties, ecomorphs, subspecies, etc.) are only used when the continuum in morphological variety fits into categories (e.g. *Caulerpa* polymorphism). These identifications below species level can be useful as certain types of morphology are related to the governing environmental parameters, which also shape marine biocoenoses. Although species concepts differ between ecologists, molecular biologists and philosophers (Hull 1997), the term "species" generally refers to an exclusive combination of morphological and anatomical traits that can be observed in the field or the laboratory. Recent molecular and culture studies, however, have shown that the existence of cryptic diversity (molecularly diverged but not pronounced so in anatomical or morphological traits, e.g. Stiller & Waaland 1993) and species complexes (a multitude of hitherto recognized species that are not supported by molecular phylogenies, e.g. Zuccarello & West 2002) might be more common than currently accepted. Consequently, biogeographic studies might indicate links with (distant) areas based on traditional identification techniques, while the respective species in fact have already molecularly or reproductively speciated into different taxa. By using a multitude of traits (e.g. inclusion of the study of post-fertilization events directly linked to the reproductive process, *chapters 2-5*), and focusing primarily on the Rhodophyta (pronounced and distinct reproductive features between species in comparison to the Phaeophyta and Chlorophyta), these problems have been partly overcome.

Macroalgae

Macroalgae or seaweeds are the common names for a polyphyletic group of photosynthetic, eukaryotic and multicellular organisms belonging to three phyla classified by their photosynthetic pigmentation, *viz.* the Rhodophyta (red algae), Phaeophyta (brown algae) and Chlorophyta (green algae). Structurally, macroalgae have been grouped in the Thallophyta: plants without a differentiation into roots, stem and leaves, and lacking the conducting tissues phloem and xylem. In contrast to the omnipresent and likewise "artificial" (non-monophyletic) group of algae (all organisms containing chlorophyll a, except the land plants), macroalgae mainly occur in marine habitats. Macroalgae are found in all seas and in various forms: filamentous, crustaceous, epiphytes and large macrophytes. Currently, about 7300 species of marine macroalgae or seaweeds are known (Smith 2002). Most seaweeds are highly adapted to a specific littoral zone (adlittoral, intertidal, subtidal fringe, subtidal) and specific environmental conditions (epilithic, epipelic, epipsammic, epiphytic, temperature, salinity, etc.) for optimal growth or population structure. Most well-developed and luxuriant algal communities are confined to hard substratum, i.e. rocky shores or solid anthropogenic constructions. The subtidal fringe and the subtidal are generally the zones that harbour the most diverse macroalgal communities (largely attributable to rhodophytes). Because of the limited tidal range in the Arabian Sea and the fact that exposed substrata are subjected to intense irradiation and wind stress (see *Sample sites defined*), this study aims at comparing the well-developed and species-rich plant communities of subtidal habitats.

Seagrasses

Besides macroalgae, a few flowering plants have readapted to a marine environment, viz. mangroves, tidal marsh plants and seagrasses. Of these flowering plants, the seagrasses are the sole ones that have colonized subtidal marine habitats. A few other flowering plants like *Ruppia* spp., however, can also thrive in brackish waters (e.g. blue holes). Seagrasses are Magnoliophyta that can constitute biologically important seagrass beds, intertidal or subtidal meadows, serving as (i) a specific biotope for certain coastal biota (e.g. dugong and seahorses), (ii) a nursing ground for various marine animals (e.g. juvenile fish and invertebrates) and (iii) an important phorophyte for epiphytic biota. Seagrasses occur on all continents except Antarctica, with the highest diversity in tropical seas (7 genera versus 5 genera in temperate waters, Phillips & Meñez 1988).

History of phycological research in the Arabian Sea

The first phycologist recognizing the peculiar biogeographic affinities of the Arabian Sea is Børgesen (1934a). This compilation of species records from Karachi (Pakistan), Okha and Dwarka (northwestern India) was based on his previous publications, new samples from Karachi and herbarium collections from the Royal Botanical Gardens, Kew. Upon listing the species and analyzing their distributions, Børgesen (1934a) concludes: “But I am of opinion that the discovery of several species so far only known from such far-off regions as Australia, Japan, Cape and even the northern Atlantic in the northern part of the Arabian Sea is of considerable plant-geographical interest”. Upwelling occurs in this part of the northern Arabian Sea during the NE monsoon (Fig. 4), differing in seasonality from the upwelling areas around Socotra and Masirah. Despite the seasonal differences, characteristic elements of the Arabian Sea flora are found throughout these upwelling locations [e.g. *Melanothamnus somalensis* Bornet & Falkenberg and *Nizamuddinia zanardinii* (Schiffner) P.C. Silva]. Besides the macroalgal studies on the eastern coasts (India, Iran and Pakistan) of the Arabian Sea (Anand 1940, 1943; Børgesen 1930, 1931, 1932a, b, 1933 a, b, 1934 a, b, 1935, 1937 a, b, 1938, 1939), phycological research in the western Arabian Sea was scarce during the mid twentieth century (Newton 1953) and renewed interest in the region arose in the two last decades of the century. Since the 1970’s, Pakistani and Indian researchers remained very productive in describing their macroalgal flora, its ecology and phycochemical aspects (e.g. Nizamuddin 1964; Nizamuddin & Gessner 1970; Nizamuddin & Begum 1973; Shameel 1978; Moazzam & Shameel 1985; Aliya & Shameel 1999; Hayee-Memon & Shameel 1999). In the western Arabian Sea, a continuation of the three basic taxonomic papers on Yemeni macroalgae (Banaimoon 1986, 1988; Wynne & Banaimoon 1990) resulted in the first comprehensive ecological study on intertidal macroalgal assemblages of an upwelling area within the Arabian Sea (Hadramout coast of Yemen, Ormond & Banaimoon 1994). The study reports on a marked seasonal pattern in algal growth and a clear zonation from the upper to the lower intertidal. These findings have been republished in a different format as Banaimoon (1998). At the same time an ecological research team, headed by L. Barratt (Barratt *et al.* 1984, 1986), investigated the upwelling regions of the Arabian Sea where they consulted the phycologists S. Hiscock, M. Nizamuddin and M.J. Wynne. Especially the cooperation with Wynne proved to be fruitful and resulted in several taxonomic publications on Omani algae (Wynne & Jupp 1998; Wynne 1999a, b, 2000, 2001; Wynne & Leliaert 2001). The resulting plethora of new records and the description of many new species and genera indicated that the area was largely understudied, and that it harbours a rich and unique flora within the Indian Ocean. Wynne (2000) stressed the biogeographic links of the Omani flora with Japan, as proposed by Børgesen (1934a), by recording eight disjunctly distributed taxa between both regions.

Socotra Archipelago

The first botanical explorations to the archipelago included small macroalgal collections. In an investigation of the Natural History of Socotra, sponsored by the British Association for the advancement of Science, Prof. I.B. Balfour led an expedition to Socotra. His team visited the island from 11 February-30 March 1880. Many zoological, geological and botanical collections were made and resulted in the description of over 200 species and 20 genera new to science. Few algae were collected and these were investigated by Dickie (1888), resulting in 16 algal species records for Socotra Island. The second published inventory of algae of the Socotra Archipelago was compiled by Holmes (1903), resulting from a joint British Museum and Liverpool Museum expedition to Socotra and Abd al-Kuri from 3 December 1897-23 February 1898. This expedition was jointly led by H. Forbes and W.R. Ogilvie-Grant and did not add a significant number of new records or species to the flora of Socotra. Holmes (1903) reported 13 macroalgae for Abd al-Kuri. After these intense research efforts at the end of the 19th century it was over 50 years until the island was again visited by a botanist (Miller 2002). In the meantime, occasionally enthusiast collectors on ships that frequented Socotra sampled algae. No publications, however, on any of such sparse collections appeared. In the late 1990's, Kemp (1998a) is the first biologist to comment on the peculiar aspects of the algal flora of the archipelago. Being an ichthyologist, the extensive stands of the large fucoid *Nizamuddinia zanardinii* (Schiffner) P.C. Silva drew his attention. He reported on the distribution of this alga, a monotypic genus endemic to the Arabian Sea, within the archipelago and noticed differences in the number of productivity peaks and a temporal shift in the growth cycles between mainland Arabia and Socotra. His research was part of the preparatory phase of a large project funded by UNDP/GEF. Subsequently, Leliaert (2000) was the first phycologist studying the marine benthic macroalgae of Socotra. In the framework of the UNDP/GEF project, he visited the island in January-February 1999 and estimated a number of 260 macroalgal species for the archipelago. Furthermore, Wynne & Leliaert (2001) reported on a striking green alga, *Pedobesia simplex* (Kützing) M.J. Wynne & Leliaert, new to the Indian Ocean. The subsequent field trip from the Phycology Research Group of Ghent University focused on ecological observations by means of quadrat sampling, being the subject of this thesis. The preliminary results of the latter field trip were presented in Schils (2002).

Masirah Island

As previously mentioned, a revival of phycological research in Oman during the late nineties started with a project of the Darwin Initiative led by L. Barratt. M.J. Wynne has been the main phycologist in charge of taxonomic issues of her team. This resulted in several taxonomic publications on the Omani flora, including a number of new species (see *History of phycological research in the Arabian Sea*). The seagrass beds off Masirah Island were included in a study on the distribution, abundance and species composition of Omani seagrass stands (Jupp *et al.* 1996). Wynne & Jupp (1998) published a general overview of macroalgae new to Oman in respect to the Indian Ocean Catalogue of Silva *et al.* (1996), the latter not incorporating a publication on the algae of the Gulf of Oman (Cordero 1993).

About half (35 out of 71) of the newly recorded species in Wynne & Jupp (1998) were collected from the vicinity of Masirah (Masirah Island and the Barr al-Hikman Peninsula) increasing the floristic knowledge of the area substantially. The subsequent communications on the marine flora of the area consist of two progress reports of the "Oman 99" field trip (Schils 1999, 2001).

OBJECTIVES

This study attempts to characterize the marine flora of various localities within the Arabian Sea by means of species inventories and relevé data. Initially, this project started off as a case study of the marine plant communities of the Socotra Archipelago and included an investigation on the seasonality of the biocoenoses. The latter aspect was hampered as the fieldwork of the UNDP/GEF project ended after the visit in 2001. Since then, SCUBA facilities were absent and the availability of motorized transport around the archipelago was limited. As a result, the seasonality study was aborted, but the preceding invitation of the Ardoukoba Association (France) to participate in a field trip to Masirah Island (Oman) compensated for this by creating an opportunity for an elaborate biogeographic study within upwelling areas of the Arabian Sea. The sequel to this "Oman 99" mission to Masirah was scheduled for September 2001. The goal of the "Oman 2001" field trip was to investigate the marine biota of the fjords of the Musandam Peninsula (Oman), being a biogeographic and biological haven for organisms dependent on hard substrata. Musandam is located in the Strait of Hormuz and connects the Persian Gulf with the Gulf of Oman, both principally consisting of soft sediments. Due to the unpredictable events following 11 September 2001 and the resulting safety precautions for traveling in the Middle East in the months thereafter, the envisioned trip was cancelled and the flora of this area could not be included in the biogeographic analyses. The observations made during both field trips, however, gave a clear insight in the seasonal appearance of macroalgae during these periods. Communication of these observations with colleagues was helpful in interpreting seasonal variations in species occurrences and biomass (e.g. seasonality of the fucoid *Nizamuddinia zanardinii*, S.C. Wilson pers. comm.).

Documenting survey data

Prior to the ecological fieldwork, the collection of Leliaert (2000) was studied. These specimens were categorized and included in the recent Arabian Sea collections. Two databases (MS Access) were developed for this purpose: "Phycobase" and "SMM relevés". The former contains (i) the collection information of the specimens, (ii) an assemblage of the majority of presently known macroalgal genera and their current systematic position, (iii) tables and queries of most of the reported macroalgal taxa for nations of the Indian Ocean. This structure allows for the identification of new species and generic records, the execution of exhaustive biogeographic comparisons, the generation of systematic listings of genera and species, etc. Additionally, hyperlinks to web pages are included, in which the diagnosis of the taxon is given and compared to literature descriptions of closely related taxa. These dynamic web pages are continuously updated as identifications proceed. The web structure is based on current systematics and contains links to higher and lower systematical levels, macro- and microscopic pictures, and personal comments of taxonomists. Currently, 1603 specimens have been entered in Phycobase, of which 1052 are samples from the Socotra Archipelago and 551 samples from Masirah Island.

The second database, "SMM relevés", collates the vegetation relevé data. The forms show for each sampling site the description, the environmental parameters and the vegetation relevés as sub-forms. The combined view of all quadrats per station is helpful in having an overview to make sound adaptations (refined species identifications) to the original field observations. All data are gathered in 2 tables, facilitating simple and thorough processing by means of various cross tables (simple statistics, extracting matrices as input for multivariate analyses, etc.).

Taxonomy of the Rhodophyta (see *chapters 2-5*)

Dependent on the scale, the purpose and the resources, organisms are identified up to a certain taxonomic level in order to use these taxa as the basic entities in ecological or biogeographic studies. Generally, "species" are chosen as the basic units for these studies (see *Ecological and biogeographic units: macroalgal and seagrass species*). The identification of species (taxonomy) is therefore an elemental part in applied biological studies. The investigated sites of this study were all marine and focused on subtidal habitats (limited intertidal diversity), where the rhodophytes accounted for the highest diversity of the macroalgal phyla. Moreover, the red algae belonging to the Florideophyceae are the most diverse macroalgal class, expressed in various distribution and biogeographic patterns on a global and local scale.

The life cycle of the Florideophyceae is trigenetic, with complex and diverse reproductive structures and fertilization events in comparison to the Bangio-, Phaeo- and Chlorophyceae. Fig. 9 shows the life cycle of a Florideophyceae based on *Reticulocaulis* species from the Arabian Sea and completed with the tetrasporophyte and young gametophyte stage of the related *Naccaria wiggii* (Turner) Endlicher (Boillot & L'Hardy-Halos 1975). Detailed studies of the reproductive structures and post-fertilization events showed the diagnostic value of these traits in respect to species identification and systematics (*chapters 2, 3*). These characters can also be used in an evolutionary context, serving as character states on phylogenetic trees based on molecular data. Taxonomic studies on Arabian Sea algae hence contribute to the knowledge of post-fertilization processes in red algae, especially the gelatinous red algae of which the gametophytes seem to develop seasonally according to the changes in day length and other environmental conditions.

Conservation

Historically, the number of marine reserves and the research efforts on marine conservation lag behind the terrestrial reserves (Sloan 2002). Ecological analyses (*chapters 6, 7*) are generally used to give insight into the distribution of species and their interactions on a local scale. Species-rich and diverse communities are generally considered to be important areas for conservation, as ecological interactions and community structure are believed to be best preserved. The occurrence of rare, threatened and endemic species add value to the proposition of sites for conservation. On a larger scale, the degree of endemism and the distribution patterns of the occurring species are indicative of the uniqueness and global importance of marine biocoenoses. Formerly, macroalgae have been rather neglected in surveys for conservation issues (Walker & Kendrick 1998), which primarily concentrated on (attractive) marine animals. Recently, scientific recommendations on marine protected areas

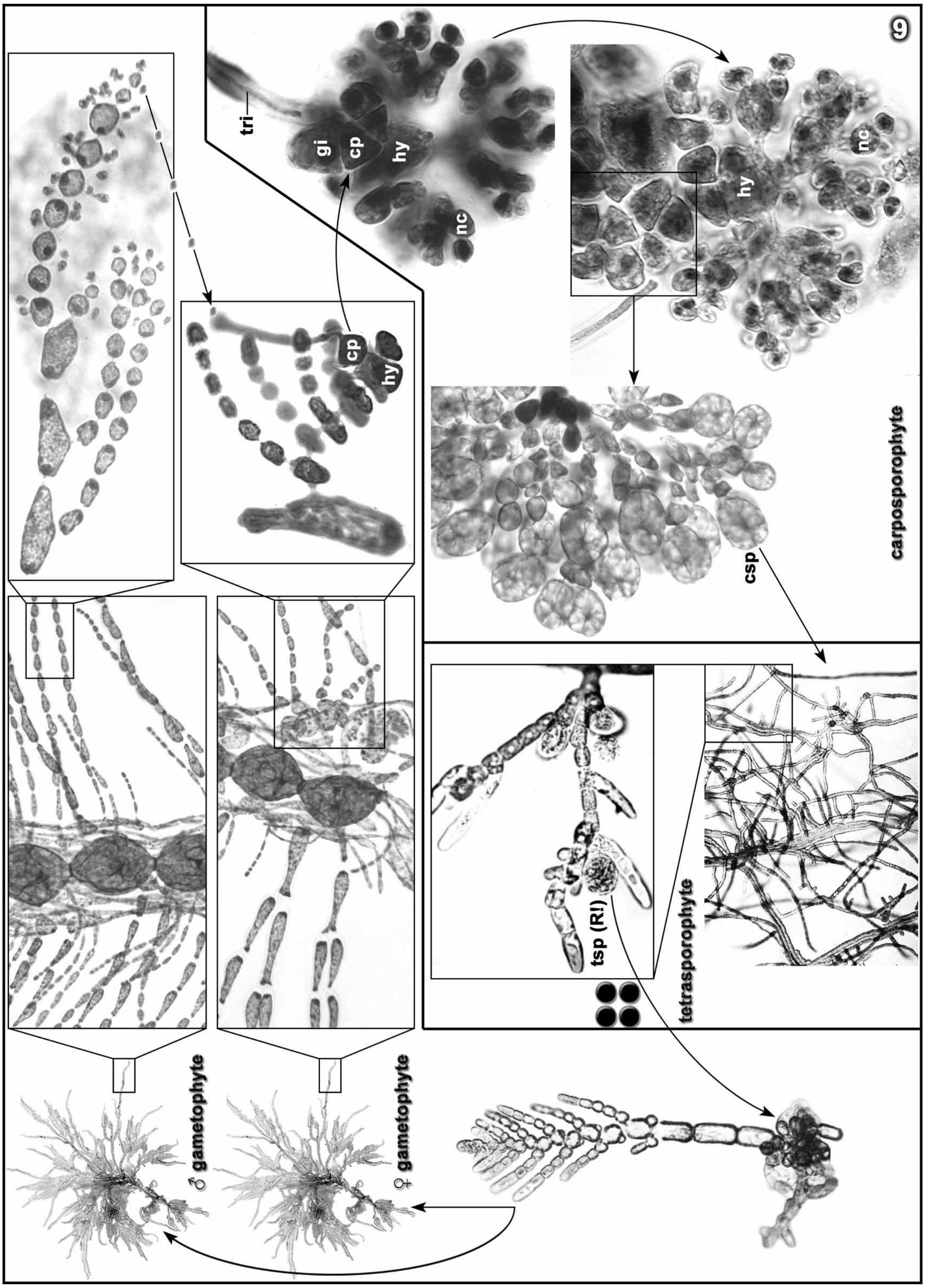

Fig. 9. Hypothesized life cycle of the genus *Reticulocaulis* (Rhodophyta; see *chapter 3*), containing pictures of the tetrasporophyte phase and a young gametophyte of *Naccaria wiggii* (Turner) Endlicher. The three *Naccaria* figures after Boillot & L'Hardy-Halos (1975). Carpogonium (cp), carposporangium (csp) gonimoblast initial (gi), hypogynous cell (hy), meiotic division (R!), nutritive cells (nc), tetraspores (tsp) and trichogyne (tri) are indicated.

try to incorporate all aspects of habitat and biotic diversity (Phillips 1998). In this respect the present studies (*chapters 6, 7*) form part of larger holistic projects. During the Ardoukoba field trip to Masirah Island eleven scientists, mainly taxonomists, visited the island and focused on the biodiversity of the sampling sites and the different ecosystems. Local experts and government officials also attended the expedition, hence encouraging local environmental awareness. The Socotra fieldwork fitted in the framework of the UNDP/GEF project for conservation and sustainable use of the archipelago. The findings of the vast number of marine experts (SCDP 2002) have been reported in several project reports. These included the development of monitoring and zoning plans for the most diverse and unique biotopes to be implemented by trained locals. These systems should preserve the biodiversity hot spots of this relatively unspoilt region. In addition, the project serves as a current status report of the marine biocoenoses and is an excellent reference tool for further environmental impact studies. In this context, a database has been produced to facilitate future use for the collected survey data (Apel *et al.* 2000). Environmental issues threatening both islands are global warming (extensive coral bleaching has been reported for the Socotra Archipelago during the El Niño of 1997-1998, Wilkinson 2002), the increase of anthropogenic influence (intensive fishing, tourism, oil pollution, increase of build up areas, etc.) and invasive species as transport by sea in the area increases.

Commercial applications

Algae are well-known natural resources in South-East Asia (Prud'homme van Reine & Trono Jr 2001) and certain other regions (e.g. Brittany, France). In the Middle East, however, this resource has been practically unexploited. In a prospective study to exploit these resources, the Oman Seaweed Project (hereafter OSP) analyzed various biochemical aspects of locally abundant and certain endemic (to the Arabian Sea) macroalgae. The OSP identified various macroalgae substances, the distribution of economically important species and data on local utilization. This included an assessment of potentially useful colloid-bearing species. These polysaccharides (agars, carrageenans and alginates) are valuable extracts with a multitude of application purposes in the fields of biochemistry, biotechnology, aquaculture and the food industry. The large *Gelidium* sp. nov. (previously referred to as a *Ptilophora* sp. and *Suhria* sp.) is locally abundant (up to 100% cover and a biomass from 0.4 to 0.9 kg m^{-2}, with an estimated total of over 300 tonnes for the Arabian Sea coasts) in intertidal habitats and contains commercially acceptable agar (an agar yield of 18% dry weight and a gel strength of 700-800 g cm^{-2}). Furthermore, these *Gelidium* populations do not seem to be affected by harvesting as they regenerate from turf-like clumps. Besides this agarophyte, the carrageenophytes *Grateloupia indica* Børgesen and *Hypnea bryoides* Børgesen are of commercial interest. Both species occur in subtidal habitats and their cultivation is necessary for the profitable exploitation of these algae. The OSP proposed the development of an integrated polyculture of macroalgae in aquaculture farms (fish or shellfish), where the algae help to remove excess waste nutrients (ammonia-N, P and other effluents). Studies on macroalgal beach cast, thrown up every year by intermittent storms during post-monsoon months, showed that *Nizamuddinia zanardinii* has the highest crude fiber and crude protein contents of the investigated Arabian Sea algae. Consequently, this endemic alga has a great potential for livestock feed supplementation. Analyses of the dominant taxa in local beach cast showed that the abundant *Sargassum* species contain the highest N contents (equivalent to 13% protein content) of these algae. In addition, the C:N ratio of *Sargassum* (9.61) is smaller than 10, being indicative for fast mineralization rates of the plants in composts, making beach cast a promising source for fertilizer production (OSP 1997, 1999a, b; Jupp 1999).

Few secondary compounds of Arabian Sea algae have been screened so far. Besides the extracts used in gross quantities (polysaccharides), many seaweeds contain smaller concentrations of bioactive natural products, often associated with chemical defense against competitors or herbivores. Such metabolites have antibiotic and feeding deterrent properties (e.g. bromoform and halogenated acetones in *Asparagopsis*, Norris & Fenical 1982). The search for these natural products is largely dependent on taxonomical research for sound field identifications and the screening of related taxa. Endemic algae seem to be of particular interest as they have certainly not been screened previously and this natural heritage can prove to be important for export purposes. This strategy was also applied while collecting Porifera and Tunicata during the Masirah Island field trip. The biochemical analyses and bioassays of these animals advance well, but the taxonomical identifications lag behind due to the limited number of taxonomic experts (Amade 2001). Similarly, a better knowledge of the Omani marine flora, especially that of the productive upwelling areas, is beneficial for future biochemical studies on well-defined taxa.

PERSONAL CONTRIBUTION TO THE THESIS

The *chapters 2-7* are cited as multi-authored publications. The analyses, drawings, field work, laboratory work, photographs and writing for the *chapters 2-4* and *6-7* were, however, carried out solely by T. Schils. The presented manuscripts were thereafter discussed, corrected and commented on by the respective coauthors (E. Coppejans, O. De Clerck and J.M. Huisman). In addition, H. Engledow kindly commented on the manuscripts and checked the complete English text. *Chapter 5* was a study in collaboration with J.M. Huisman during a research stay in Murdoch University (Western Australia). Certain specimens studied in *chapter 4* were collected by F. Leliaert (Ghent University) during an expedition to Socotra Island preceding this project (13 January-20 February 1999). These specimens were very helpful in gaining insight into the specific marine flora. The subsequent collecting trip to Masirah Island (2-30 November 1999) was executed by T. Schils with the support of the Ardoukoba Association (France). Vegetation and specimen sampling on Socotra (26 March-7 May 2000) were also performed by T. Schils, in collaboration with the Senckenberg Research Institute (Germany) and the personnel of the project implementation unit (UNDP). The field work comprised largely SCUBA diving, snorkeling, and intertidal collecting. The procedure of vegetation sampling is explained in the *Materials and Methods* of *chapter 6*. The photographs in this thesis were taken under standard light microscopes with a 35-mm camera and two types of digital cameras (for further details, see *Materials and Methods* of the respective chapters). Drawings were made with a camera-lucida on the microscopes, upon which they were scanned with an Agfa Snapscan e50. The different dyes that were used for staining the specimens for microscopical examination are listed in the *Materials and Methods* of the *chapters 2-5*.

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CHAPTER 2

Gelatinous red algae of the Arabian Sea, including *Platoma heteromorphum* sp. nov. (Gigartinales, Rhodophyta)

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ABSTRACT

This study reports on the gelatinous red algae of the Arabian Sea (Masirah Island, Oman and Socotra Island, Yemen) belonging to the families Dumontiaceae, Nemastomataceae and Schizymeniaceae. *Dudresnaya capricornica*, *Gibsmithia larkumii*, *Predaea laciniosa*, *P. weldii* and *Titanophora pikeana* are new records for the region. The morphological and reproductive features of these species are presented, with emphasis on post-fertilization events. *Platoma heteromorphum* Schils *sp. nov.* is described from an upwelling region along the eastern coast of Masirah Island. Based on similarities in morphology and post-fertilization events, this species is closely related to *P. ardreanum*, *P. cyclocolpum* (the generitype) and *P. izunosimense*. The connecting filament initiation in *P. heteromorphum* is comparable to *Titanophora*, but the post-fertilization processes observed in *P. heteromorphum* and *T. pikeana* clearly demarcate both genera within the Schizymeniaceae. A first impression of the gelatinous red algae in the Arabian Sea suggests a high biogeographical affinity with Australia, but additional records from the Indian Ocean indicate that their distribution may be more widespread than is currently accepted.

INTRODUCTION

The study of the benthic marine algal flora of the Arabian Sea started with Børgesen (1934), who stressed the peculiar composition of the algal flora relative to adjacent areas and suggested biogeographical links with distant regions, e.g. Australia, Japan, South Africa and the northern Atlantic. Renewed interest in the phycology of this region occurred in the 1990s, resulting in various new records and new species descriptions (Wynne & Banaimoon 1990; Kemp 1998; Wynne & Jupp 1998; Wynne 1999a, b, 2000, 2001). Despite the recent increase in taxonomic studies in the northern Indian Ocean (Djibouti, India, Iran, Laccadive Islands, Maldives, Oman, Pakistan, Socotra, Somalia, Yemen), information on the gelatinous red algae of the region remains scarce (Holmes 1903; Silva *et al.* 1996). For each of the families (Dumontiaceae, Nemastomataceae and Schizymeniaceae) we studied in this paper, only a single species has previously been recorded for the northern Indian Ocean, viz. *Dudresnaya japonica* Okamura (Oman: Wynne 2000), *Predaea feldmannii* Børgesen var. *indica* M.S. Balakrishnan & Chawla (India: Balakrishnan & Chawla 1984) and *Schizymenia apoda* (J. Agardh) J. Agardh (Somalia: Hauck 1889).

MATERIAL AND METHODS

Specimens were collected by the first author during field trips to the islands of Masirah, Oman (November 1999) and Socotra, Yemen (March–May 2000). Specimens were collected in plastic zip-lock bags during SCUBA dives and afterwards pressed as herbarium specimens (lodged in GENT: Ghent University Herbarium, Krijgslaan 281 (S8), 9000 Ghent, Belgium) or preserved in a 5% formaldehyde–seawater solution or dried in silica gel.

After staining of specimens with Aniline Blue, Fast Green or Lugol's solution, slides were made by mounting the specimens in a 50% corn syrup-water solution (containing a few drops of phenol). Subsequently, the samples were studied using a light microscope (Leitz Diaplan). ImageTool 2.00 (The University of Texas Health Science Center in San Antonio, Texas) and a digital camera (Olympus DP50) were used for microscopical measurements, which are presented in the text as length × width.

RESULTS

Dudresnaya capricornica Robins & Kraft 1985, p. 23 (Dumontiaceae)

Figs 1–4

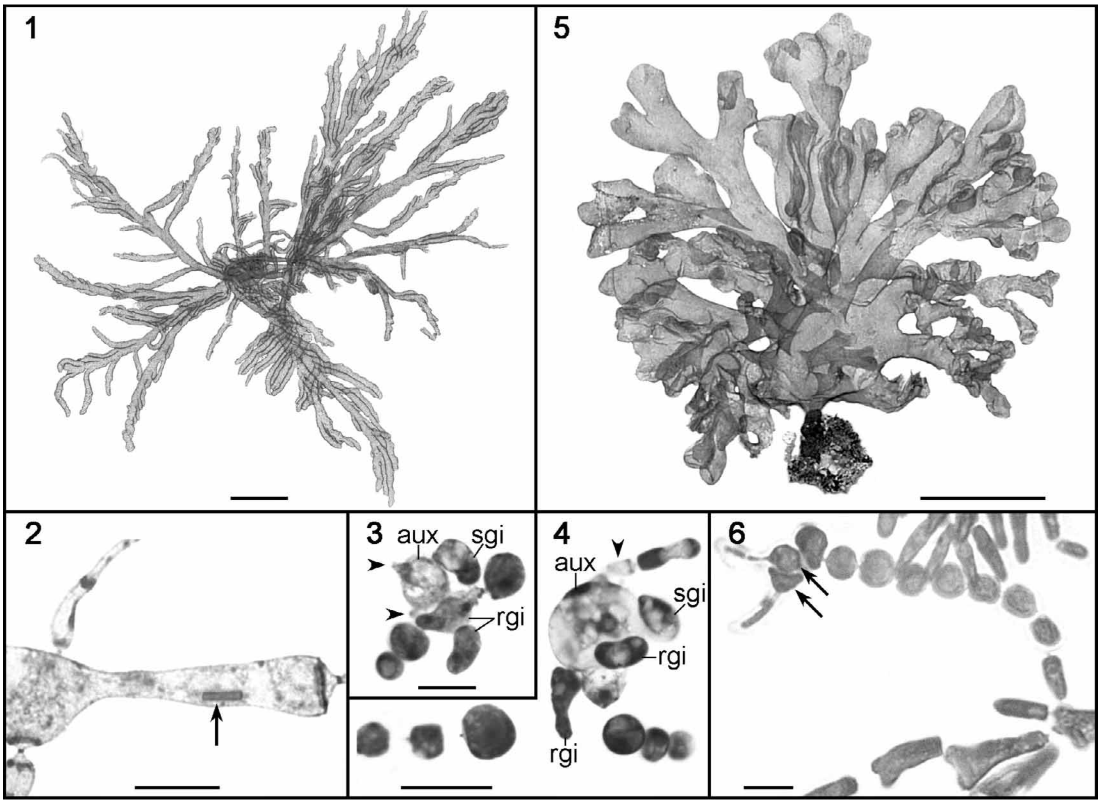
SPECIMENS EXAMINED: **Yemen**: Socotra, east of Bidholih (ALG-41: 12°19'19"N, 54°02'2"E), 1 May 2000, subtidal: –19.4 m, leg. T. Schils (SMM 480).

DISTRIBUTION: Australia, Norfolk Island, Papua New Guinea, Saudi Arabia, Tanzania, Yemen [Robins & Kraft 1985; Huisman & Walker 1990; De Clerck & Coppejans 1996 (as *Dudresnaya* sp. det. A. Millar, 14 August 1998); Silva *et al.* 1996; Huisman 1997; Phillips 1997; Millar *et al.* 1999; Coppejans *et al.* 2000; Tai *et al.* 2001; this paper].

Plants are bright red plant with a terete thallus (11 cm tall; Fig. 1) and grow epilithically. Axial cells are marked by the presence of longitudinally elongated hexagonal protein crystals (8.5–17 µm × 2–4.5 µm) which are visible using bright field optics (Fig. 2) or ultraviolet fluorescence. Initially, the distinct primary axes produce cortical filaments in a secund arrangement, resulting in an irregular multiple branching pattern. The outer cortical cells are cylindrical (5.5–40 µm × 2–9 µm) and hairs are absent. Rhizoids (3.5–15 µm in diameter) develop from the basal cells of the cortical filaments.

A single female gametophyte was collected. The reproductive filaments lack a mucilaginous coat. The carpogonial filaments consist of 8–22 cells, with a terminally deflexed carpogonium (4.5–9.5 µm × 5.5–8.5 µm) resulting from a single oblique division. The trichogyne can reach a length of 0.5 mm. The auxiliary-cell filaments consist of 8–40 cells, with a subspherical to rectangular generative auxiliary cell (8.5–12 µm × 8.5–13 µm) situated amongst large, dark-staining cells. Adventitious laterals and rhizoids develop from carpogonial and auxiliary-cell filaments. Fusion of the connecting filament with the auxiliary cell causes the latter to swell and form a bulge at the site of contact, resulting in a latero-pyriform shape (18–27 µm × 22–35 µm). Three gonimoblast initials are formed. Two are recurved (reniform) (13.5–19 µm × 7–11 µm) and the third is generally larger and reniform to subspherical (Figs 3, 4). These gonimoblast initials give rise to an uncleft cystocarp (up to 265 µm in diameter) that completely encircles the auxiliary-cell filaments. Carposporangia reach a diameter of 9.5–17 µm.

REMARKS: Of the 17 currently recognized *Dudresnaya* P. & H. Crouan species (Robins & Kraft 1985; Searles & Ballantine 1986; Kajimura 1993, 1994; Tabares *et al.* 1997; Afonso-Carrillo *et al.* in press), D. hawaiiensis R.K.S. Lee is the only well documented species for the Indian Ocean (South Africa: Norris 1992). Wynne (2000) reported on *D. japonica* from the Dhofar coastline of Oman and commented on the ill-defined mucilage coat surrounding the auxiliary-cell filament and the cystocarps being indistinctly cleft. Robins & Kraft (1985) use the latter feature to classify Dudresnaya species into two groups. Our specimen, from Socotra, agrees with *D. japonica* as described by Wynne (2000), but it should be referred to *D. capricornica* owing to its irregular radial branching, the absence of a thick mucilaginous coat around the reproductive filaments, the reniform gonimoblast initials, and cystocarps that completely surround the auxiliary-cell filaments. Future studies should elucidate the species diversity and the variability of the genus in the region.



Figs 1–4. *Dudresnaya capricornica.*

Fig. 1. Habit of a female gametophyte, SMM 480. Scale bar = 2 cm.

Fig. 2. Axial cell, showing a single longitudinally elongated hexagonal protein crystal (arrow). Slide SMM 480f. Scale bar = 25 µm.

Figs 3, 4. Two reniform (rgi) and a third larger subspherical to reniform gonimoblast initial (sgi) developing from a diploidized auxiliary cell (aux), with incoming and outgoing connecting filaments (arrowheads). Slide SMM 480d. Scale bars = 25 µm.

Figs 5, 6. *Gibsmithia larkumii.*

Fig. 5. Habit of a female gametophyte, SMM 496. Scale bar = 2 cm.

Fig. 6. Carpogonial filament bearing two carpogonia (arrows). Slide SMM 496a. Scale bar = 10 µm.

Gibsmithia larkumii Kraft 1986, p. 439 (Dumontiaceae)

Figs 5, 6

SPECIMENS EXAMINED: **Yemen:** Socotra, Qatanhin, Permanent Transect IX (ALG-23: 12°21'18"N, 53°32'40"E), 9 April 2000, subtidal: –10.5 m, leg. T. Schils (SMM 257); Socotra, east of Bidholih (ALG-41: 12°19'19"N, 54°02'02"), 1 May 2000, subtidal: –19.4 m, leg. T. Schils (SMM 496, SMM 497). **Tanzania:** Ruvula Beach (Mnazi Bay, Mtwara area), 26 July 2000, subtidal: –20 m, leg. E. Coppejans, O. Dargent & G. Bel (HEC 12898); Ruvula Beach, in front of the lodge (Mnazi Bay, Mtwara area), 7 August 2000, subtidal: –25 m, leg. E. Coppejans, O. Dargent & G. Bel (HEC 14197).

DISTRIBUTION: Australia, Papua New Guinea, Tanzania, Yemen (Kraft 1986; Millar *et al.* 1999; this paper).

Thalli are bright red, gelatinous, up to 7 cm tall and 8.5 cm broad (Fig. 5). They are attached by a cartilaginous disc (0.5 cm in diameter), which lacks the characteristic perennial stipe of other species of *Gibsmithia* Doty. The pseudodichotomous cortical filaments consist of subrectangular cells (5–35 µm × 2.5–9 µm). Apical cortical cells are blunt, lacking terminal hairs. Inner cortical cells give rise to medullary filaments, 2.5–8.5 µm in diameter.

The unfertilized female gametophytes contain carpogonial filaments (6–12 cells long) with an enlarged subterminal hypogynous cell, which initiates a carpogonium by an oblique division. The occurrence of two carpogonia on a single carpogonial filament was scarcely ever observed (Fig. 6). Auxiliary-cell filaments are 6–13 cells long. The subrectangular auxiliary cell is flanked by two enlarged, deeply staining cells. Adventitious laterals and rhizoidal filaments develop to various extents on carpogonial and auxiliary-cell filaments. Tetrasporophytes bear obovoid, cruciate tetrasporangia (16–29 µm × 11–23 µm) terminally on the cortical filaments.

This alga was sampled from the site with the highest species diversity yet found in the Socotra Archipelago (30 ± 2 species per 0.25 m^2). Very strong currents were observed around this eastern extremity of Socotra. The rocky substratum contained a high diversity of red algae, intermixed with bare sandy patches.

REMARKS: Two other *Gibsmithia* species have previously been recorded for the Indian Ocean: *G. hawaiiensis* Doty (Australia, Kenya, Seychelles and Tanzania: Silva *et al.* 1996; Coppejans *et al.* 2000) and a *Gibsmithia* sp. from Zanzibar, Tanzania (Coppejans *et al.* 2000). We have recently recollected both species in Tanzania (Mnazi Bay), indicating that the lack of *Gibsmithia* records for the Indian Ocean most probably results from the lack of subtidal phycological studies in this area.

Platoma heteromorphum Schils, sp. nov. (Schizymeniaceae)

Figs 7–17

Plantae atrorubrae foliosae ad subcylindricae. Hapteron discoideum (1 mm crassum), stipite brevi (6–9 mm longo). Cortex 4–8 cellulis externis corticalibus, numerosas intercalares glandicellulas continentibus, cellulis internis corticalibus elongatis (includentibus cellulas X- et V-formes) filamenta medullosa edentibus. Interdum cellulae steriles in ramis carpogonialibus tricellularibus praesentes. Carpogonium post fecundationem longitudinaliter dimidiatum, ambo dimidia ad contiguas cellulas auxiliares subsidiarias *conjugentia. Una ex quibus et una cellula distalis producentes filamenta conjunctiva septata directe. Cellulae auxiliares generativae intercalares in fasciculis corticalibus separatis, perspicuae forma obpyriformi (16–21 µm longae et 11–13 µm crassae) et coloratae atrocyaneae. Post conjunctionem laterale fili conjunctivi cum cellula auxiliari generativa, illa crescens porrecto et peragrans. Cellula auxiliaris diploidea in prima cellula gonimoblasti (6.5–9.5 µm longa et 6–10 µm crassa) transverse dividens. Duo gonimolobos producens, maturescentes sequenter et produscentes carposporangia angulares (11.5–30 µm diametro). Tetrasporangia et spermatangia incognita.*

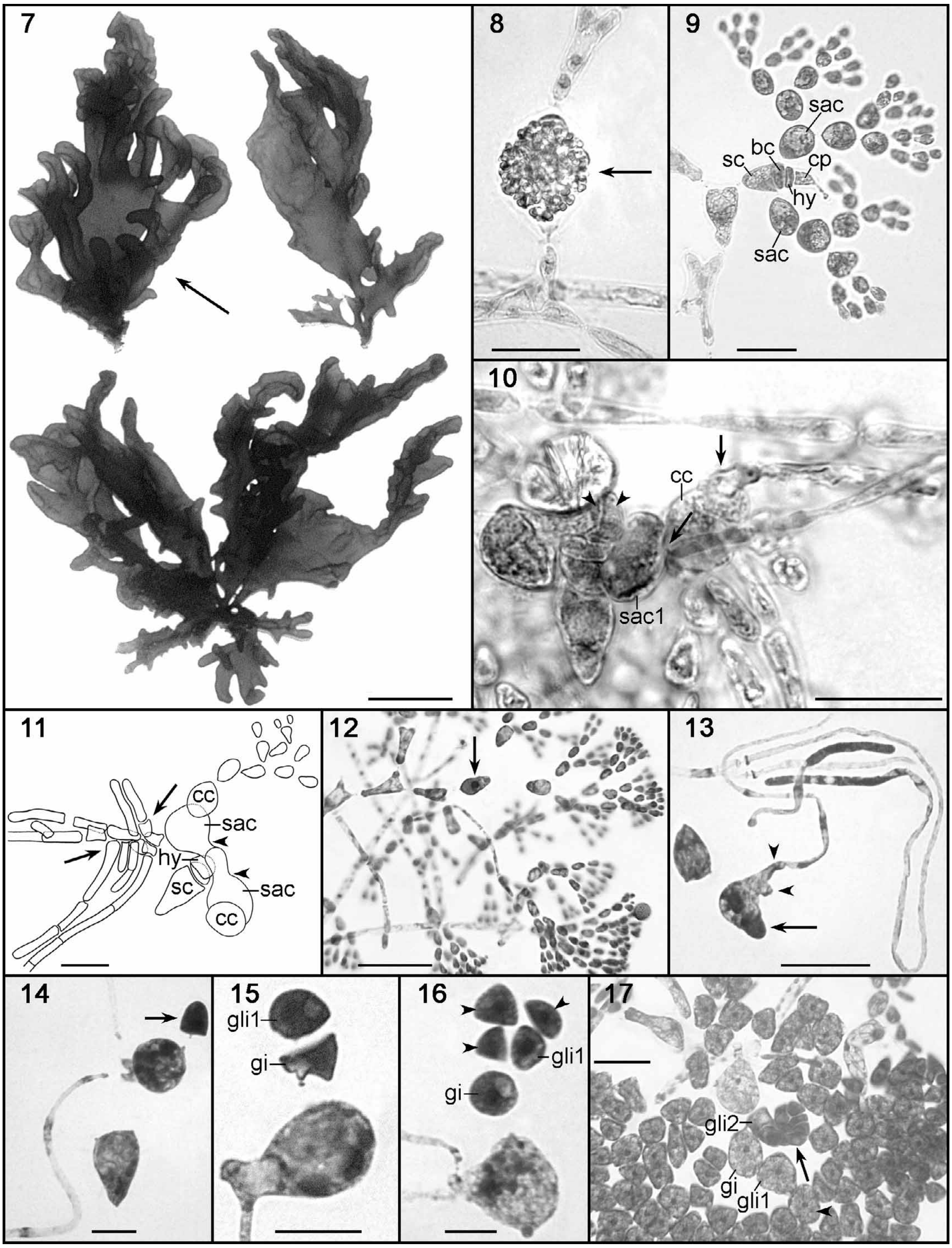
Deep red plants, foliose to subcylindrical in shape. Multiple blades with short stipes (6–9 mm long) arise from a single discoid holdfast (1 mm across). Cortex consists of 4–8 outer cortical cells, containing numerous intercalary gland cells, and an inner layer of elongated cells (including X- and V-shaped cells) giving rise to medullary filaments. Three-celled carpogonial branches occasionally bear sterile cells. The fertilized carpogonium divides longitudinally into two halves, fusing with adjacent subsidiary auxiliary cells. One of the diploidized subsidiary cells and the cell distal to it initiate septate connecting filaments directly. Generative auxiliary cells are formed in an intercalary position in separate cortical filaments and are characterized by their obpyriform shape (16–21 µm × 11–13 µm) and a deep aniline staining. After lateral fusion of a connecting filament with a generative auxiliary cell, the former continues to grow and effects further diploidizations. The diploidized generative auxiliary cell divides transversely, producing a conical gonimoblast initial (6.5–9.5 µm × 6–10 µm). Two gonimolobes are formed, which mature sequentially and produce angular carposporangia (11.5–30 µm in diameter). Tetrasporangia and spermatangia unknown.

HOLOTYPE: MAS 139, upper left specimen on herbarium sheet (field picture: Fig. 7).

ETYMOLOGY: The specific epithet alludes to the combination of compressed and subcylindrical parts of the thallus.

TYPE LOCALITY AND SPECIMENS EXAMINED: **Oman:** Masirah Island, close to Ra's Zarri (site 09: 20°11'85"N, 58°42'55"E), 9 November 1999, subtidal: –9 m, leg. T. Schils (MAS 139). Species-rich algal flora, dominant species are *Spatoglossum asperum* J. Agardh, *Sebdenia flabellata* (J. Agardh) P.G. Parkinson, *Dictyota* spp. and *Padina* spp. Rocky platform with grooves and rocky outcrops; Masirah Island, Close to Ra's Zarri (site 22), 20 November 1999, subtidal: –9 m, leg. T. Schils (MAS 374) (holotype).

The plants are up to 8.5 cm tall, deep red in colour (bright red when dried) and gelatinous in texture (Fig. 7). A distinctive feature of the species, consistent with the most recent etymological interpretation of *Platoma* Schousboe *ex* Schmitz ('becoming wide': Athanasiadis 2000), is the flattened subcylindrical thallus shape with irregular lobes (cf. certain *Nemastoma* J. Agardh and *Predaea* De Toni spp.), which do not fuse. The thallus occasionally has surface proliferations, but lacks marginal calluses. There is a short stipe (6–9 mm), attached by a small discoid holdfast, 1 mm across.



Figs 7–17. *Platoma heteromorphum.*

Fig. 7. Habit of female gametophytes, including the holotype (arrow), MAS 139. Scale bar = 2 cm.

Fig. 8. Large intercalary gland cell (arrow) in the inner cortex. Slide MAS 139x. Scale bar = 25 µm.

Fig. 9. A three-celled carpogonial branch consisting of an oval basal cell (bc), a subrectangular hypogynous cell (hy) and a conical carpogonium (cp). The supporting cell (sc) bears two subsidiary auxiliary cells (sac). Slide MAS 139x. Scale bar = 25 µm.

Fig. 10. Longitudinal division of the fertilized carpogonium and fusion of both halves (arrowheads) with the adjacent subsidiary auxiliary cells. One diploidized subsidiary auxiliary cell (sac1) and the cortical cell distal to it (cc) initiate septate connecting filaments (arrows) directly. Slide MAS 139af. Scale bar = 25 µm.

Fig. 11. Both halves of a divided carpogonium fuse (arrowheads) with the subsidiary auxiliary cells (sac). The connecting filaments (arrows) arise from one of the subsidiary auxiliary cells and branch profusely. Supporting cell (sc), hypogynous cell (hy) and cortical cells (cc) are indicated. Drawing from slide MAS 139af. Scale bar = 25 µm.

Fig. 12. Undiploidized generative auxiliary cell (arrow) in an intercalary position in a cortical filament. Slide MAS 139ae. Scale bar = 50 µm.

Fig. 13. Incoming and outgoing septate connecting filaments (arrowheads) on a fertilized generative auxiliary cell, which protrudes distally (arrow). Slide MAS 139p. Scale bar = 25 µm.

Fig. 14. A transverse division of the diploidized generative auxiliary cell results in a conical gonimoblast initial (arrow). Slide MAS 139p. Scale bar = 10 µm.

Fig. 15. An oblique division of the gonimoblast initial (gi) gives rise to the first gonimolobe initial (gli1). Slide MAS 139p. Scale bar = 10 µm.

Fig. 16. Development of gonimoblast cells (arrowheads) from the first gonimolobe initial (gli1), on top of the gonimoblast initial (gi). Slide MAS 139p. Scale bar = 10 µm.

Fig. 17. The gonimoblast initial (gi), the primary gonimolobe initial (gli1) and an inner gonimoblast cell (arrowhead) are perceptible as large, globose cells in a maturing carposporophyte. A second gonimolobe (arrow) develops from the secondary gonimolobe initial (gli2). Slide MAS 139f. Scale bar = 25 µm.

The moniliform outer cortex consists of discrete, dichotomous branch systems that are 4–8 cells long with blunt apices. The inner cortical cells are elongate and include X- [cf. *P. abbottianum* J.N. Norris & Bucher (1977) and *P. izunosimense* Segawa (Kajimura 1997)] and V-shaped cells (cf. *Itonoa*: Masuda & Guiry 1995); they initiate rhizoidal filaments. In accordance with the other well studied *Platoma* species (Kraft & Abbott 1997), the cortical fascicles contain intercalary and subterminal subspherical gland cells (6.5–40 µm in diameter), which stain deeply with Aniline Blue. Certain gland cells close to the inner cortex become very large (Fig. 8). The cell content of small gland cells is dense and that of the large gland cells is coagulated and contains a single large spherical protein inclusion (3.5–15 µm in diameter).

Only dioecious female gametophytes were observed. The carpogonial branches (Fig. 9) develop at the terminal end of an inner cortical cell (an apically depressed obovate supporting cell, 15–18 µm × 12–15.5 µm), positioned in the dichotomy of a cortical fascicle. The three-celled carpogonial branches consist of an oval basal cell (4.5–9 µm × 9.5–12 µm), a subrectangular hypogynous cell (3–5 µm × 8.5–10.5 µm), and a distal carpogonium (conical in shape, 9–10.5 µm × 6–8 µm) with a straight trichogyne that is some 0.2 mm long. Occasionally, sterile cells were noticed on the basal and hypogynous cells. The two cortical cells on top of the supporting cell become subsidiary auxiliary cells (or epi-supporting cells, 13.5–22.5 µm in diameter; Fig. 9). Following presumed fertilization, the carpogonium divides longitudinally and both halves fuse with the adjacent subsidiary auxiliary cells (Fig. 10). One diploidized subsidiary auxiliary cell and the cortical cell distal to it then initiate septate connecting filaments directly; these filaments branch abundantly near their site of origin (Fig. 11). By traversing the thallus, the connecting filaments can ultimately fuse with a generative auxiliary cell. The latter cells are formed in an intercalary position in cortical filaments separate from those containing supporting cells. Prior to fusion with connecting filaments, these generative auxiliary cells (16–21 µm × 11–13 µm) differ from normal vegetative cells by their obpyriform shape and their dark staining with Aniline Blue (Fig. 12). Most connecting filaments continue to grow from the point of contact with the generative auxiliary cell, giving rise to a crescent-shaped lateral extension on the auxiliary cell. Upon diploidization, the generative auxiliary cell protrudes distally (Fig. 13) and divides transversely to form a conical gonimoblast initial (6.5–9.5 µm × 6–10 µm; Fig. 14). A subsequent oblique division of the gonimoblast initial forms the first gonimolobe initial

(6–9 µm × 7–9 µm; Fig. 15), which continues to divide (Fig. 16) to produce the first gonimolobe. A second gonimolobe initial (Fig. 17) develops later and the resulting gonimolobe matures sequentially. The gonimoblast initial, the primary gonimolobe initial and inner gonimoblast cells are discernible as large globose cells (17–22 µm in diameter; Fig. 17) in the mature nonostiolate cystocarp (90–210 µm in diameter). The angular carposporangia are 11.5–30 µm in diameter. During cystocarp development, the cortical filament cells adjacent to the generative auxiliary cell enlarge and elongate to some extent.

REMARKS: *Platoma heteromorphum* fits the generic definitions of female reproductive structures and postfertilization events presented by Masuda & Guiry (1994). The presence of gland cells and subsidiary auxiliary cells, together with various morphological features (Norris & Bucher 1977; Kajimura 1997; Kraft & Abbott 1997) clearly demarcates the Omani species from less studied species, such as *P. abbottianum*, *P. australicum* Womersley & Kraft, *P. fanii* Dawson, *P. foliosum* Womersley & Kraft, *P. incrassatum* Schousboe *ex* De Toni and *P. tenue* Howe & Taylor. Its morphology and especially the postfertilization events (Table 1) differ from the well documented (Itono 1984; Kajimura 1997) Japanese species, *P. izunosimense*. In that species, the fertilized carpogonium does not divide in two but fuses with one or both subsidiary auxiliary cells or a cortical cell distal to one of the latter. A monopodial connecting filament–initial branch then initiates the connecting filaments indirectly. Compared to *P. ardreanum* Kraft & Abbott (1997), *P. heteromorphum* lacks the distinctive calluses and blade ruffling and has a stipe. Some carpogonial branch cells bear sterile cells, as in *P. ardreanum*. Multicellular laterals and sterile cells on the supporting or epi-supporting cells were not observed, however, but cannot be said never to occur, because carpogonial branches with sterile cells were scarce in the material. Like the Hawaiian species, the fertilized carpogonium divides into two halves, which fuse with the adjacent subsidiary auxiliary cells. Conversely, the connecting filament initiation in *P. heteromorphum* is not restricted to a subsidiary auxiliary cell. Besides the morphological differences (stipe, surface proliferations), these postfertilization events also distinguish the new *Platoma* species from *P. cyclocolpum* (Montagne) F. Schmitz, the type of the genus. In *P. cyclocolpum*, the fertilized carpogonium can fuse with one or two subsidiary auxiliary cells (Masuda & Guiry 1994; Huisman 1999) and the connecting filaments can develop from both fusion cells and supplementary cortical cells. Itono (1984) observed that connecting filaments in *Titanophora* (J. Agardh) Feldmann also arose from the cell distal to one of the two subsidiary auxiliary cells. In this respect, *P. cyclocolpum*, *P. heteromorphum* and *P. izunosimense* illustrate close similarities in postfertilization events between *Platoma* and *Titanophora*.

Predaea laciniosa **Kraft 1984, p. 11 (Nemastomataceae)**

Figs 18–27

SPECIMENS EXAMINED: **Oman:** Masirah Island, in between Ra’s Abu Rasas and Ra’s Zarri (site 25), 22 November 1999, subtidal: –11 m, leg. T. Schils (MAS 530). **Yemen:** Darsa Island, south coast (ALG-21: 12°06'36"N, 53°17'48"E), 8 April 2000, subtidal: –21 m, leg. T. Schils (SMM 209). Rocky platform with large concave grooves (vertical walls and obscured areas); abundance of soft corals.

Table 1. Comparison of *Platoma heteromorphum* with closely related species. Based on Masuda & Guiry (1994), Kajimura (1997), Kraft & Abbott (1997), Huisman (1999), Guiry & Nic Dhonncha (2001), and the present study.

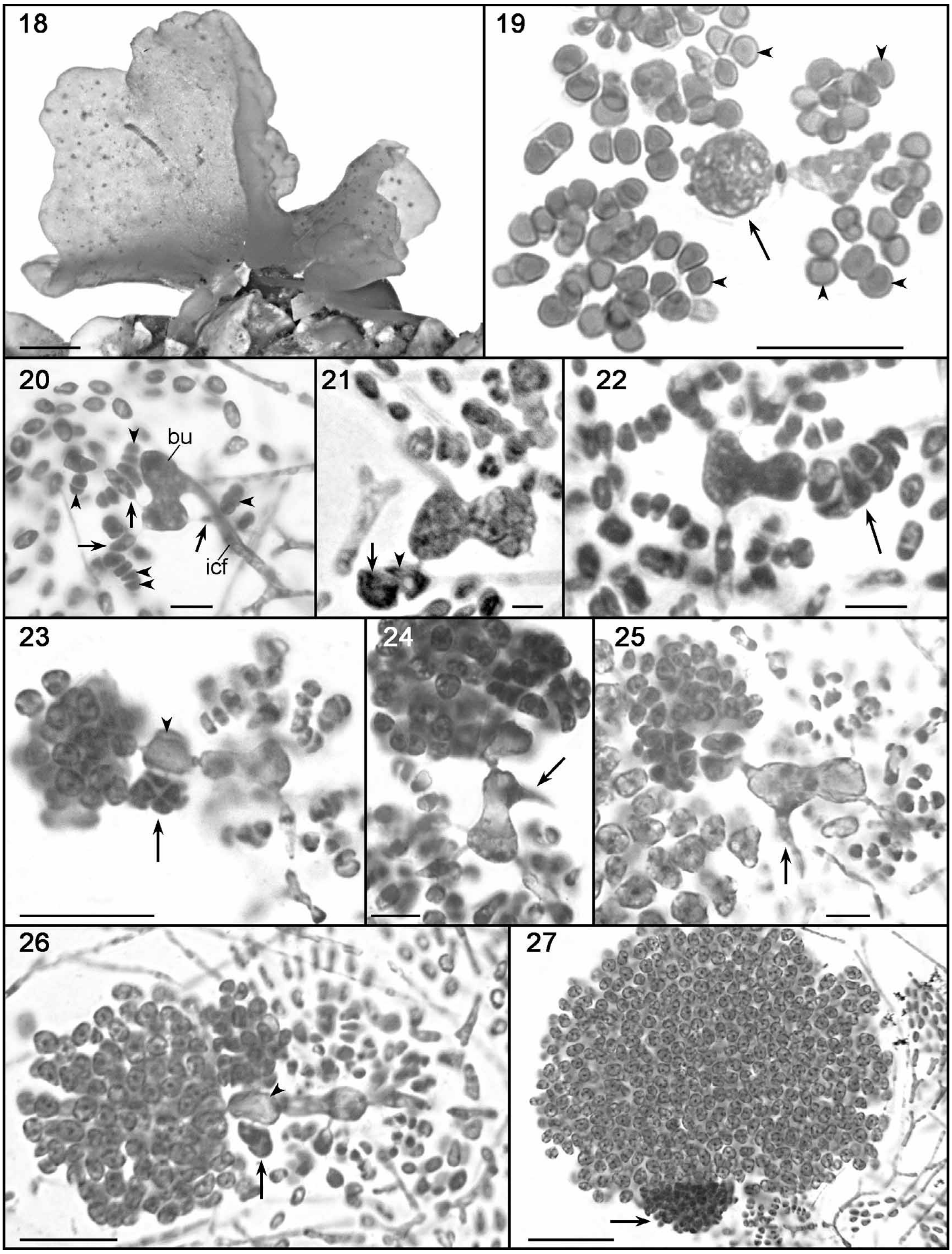
Feature	*P. ardreanum*	*P. cyclocolpum*	*P. heteromorphum*	*P. izunosimense*
Branching pattern	broadly lobed, with deep incisions	irregular with rounded bifurcations at the apices, non-undulate	irregularly lobed	irregularly pinnate, often with forked branch apices, also palmate or irregular; surfaces undulate
Thallus shape	foliose with apparent calluses, blunt lobes, and dentate to narrowly proliferous margins or ruffles	foliose to subcylindrical, with marginal proliferations	foliose to subcylindrical, with no calluses, no blade ruffling, but occasionally with proliferations	foliose, with or without proliferations
Thallus colour	deep reddish-brown	light pink to reddish-brown	deep red to bright red when dry	reddish-brown to pinkish red when dry
Stipe	absent	absent	present	present or absent
Intercalary gland cells	present	present	present	present
Carpogonial branch	3(-4)-celled	3-celled	3-celled	3-celled
Sterile cells on carpogonial branch	present	probably absent	occasionally present	probably absent
Division of fertilized carpogonium	yes	?; direct fusion without division is observed	yes	no
Origin of connecting filament initiation	one of the two contacted subsidiary auxiliary cells	one or both diploidized subsidiary auxiliary cells and a cortical cell distal to one of them	one of the two contacted subsidiary auxiliary cells and the cortical cell distal to it	one or both diploidized subsidiary auxiliary cells and a cortical cell distal to one of them
Distribution	Hawaiian Islands	Caribbean, Mediterranean, north-eastern Atlantic, Western Australia	Oman (Arabian Sea)	southern Japan

DISTRIBUTION: Australia, French Polynesia, Hawaii, Oman, Papua New Guinea, Yemen (Kraft & Abbott 1971; Kraft 1984; Huisman 1997; Abbott 1999; Millar *et al.* 1999; Payri *et al.* 2000; this paper).

The plants are small, up to 1.8 × 2.5 cm, and grow on coralline red algae and shell debris (Fig. 18). Four to eight oval, outer cortical filament cells (3–9 µm × 2–5 µm) originate from elongated subcortical cells. Large spherical gland cells (12–24 µm × 10–21 µm) are prominent, and are intercalary or terminal in cortical filaments. Rhizoidal filaments develop from the inner cortical cells and constitute the medulla, their cells 5–280 × 2–3 µm.

Only dioecious female gametophytes were collected. Although were observed at different stages of development, carpogonial branches were absent. The cortical filament cells (7–14 µm × 3–6 µm), attached to the auxiliary cell (21–26 µm × 9–14 µm; Fig. 19), bear aggregations (generally 4 branching tiers, each consisting of 3–15 cells) of small subspherical nutritive cells (2–5 µm × 2.5–7 µm). Connecting filaments fuse baso-laterally with the auxiliary cell. The incoming connecting filament initiates a bulge (Fig. 20), which gives rise to a gonimoblast initial (Fig. 21) opposite to the site of contact with the auxiliary cell. The gonimoblast initial swells, becoming subspherical (reaching a size of 6.5–18 µm in diameter) and cutting off the primary gonimolobe initial (Fig. 21). The resulting gonimoblast cells divide profusely and initiate a large subspherical primary gonimolobe (up to 180 µm × 220 µm). The remains of the incoming connecting filament are visible as a spine-like protuberance on the auxiliary cell (Figs 24, 25). Secondary (Fig. 23) and tertiary gonimolobes (Fig. 26) are initiated sequentially, lateral to the first gonimolobe. The subspherical to isodiametric carposporangia (5–13 µm in diameter) mature asynchronously and small clusters of secondary and tertiary carposporangia are evident at the base of the prominent primary gonimolobe (Fig. 27).

REMARKS: The Arabian Sea specimens lacked the ruffled surface originally thought characteristic of *P. laciniosa* (Kraft 1984). *Predaea tokidae* Kajimura differs from *P. laciniosa* by having a lobed thallus without surface ruffles. Besides this difference in habit, the vegetative structure and reproductive traits of both species are remarkably similar (Kajimura 1987, 1995). Since *P. laciniosa* would have priority over *P. tokidae* if the two species were combined, and since our observations of Omani and Socotran specimens are completely consistent with the description of *P. laciniosa* (Kraft 1984), apart from the ruffled surfaces, MAS 530 and SMM 209 are identified as *P. laciniosa*; an additional feature in favour of this identification is the presence of three gonimolobes in the Arabian Sea specimens. The high degree of morphological variability in these gelatinous red algae, the disjunct distribution pattern of *P. laciniosa*, and the floristic affinity between the northern Arabian Sea and the Sea of Japan (Børgesen 1934; Wynne 2000) may be indicative of a greater distribution range of the species than currently accepted. Detailed studies on *P. tokidae* and *P. laciniosa* should clarify the morphological and developmental differences between both species.



Figs 18–27. *Predaea laciniosa*.

Fig. 18. Habit of a female gametophyte, MAS 530. Scale bar = 1 mm.

Fig. 19. Nutritive cells (arrowheads) and an undiploidized generative auxiliary cell (arrow) in an intercalary position in a cortical filament. Slide SMM 209b. Scale bar = 25 μm.

Fig. 20. Diploidized auxiliary cell with (laterally) an incoming connecting filament (icf), initiating a bulge (bu) prior to gonimoblast initiation. The contiguous cortical cells (arrows) of the auxiliary cell bear nutritive cells (arrowheads). Slide SMM 209a. Scale bar = 10 μm.

Fig. 21. The gonimoblast initial (arrowhead) and the gonimolobe initial (arrow) arise outwardly from the connecting filament bulge. Slide SMM 209b. Scale bar = 5 μm.

Fig. 22. Development of the first gonimolobe (arrow). Slide SMM 209a. Scale bar = 10 μm.

Fig. 23. Initiation of a secondary gonimolobe (arrow) from the gonimoblast initial (arrowhead). Slide SMM 209a. Scale bar = 25 μm.

Fig. 24, 25. Prominent spike-like projection on the auxiliary cell (arrow), representing the remains of the connecting filament. Slide SMM 209a. Scale bar = 10 µm.

Fig. 26. Development of a tertiary gonimolobe (arrow) on the side of the gonimoblast initial (arrowhead). Slide SMM 209a. Scale bar = 25 µm.

Fig. 27. Sequentially maturing secondary carposporangia (arrow) at the base of the primary gonimolobe. Slide SMM 209a. Scale bar = 50 µm.

Predaea weldii **Kraft & I. A. Abbott 1971, p. 194 (Nemastomataceae)**

Figs 28–35

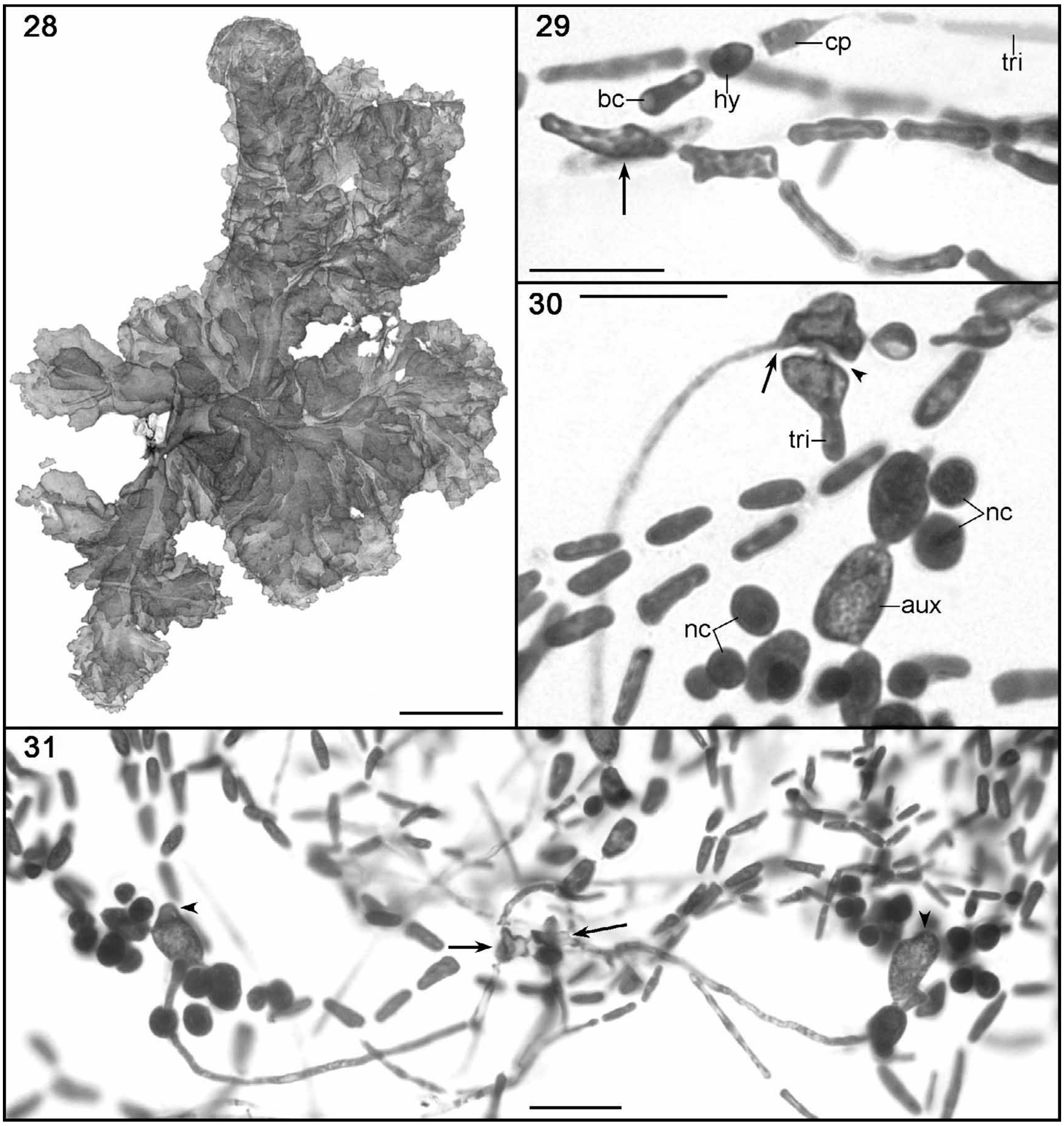
SPECIMENS EXAMINED: **Oman:** Masirah Island, Coral Garden (site 01: 20°10'15"N, 58°37'80"E), 3 November 1999, subtidal: –3 m, leg. T. Schils (MAS 002); Masirah Island, 6 November 1999, subtidal, leg. A. Couté (MAS 077); Masirah Island, around the rock (site 07: 20°12'51"N, 58°36'87"E), 8 November 1999, subtidal: –8 m, leg. T. Schils (MAS 111). Platforms with dominant *Spatoglossum asperum* vegetations. Many *P. weldii* specimens growing on the boulders of the rocky platform.

DISTRIBUTION: Australia, Fiji, Hawaii, Oman, Papua New Guinea, Puerto Rico, South Africa, Venezuela (Kraft 1984; Millar 1990; N'Yeurt *et al.* 1996; Ballantine & Aponte 1997; Huisman 1997; Phillips 1997; Abbott 1999; Coppejans & Millar 2000; Huisman 2000; De Clerck *et al.*, in press; this paper).

Thalli are bright red, mucilaginous and foliaceous, with numerous blunt, tapering branchlets, and grow up to 12 cm tall (Fig. 28). The pseudodichotomous cortical filaments consist of 12–21 rectilinear cells (11–17 µm × 3.5–5.5 µm), some producing rhizoidal filaments. Inner cortical cells measure 20–75 µm × 5–12 µm. Gland cells are absent. Medullary filaments vary in size from 28–205 µm × 2–5 µm.

Three-celled carpogonial branches (Fig. 29) develop from a cortical filament cell (the supporting cell, 10.5–19 µm × 5.5–7.5 µm). The basal cell is cylindrical in shape (6.5–13.5 µm × 4–6.5 µm), the hypogynous cell subspherical (5.5–9 µm × 4.5–7 µm); the conical carpogonium has a blunt distal end (9.5–13 µm × 3.5–5 µm) and bears a straight terminal trichogyne. After presumed fertilization, the zygote enlarges and divides transversely (Fig. 30). The basal part then produces connecting filaments prior to the degeneration of the trichogyne (Fig. 30). Throughout the thallus, the branched connecting filaments occasionally develop small cells (Fig. 31) that give rise to multiple connecting filaments extending out in all directions. The auxiliary cell develops in an intercalary position in a cortical filament and is often uteriform in shape (16.5–22.5 µm × 9–13 µm). Small aggregations [1–4 tiers, each consisting of 1–2(–3) cells] of large spherical nutritive cells (5.5–10 µm in diameter) are attached to the cortical cell, subtending the auxiliary cell and the distal two cortical cells that originate from it (Figs 30, 31). After the fusion of a connecting filament at the basal side of an auxiliary cell, the latter protrudes terminally (Fig. 31; 24–37.5 µm × 9.5–14 µm) and divides transversely at its terminal end, initiating a gonimoblast initial (7–10 µm in diameter; Fig. 32). This is followed by a distal transverse division of the gonimoblast initial, giving rise to the primary gonimolobe initial (Fig. 32). The latter divides first transversely and then twice obliquely (perpendicular to one another) to develop the first gonimoblast cells. These cells continue to divide along different axes and constitute the first gonimolobe. Secondary and tertiary gonimolobes (Figs 33, 34) develop sequentially from the sides of the gonimoblast initial, but the carposporangia (up to 12 µm in diameter) mature synchronously.

During cystocarp development the cells bearing the nutritive cell aggregations stain deeply with Aniline Blue and enlarge, and the pit connections towards the auxiliary cell expand.



Figs 28–31. *Predaea weldii.*

Fig. 28. Habit of a female gametophyte, MAS 002. Scale bar = 2 cm.

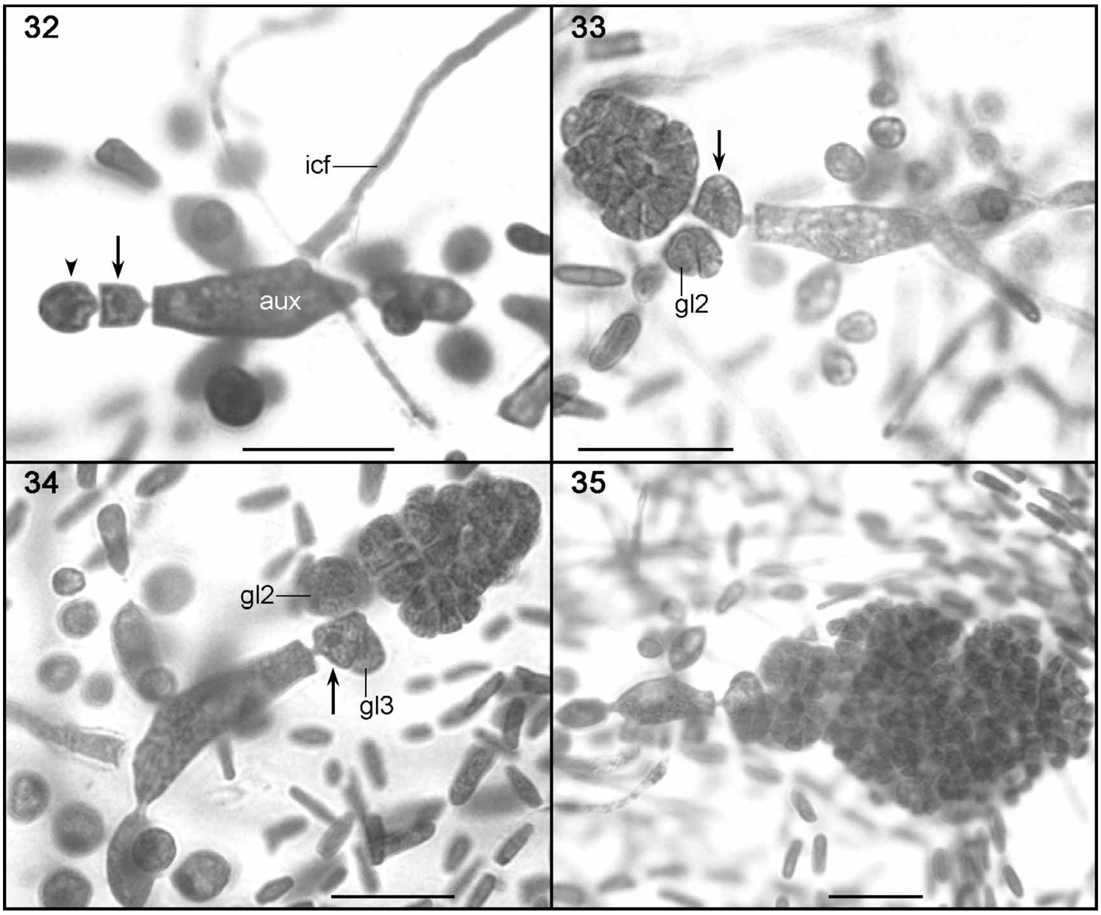
Fig. 29. In an intercalary position in a cortical filament, a supporting cell (arrow) bears a three-celled carpogonial branch consisting of a cylindrical basal cell (bc), a subspherical hypogynous cell (hy) and a conical carpogonium (cp) with a straight terminal trichogyne (tri). Slide MAS 002b. Scale bar = 25 μm.

Fig. 30. Upon enlargement, the fertilized carpogonium divides transversely (arrowhead) and the basal part initiates connecting filaments (arrow). The trichogyne (tri) remains perceptible on the distal part of the carpogonium. The cortical filament supports a carpogonial branch as well as an undiploidized auxiliary cell (aux). The cortical cells adjacent to the auxiliary cell bear large subspherical nutritive cells (nc). Slide MAS 111a. Scale bar = 25 μm.

Fig. 31. Small cells (arrows), in an intercalary position in connecting filaments, give rise to multiple connecting filaments that branch throughout the thallus and diploidize auxiliary cells. The diploidized auxiliary cells protrude distally (arrowheads) before gonimoblast initiation. Slide MAS 002b. Scale bar = 25 μm.

REMARKS: The Omani material differs from the original description of *P. weldii* (Kraft & Abbott 1971) in the transverse division of the zygote prior to connecting filament initiation. Millar & Guiry (1989) discussed this feature in *P. kraftiana* and noted that Lemus &

Ganesan (1977) depicted this trait for *P. weldii*, without mentioning it. Previous doubts (Kraft & Abbott 1971; Kraft 1984; Millar & Guiry 1989) concerning the conspecificity of *P. pusilla* and *P. weldii* were clarified by Verlaque (1990), who showed that the difference in gonimoblast initiation (lateral versus terminal) is the main diagnostic feature separating these species. Our Omani *P. weldii* specimens were gathered during the same season as when the species is abundant in eastern Australia (Kraft 1984).



Figs 32–35. *Predaea weldii.*

Fig. 32. A diploidized auxiliary cell (aux) with an incoming connecting filament (icf) laterally. Two subsequent transverse divisions of the diploidized auxiliary cell originate in a gonimoblast initial (arrow) and the first gonimolobe initial (arrowhead). Slide MAS 002b. Scale bar = 25 µm.

Figs 33, 34. Development of a secondary (gl2) and tertiary gonimolobe (gl3) from the gonimoblast initial (arrows). Slide MAS 002a. Scale bar = 25 µm.

Fig. 35. Carposporophyte with synchronously maturing gonimolobes. Slide MAS 002a. Scale bar = 25 µm.

Titanophora pikeana (Dickie) Feldmann 1942, p. 111 (Schizymeniaceae)

Figs 36–44

SPECIMENS EXAMINED: **Yemen:** Socotra, west of Rhiy di-Diblih (ST-021: 12°19'31"N, 53°59'59"E), 12 March 1999, subtidal: –6 m, leg. F. Leliaert (SOC 347); Socotra, Steroh (ST-037: 12°19'00"N, 53°52'51"E), 14 March 1999, subtidal: –15 m, leg. F. Leliaert (SOC 356); Socotra, east of Qatanhin, Quray (ALG-22: 12°18'55"N, 53°37'23"E), 9 April 2000, subtidal: –17 m, leg. T. Schils (SMM 216); Socotra, west of Bidholih (ALG-40: 12°18'46"N, 53°58'47"E), 30 April 2000, subtidal: –20 m, leg. T. Schils (SMM 448, SMM 496, SMM

497); **South Africa:** Sodwana Bay, dive site ‘Deep Sponge’, 11 February 2001, subtidal: –30 m, leg. O. De Clerck, S. Fredericq, W. Freshwater, F. Leliaert, A. Millar, T. Schils & E. Tronchin (KZN 2128).

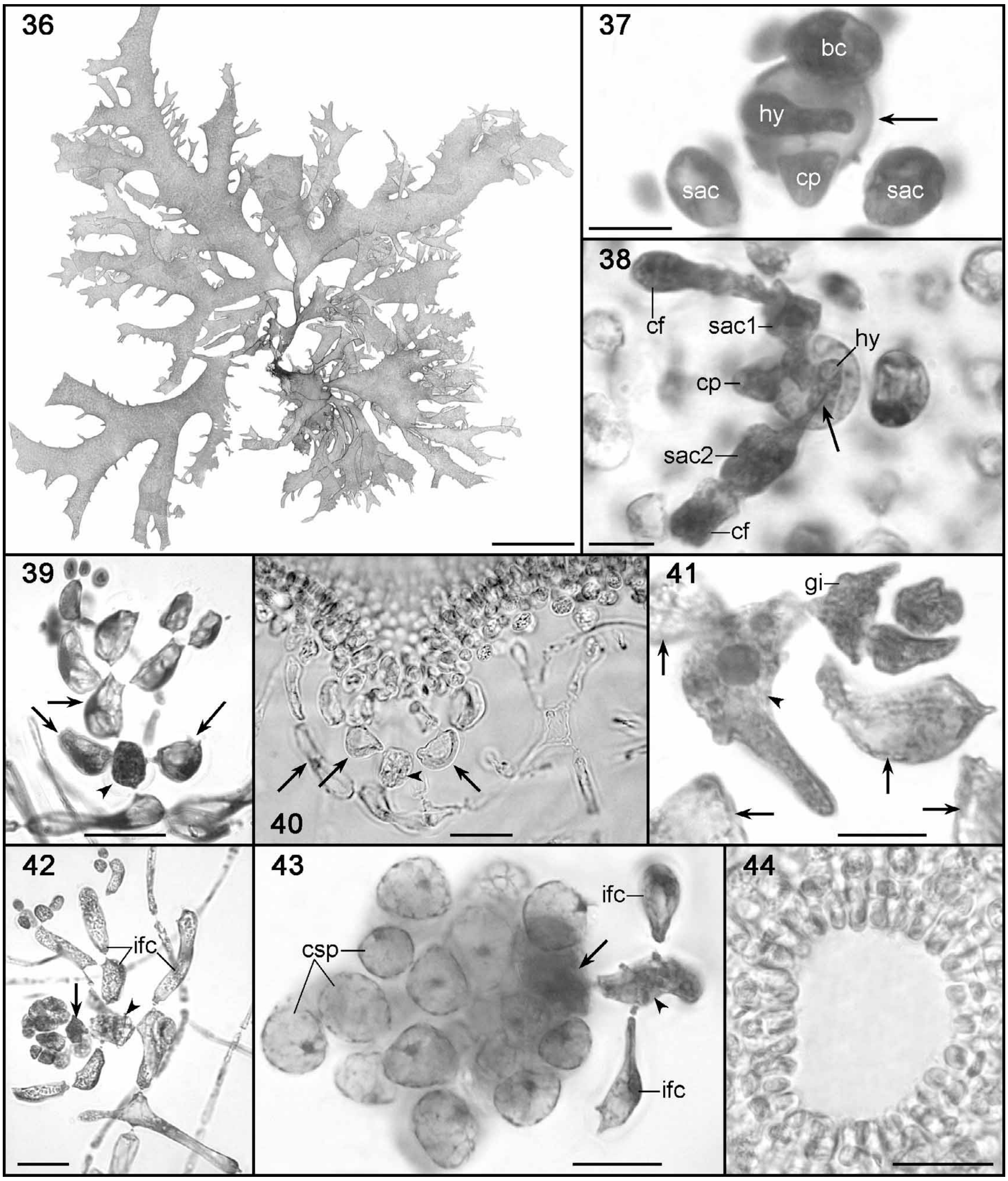
DISTRIBUTION OF *T. PIKEANA*: Egypt, Hawaii, Madagascar, Mauritius, Réunion, South Africa, Sri Lanka, Tanzania, Yemen (Nasr 1940; Feldmann 1942; Børgesen 1943, 1949, 1950; Mshigeni & Papenfuss 1980; Payri 1985; Bucher & Norris 1992; Norris 1992; Abbott 1999, Coppejans *et al.* 2000, this paper).

DISTRIBUTION OF *T. WEBERAE* BØRGESEN (SEE BELOW): Australia, French Polynesia, Indonesia, Japan, Kenya, Madagascar, Tanzania (Weber-van Bosse 1921; Børgesen 1943; Itono 1972; Farghaly 1980; Mshigeni & Papenfuss 1980; Huisman 1997; Huisman 2000; Payri *et al.* 2000).

Plants are whitish pink in colour. The flat thalli (420–725 µm thick) are narrow to broad, occasionally pertusate, with varying degrees of marginal proliferation (Fig. 36). Certain specimens lack calcification and in others the aragonite deposits are restricted to the medullary layer. The vegetative thallus consists of medullary filaments with large axial filaments (Norris 1992) in the central medulla, often resulting in X- and V-shaped cells as noted in other Nemastomataceae and Schizymeniaceae (Masuda & Guiry 1995). Cortical filaments are composed of four or five cells; the ultimate cells are oval to elongate (3.5–10 µm × 2–5 µm) and the underlying ones are subspherical in outline (4.5–21.5 µm in diameter). Prominent subspherical gland cells (17–65 µm in diameter) occur throughout the outer cortex. Cylindrical to club-shaped gland cells are found in an intercalary position in the medullary filaments. As in other Nemastomataceae and Schizymeniaceae taxa, the gland cell contents vary widely in appearance from dense and homogeneous, through coagulated, to granulate.

Only female gametophytes were present in our collections. A large subspherical supporting cell (13.5–17 µm) bears a three-celled carpogonial branch distally (Fig. 37), which is aligned in a plane parallel to the thallus surface. The oval basal cell measures 7–9.5 µm × 10.5–12.5 µm, the subrectangular hypogynous cell 4.5–7 µm × 9–16 µm, and the carpogonium 5.5–10 × 7–9 µm. Two deeply staining cortical cells (epi-supporting cells) flank the supporting cell, functioning as subsidiary auxiliary cells. Upon presumed fertilization of the carpogonium, one subsidiary auxiliary cell fuses with the carpogonium and the hypogynous cell. The diploidized subsidiary auxiliary cell initiates a connecting filament. The second subsidiary auxiliary cell then fuses with this complex at the hypogynous cell and initiates a connecting filament (Fig. 38). The connecting filaments disperse throughout the cortex and diploidize distant generative auxiliary cells. In contrast to the specimens investigated by Norris (1992), many undiploidized generative auxiliary cells were present in the cortex of the Socotran plants (Fig. 39). The latter cells (10.5–20 µm in diameter) are formed in an intercalary position in cortical filaments separate from those containing supporting cells and stain darkly with Aniline Blue. Recurved and elongate involucral cells (Figs 40–43) develop from the auxiliary cell and underlying branch systems prior to diploidization of the latter. The involucral cells branch di- or trichotomously and constitute involucral filaments of 3–5 cell layers. After fusion of a connecting filament with a generative auxiliary cell, the latter divides transversely and initiates an elliptical gonimoblast initial (7–22 µm × 13–32 µm). The gonimoblast initial generally produces two gonimolobe initials sequentially, giving rise to gonimolobes with carposporangia of different developmental stages. During cystocarp development, an ostiole is formed (Fig. 44);

cystocarps are 60–200 µm in diameter. Mature carposporangia are subspherical to ellipsoidal and measure 12–45 µm in diameter.



Figs 36–44. *Titanophora pikeana.*

Fig. 36. Habit of a female gametophyte, SMM 448. Scale bar = 3 cm.

Fig. 37. A large subspherical supporting cell (arrow) bears a three-celled carpogonial branch distally, consisting of an oval basal cell (bc), a subrectangular hypogynous cell (hy) and a carpogonium (cp). Two subsidiary auxiliary cells (sac) flank the supporting cell. Slide SMM 216d. Scale bar = 10 µm.

Fig. 38. One subsidiary auxiliary cell (sac1) fuses with the fertilized carpogonium (cp) and the hypogynous cell (hy). Upon diploidization, the former initiates a connecting filament (cf). Subsequently, the second subsidiary auxiliary cell (sac2) fuses with the hypogynous cell (arrow) and itself initiates a connecting filament (cf). Slide SMM 216d. Scale bar = 10 µm.

Fig. 39. Dark-staining undiploidized generative auxiliary cell (arrowhead) with involucral filament initiation (arrows). Slide SMM 216c. Scale bar = 25 µm.

Fig. 40. Recurved and elongated involucral cells (arrows) develop from the generative auxiliary cell (arrowhead) and the underlying branch systems prior to diploidization. Slide SMM 216e. Scale bar = 25 µm.

Fig. 41. The diploidized generative auxiliary cell (arrowhead), which bears involucral filament cells (arrows) and initiates the gonimoblast initial (gi) and gonimoblast cells. Slide SOC 356a. Scale bar = 10 μm.
Fig. 42. Developing carposporophyte with the auxiliary cell (arrowhead), the gonimoblast initial (arrow) and involucral filament cells (ifc). SMM 216b. Scale bar = 25 μm.
Fig. 43. Maturing carposporophyte with the auxiliary cell (arrowhead), the gonimoblast initial (arrow), involucral filament cells (ifc) and carposporangia (csp). Slide SOC 356a. Scale bar = 25 μm.
Fig. 44. Surface view of the ostiole of a mature cystocarp. Slide SMM 216e. Scale bar = 25 μm.

REMARKS: Differences in habit were the main characteristics used at first to distinguish *Titanophora* species (Børgesen 1943, 1949). Mshigeni & Papenfuss (1980), Bucher & Norris (1992) and Norris (1992) reported on variability of habit and on minor differences in thallus shape and reproductive structures among these species. Later species descriptions (Itono & Tsuda 1980; Bucher & Norris 1992) were based predominantly on anatomical characteristics. Conspecificity of *T. pikeana* and *T. weberae* has been proposed by various authors (Mshigeni & Papenfuss 1980; Norris 1992; Abbott 1999), and there is a need for developmental studies on pre- and postfertilization events in *Titanophora* species (Masuda & Guiry 1994). The Socotran plants fitted both species descriptions and the specimens were identified as *T. pikeana*, which is the earlier name. Additionally, the specimens agree with the description of *T. mauritiana* Børgesen, which is distinguished principally by the restriction of calcium carbonate crystals to the medullary layer. Variation in thallus shape and calcification was observed throughout the Socotran samples, without clear differences in reproductive or anatomical structures. Therefore, we conclude that the Socotran plants represent one species with diverse morphotypes. In supporting Norris' point of view (1992) on the conspecificity of *T. pikeana* and *T. weberae*, we additionally compared the Socotran samples with a female gametophyte from the locality he included in his study (Sodwana Bay, South Africa). No differences in the above-described characteristics could be observed among the *Titanophora* plants of Socotra and South Africa.

Owing to the low degree of calcification, the specimens were analysed by transverse sections without an HCl treatment prior to microscopy. This might explain why the compact cortex remained intact (versus separated filaments) and hence the difference in carpogonial branch organization compared to the observations of Mshigeni & Papenfuss (1980).

Our account of postfertilization events in *Titanophora* corresponds to Itono's (1984) observations, viz. initiation of connecting filaments from both subsidiary auxiliary cells. However, the connecting filaments did not develop from the cells distal to one of the subsidiary auxiliary cells (Itono 1984; see above: *Platoma heteromorphum*), probably as a consequence of the fact that the carpogonial complex we observed was in an early postfertilization stage. In addition, the diploidization events differed for both subsidiary auxiliary cells. The fertilized carpogonium in *T. pikeana* fuses entirely with a single subsidiary auxiliary cell and the hypogynous cell. The second subsidiary auxiliary cell then fuses with this complex at the hypogynous cell. Further studies should demonstrate if the latter postfertilization events could be used as a diagnostic feature for the genus within the Schizymeniaceae.

DISCUSSION

The species we studied from the Arabian Sea suggest a great affinity with the gelatinous red algal flora of Australia and especially of the Great Barrier Reef. However, the new records of *Dudresnaya capricornica* from Saudi Arabia, *Gibsmithia larkumii* from Tanzania, and *Predaea weldii* from South Africa show that many gelatinous red algae may have a wider distribution range within the Indian Ocean. Hommersand (1986) states that these rather 'primitive' algae are widely distributed in the tropics and in regions that bordered the original Tethyan Ocean. A report of two *Reticulocaulis* I.A. Abbott species from Oman and Yemen (our unpublished observations) seems to support the latter hypothesis by their disjunct distribution pattern in the Arabian Sea and Hawaii (Abbott 1985, 1999). The scarce reports of gelatinous red algae in the Indian Ocean are probably a result of their seasonal appearance and a lack of sublittoral studies. Indeed, previous claims of biogeographical links with distant areas, such as Australia, Japan and South Africa (Børgesen 1934; Wynne 2000) cannot be confirmed using representatives of the Dumontiaceae, Nemastomataceae and Schizymeniaceae. The disjunct distribution of gelatinous rhodophytes of the Arabian Sea is therefore an artefact of the research done in the Indo-Pacific, as many of the intervening regions have been studied inadequately.

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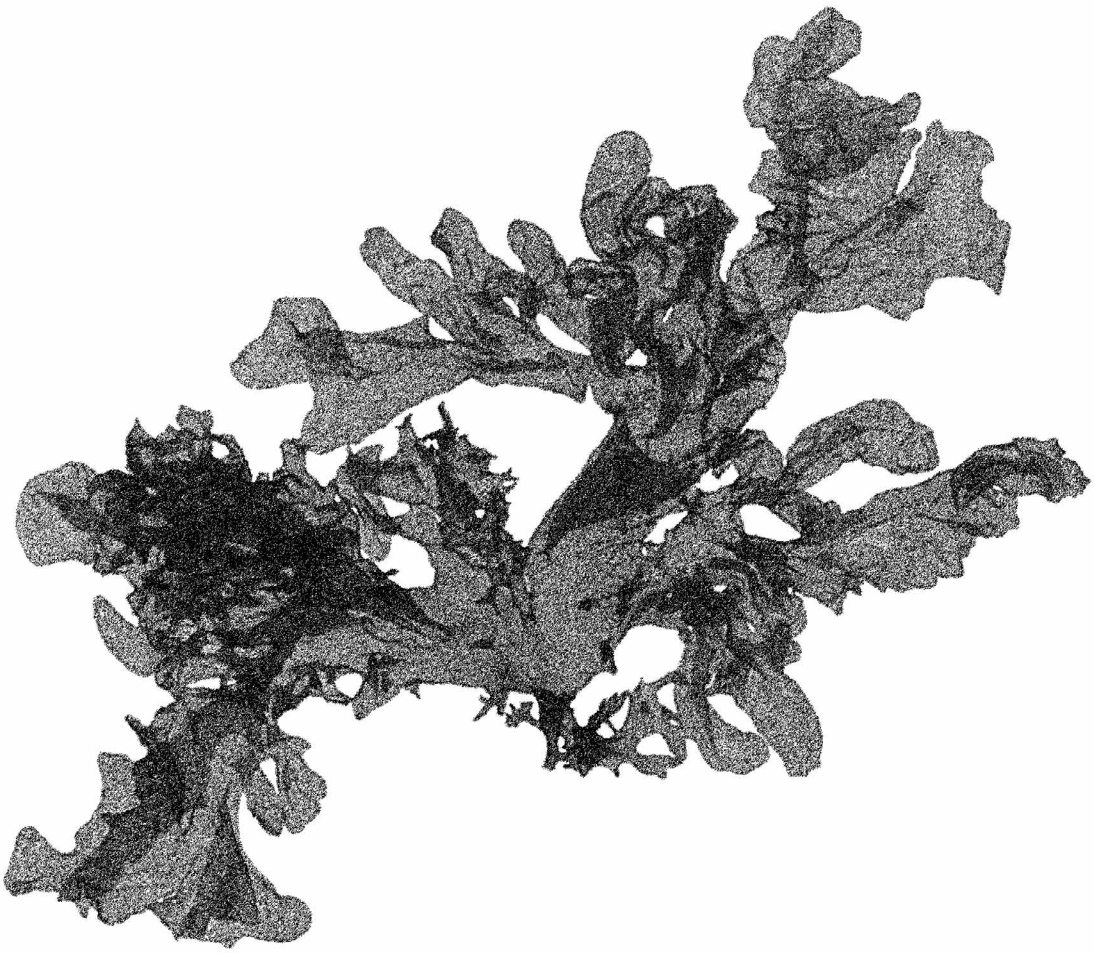

Platoma heteromorphum Schils: a new red algal species described from the southeast coast of Masirah Island (see *chapter 2*).

CHAPTER 3

The red algal genus *Reticulocaulis* from the Arabian Sea, including *R. obpyriformis* sp. nov., with comments on the family Naccariaceae

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ABSTRACT

Reticulocaulis obpyriformis Schils, *sp. nov.*, is described from the south coast of Socotra Island (Yemen), and a second species, *R. mucosissimus*, is recorded from a similar upwelling area in the Arabian Sea (Masirah Island, Oman). These are the first published records of Naccariaceae for the Indian Ocean and end the monospecific, Hawaiian-endemic status of *Reticulocaulis*. Features distinguishing *R. obpyriformis* from *R. mucosissimus* include its more sparsely branched thallus, obpyriform rather than cylindrical inner cortical cells, the presence of short moniliform laterals of small spherical cells on the cortical filaments, monoecious rather than dioecious gametophytes, and the direct development of spermatangia from catenate mother cells. The morphology and anatomy of the gametophytes of this heteromorphic genus are discussed in relation to those of other naccariacean genera.

INTRODUCTION

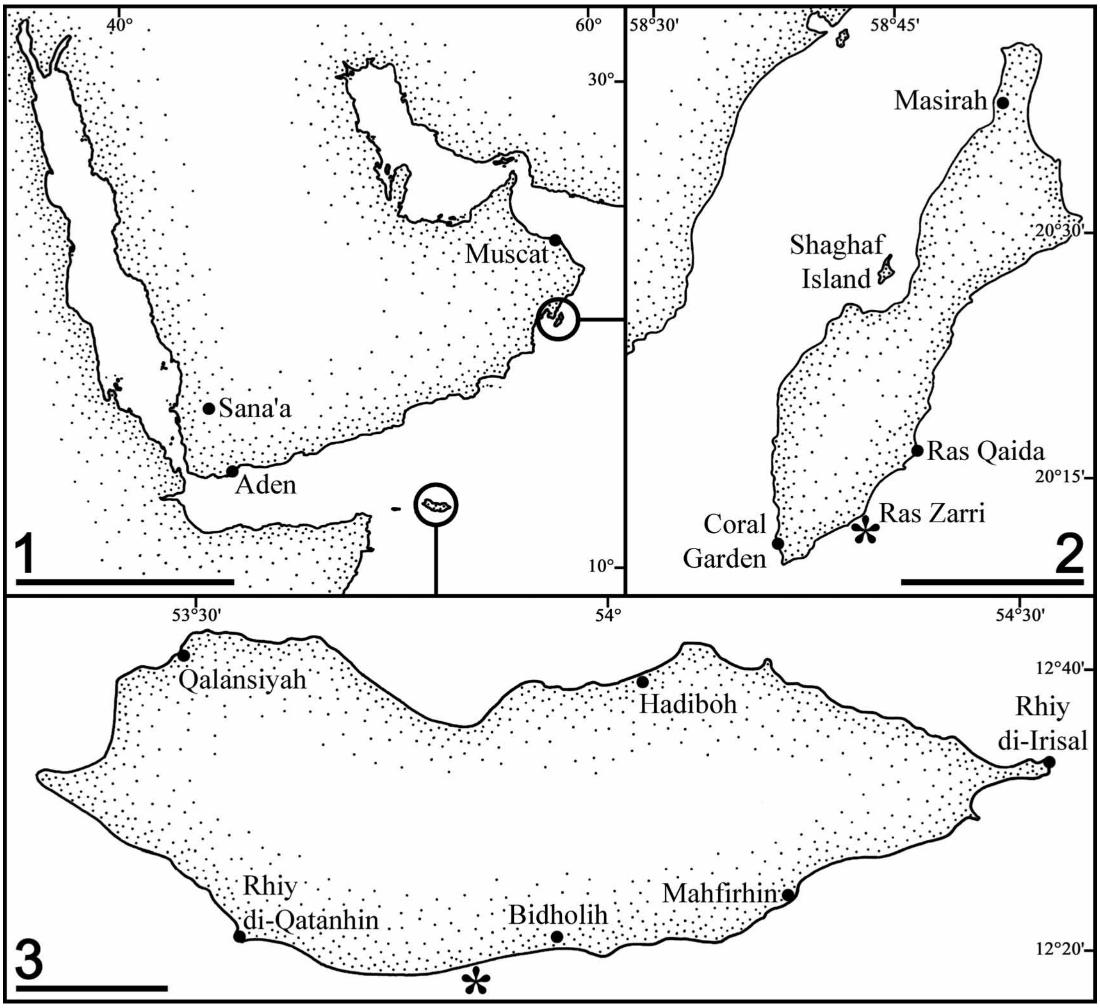
Recent phycological studies in the Arabian Sea and the northern Indian Ocean have resulted in the description of new taxa (Wynne 1999a) and a plethora of new records (Wynne & Banaimoon 1990; Wynne & Jupp 1998; Wynne 1999b, 2000) indicative of a unique marine benthic flora. The south-west monsoon that results in upwelling along the south-eastern coastline of the Arabian Peninsula (Currie *et al.* 1973; Ormond & Banaimoon 1994) is an important physical phenomenon influencing these neritic ecosystems and their biotas, particularly those of Masirah Island (Oman) and the Socotra Archipelago (Yemen), which support a seasonally rich diversity of gelatinous red algae (Schils & Coppejans 2002). Among the more unexpected of the algae recently discovered, there are two species of *Reticulocaulis*, a hitherto monotypic genus thought to be confined to Hawaii in the central Pacific Ocean and a member of the relatively little-known and infrequently encountered family Naccariaceae.

Following the recommendations of Kylin (1928), Svedelius (1933) and Feldmann & Feldmann (1942), the Naccariaceae is generally included in the order Bonnemaisoniales, based on details of gonimoblast development and the presence of nutritive-cell clusters on the carpogonial branch (Chihara & Yoshizaki 1972), an ordinal placement supported by ultrastructural characters of the pit plugs (Pueschel & Cole 1982). Womersley (1996), however, commented that the family might not be related to the Bonnemaisoniaceae, because of some seemingly major differences in the carposporophyte, such as a diffuse rather than compact gonimoblast and the complete absence of a pericarp. Abbott (1999) recently placed the Naccariaceae in the Gigartinales without specifying her reasons for the transfer. The Naccariaceae currently comprises the genera *Atractophora* P. Crouan & H. Crouan, *Naccaria* Endlicher and *Reticulocaulis* I.A. Abbott. Despite consisting of only seven species, of which five belong to *Naccaria*, the family is widely distributed throughout the Atlantic and Pacific Oceans. Although a single robust female gametophyte of *Naccaria naccarioides* (J. Agardh) Womersley & I.A. Abbott is known from the Indian Ocean coast of Western Australia (GEN-10793e, MELU: *leg.* G.T. Kraft & G.W. Saunders, 7.x.1995, Pinaroo, Western Australia, 32.20°S, 115.45°E), the present paper is the first published report of a member of the Naccariaceae from anywhere in the Indian Ocean.

MATERIAL AND METHODS

The east coast of Masirah Island (Oman; 20.42°N, 58.79°E; Figs 1, 2) and the south coast of Socotra (Yemen; 12.47°N, 53.87°E; Figs 1, 3) are influenced by a seasonal coastal upwelling from May to September, during the south-west monsoon. The specimens of this report were found in similar habitats around Masirah and Socotra, viz. rocky platforms at 10–20 m depth on which macroalgae were the most abundant benthic organisms, interspersed with isolated small hard and soft coral colonies. Gelatinous red algae such as *Dudresnaya* P. Crouan & H. Crouan, *Gibsmithia* Doty, *Platoma* Schousboe *ex* Schmitz and *Predaea* De Toni species (Schils & Coppejans 2002) were particularly conspicuous during early winter and late spring periods, other associated algae being *Amphiroa* J.V. Lamouroux spp., *Callophycus* Trevisan sp., *Caulerpa peltata* J.V. Lamouroux, *Euptilota fergusonii* Cotton, *Galaxaura marginata* (Ellis & Solander) J.V. Lamouroux, *Halimeda* J.V. Lamouroux spp., *Lobophora variegata* (J.V. Lamouroux) Womersley *ex* Oliveira, *Rhodymenia* Greville spp., *Spatoglossum asperum* J. Agardh, and *Udotea indica* A. Gepp & E. Gepp.

Specimens of *Reticulocaulis* were collected by the first author during field trips to Masirah Island in 2–30 November 1999 and Socotra in 26 March–7 May 2000, the subtidal habitats being accessed by means of SCUBA. Collected algae were pressed on herbarium sheets, with portions preserved in a 5% formalin–seawater solution. Herbarium sheets, wet specimens and microscope slides are deposited in GENT (Ghent University Herbarium, Krijgslaan 281 / S8, 9000 Ghent, Belgium). Slides and formalin-preserved samples of Hawaiian *Reticulocaulis mucosissimus* I.A. Abbott were kindly supplied by I.A. Abbott of the Bernice Bishop Museum (BISH). Herbarium sheets of *Naccaria corymbosa* J. Agardh and *N. wiggii* (Turner) Endlicher were borrowed from the National Herbarium of the Netherlands (L). Material for microscopical examination was stained with Aniline Blue, Fast Green or Lugol's Iodine (for rhodoplasts). Material for nuclear and pit-connection studies was stained using Wittmann's aceto-iron-haematoxylin–chloral hydrate (Wittmann 1965), following the procedures of Hommersand & Fredericq (1988). Anatomical and reproductive characteristics were observed from tissue squashes (whole-mounts in a 50% corn syrup-water solution, containing a few drops of phenol) using light microscopy (Leitz Diaplan). Photographs were taken with a Wild MPS51 35-mm camera and on an Olympus DP50 digital camera.



Figs 1–3. Collection sites of *Reticulocaulis* in the Arabian Sea. Scale bars = 1000 km (Fig. 1) or 20 km (Figs 2, 3).

Fig. 1. The Arabian Peninsula showing Masirah Island and Socotra.

Fig. 2. Sample Site 9 (asterisk; 20.199°N, 58.715°E), near Ras Zarri, off Masirah Island, Oman.

Fig. 3. Sample site ALG-40 (asterisk; 12.303°N, 53.843°E), west of Bidholih, off Socotra, Yemen.

RESULTS

Reticulocaulis mucosissimus I.A. Abbott 1985, p. 555

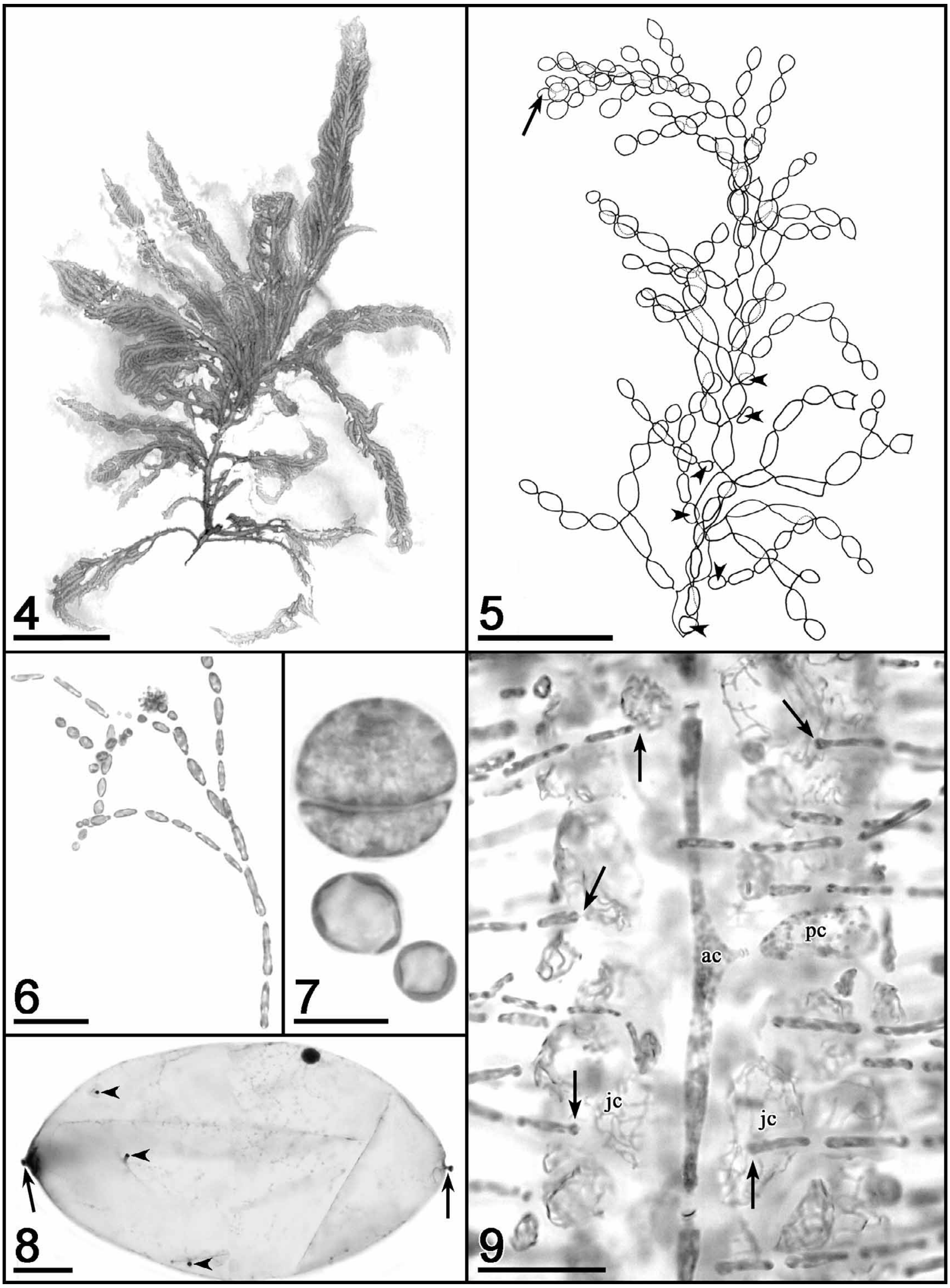
SPECIMENS EXAMINED: **Oman.** Masirah Island (Figs 1, 2): Sample site 9 (20.199°N, 58.715°E), close to Ras Zarri. A rocky platform at 9 m depth with scattered rocky outcrops in an area of strong surge (*Schils*, 9.xi.1999). MAS 138: female (Fig. 4) and male gametophytes. **Hawaii.** Mahukona, north-west coast of Hawaii. Plants growing on dead coral at a depth of 9 m (*K. J. McDermid*, 26.v.1998). Formalin sample IA 23471 (female gametophyte) and slide KM 4481 (female gametophyte); Kawailoa, Oahu Island (*W. H. Magruder & S. Carper*, 10.v.1985). Slide IA 17225: female gametophyte.

Thalli are bright red, mucilaginous, and attached by a discoid holdfast (Fig. 4). Omani plants reach 13 cm in length and grow from dome-shaped apical cells that divide obliquely, the immediate daughter cells being aligned in a nearly straight row (Fig. 5). The axial cells are slender and elongate, those lying 1 mm away from the apical cells having length : width ratios of > 4 : 1. The first periaxial cell (the ‘superior’ periaxial) is cut off three axial cells from the apex and superior periaxial cells on successive segments are produced in an irregular 1/4 spiral. A second periaxial cell (the ‘inferior’ periaxial) is always positioned proximal to the first. It is generally cut off in cells positioned 15–20 cells away from the apex (Fig. 5) and at a 90° angle to the first periaxial cell. At the same time, several rhizoidal outgrowths develop from both periaxial cells; these outgrowths branch. Besides differing in the timing of their initiation, the shapes of the two periaxial cells are also dissimilar: the superior periaxial cell becomes elongated and rectilinear, whereas the inferior one remains spherical (Fig. 5). The inferior lateral becomes the more developed of the two laterals and occasionally gives rise to indeterminate branches as it continues growing and initiates periaxial cells. Infrequently, an axial cell can initiate a third periaxial cell, which develops like the superior lateral. The derivatives of the periaxial cells (from about the 15th axial cell) differentiate rapidly by branching and cell elongation into determinate filaments that constitute the cortex. The inner cortical cells are cylindrical (Fig. 6), whereas the outer cells remain ovoid to (sub)spherical.

Two-celled propagules, reaching 16.5 µm in diameter (Fig. 7) and developing terminally on many of the cortical filaments, were observed in slide IA 17225 of a specimen from Hawaii. One or two axial cells below the site where the second periaxial cell first forms, both periaxial cells initiate rhizoidal downgrowths. The periaxial cells and the rhizoidal downgrowths inflate into what were termed ‘jacket cells’ by Abbott (1985), viz. cells that mutually cross-connect by lateral secondary pit connections (Fig. 8) and constitute a sheath around the central-axial strand (Fig. 9). While maturing, the pit connections of the jacket cells attenuate and become difficult to distinguish, which results in a seemingly parenchymatous covering. Before the covering is complete, the jacket cells initiate secondary cortical filaments that are either fasciculate or unbranched, as well as secondary rhizoidal downgrowths. In older parts of the thallus, the jacket cells become densely covered by these secondary rhizoidal filaments, which rarely branch and form uniseriate rows that cross one another, but actually constitute a single layer.

The rhodoplasts are discoid but like erythrocytes in shape (2-4 µm in diameter), having centres that are thinner than the margins.

Female gametophytes have carpogonial branches that are of accessory origin; they were found throughout the thallus in various stages of development. Near the apex, carpogonial branches arise singly from either of the periaxial cells. Further down the thallus, they also develop from other jacket cells (rhizoidal filament cells) and the lower cortical filament cells. Pairs of carpogonial branches on a single supporting cell are infrequently seen. The branches consist of 7–13 equally-staining cells, which, following the terminology of Lindstrom (1984), can be designated by numbers starting with the carpogonium (#1). Eccentric positioning of the primary pit connections results in a zigzag arrangement of carpogonial-branch cells when viewed dorsally or ventrally (Fig. 12). The carpogonial branch curves sharply toward the axis bearing it and the carpogonium arises adaxially on cell #2, the hypogynous cell (Figs 10, 11). The initially short and reflexed trichogyne can elongate to over 500 µm (Figs 12, 13; Abbott 1985).



Figs 4–9. *Reticulocaulis mucosissimus*. ac = axial cell; jc = jacket cell; pc = periaxial cell. Vegetative features. Scale bars = 2 cm (Fig. 4); 50 μm (Figs 5, 6); 10 μm (Fig. 7); 50 μm (Fig. 8, 9).

Fig. 4. Female gametophyte (pressed herbarium specimen) from Masirah Island; MAS 138.

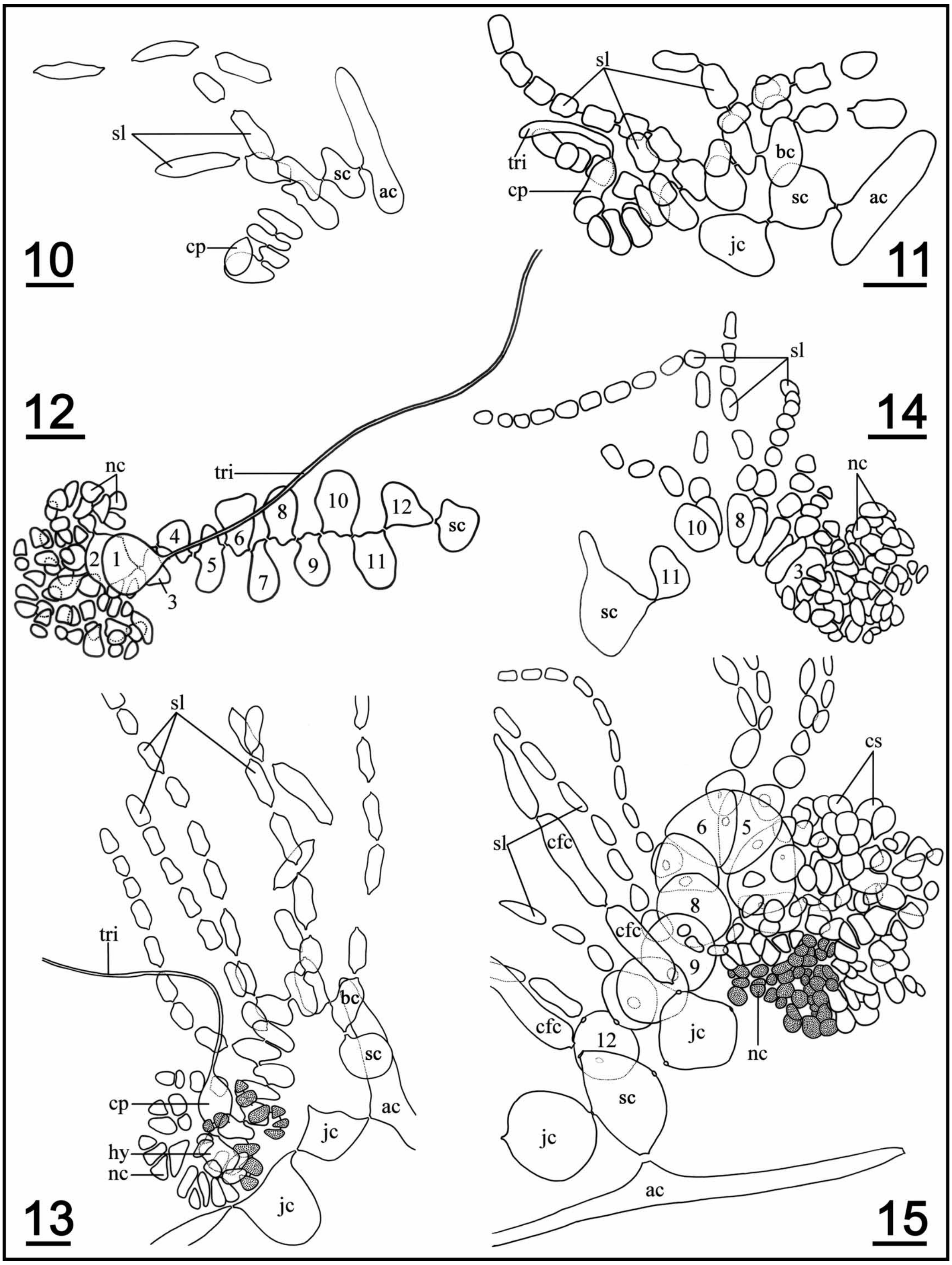
Fig. 5. Apex of an indeterminate axis, showing the apical cell (arrow) and periaxial cells (arrowheads); KM 4481.

Fig. 6. The transition from cylindrical inner- to spheroidal outer-cortical cells; MAS 138.

Fig. 7. Two-celled propagules on a Hawaiian specimen; IA 17225.

Fig. 8. Detail of an inflated jacket cell in a Hawaiian specimen, showing primary (arrows) and lateral secondary pit connections (arrowheads); IA 23471.

Fig. 9. Sheath of jacket cells around the central-axial strand, showing secondary cortical filament initiation (arrows); MAS 138.



Figs 10–15. *Reticulocaulis mucosissimus*. Carpogonial and carposporophyte morphology (MAS 138). ac = axial cell; bc = basal cell of carpogonial branch; cfc = cortical filament cells; cp = carpogonium; cs = carposporangium; jc = jacket cell; nc = nutritive-cell cluster; sc = supporting cell of carpogonial branch; sl = sterile lateral; tri = trichogyne. Scale bars = 10 μm.

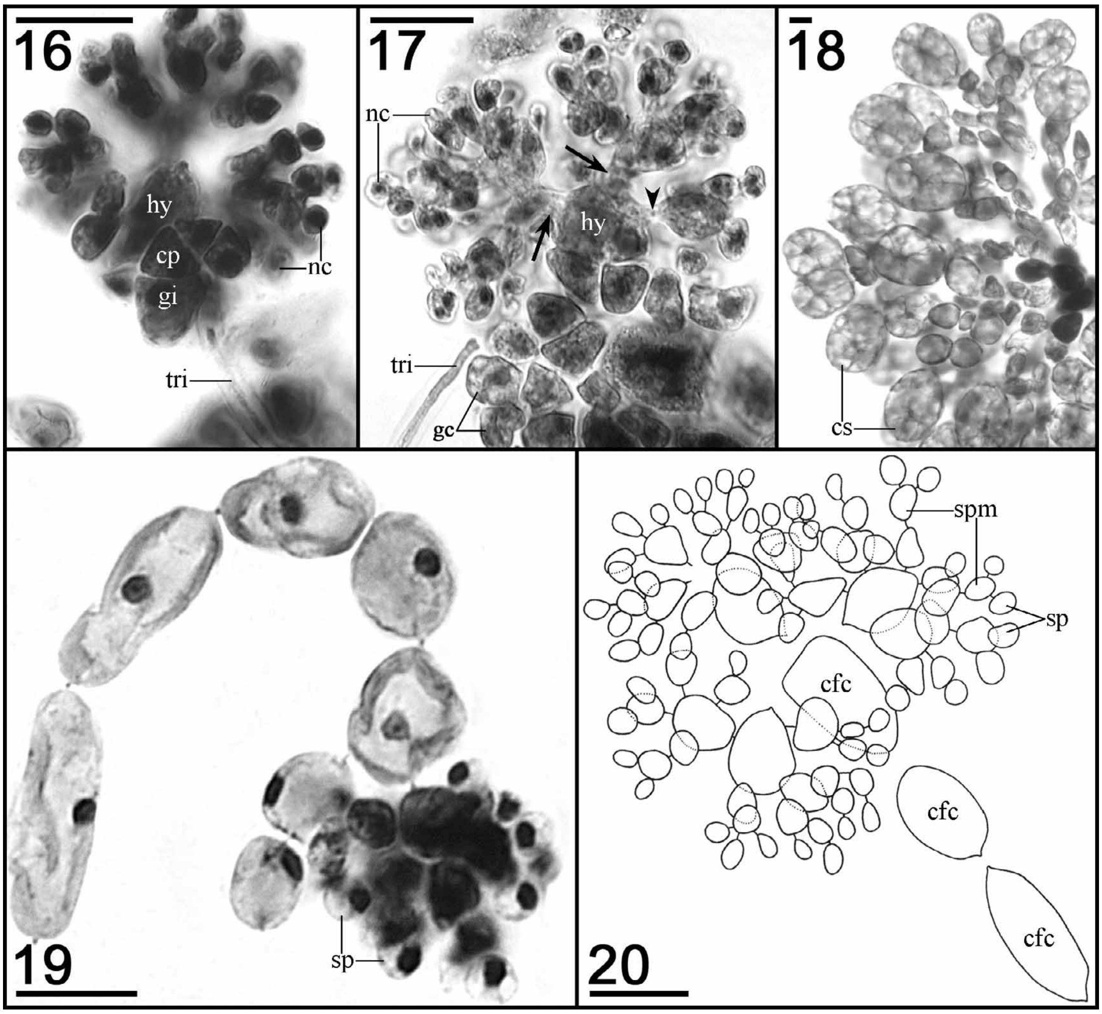
Fig. 10. Seven-celled carpogonial branch before elongation of trichogyne from the carpogonium, with sterile laterals growing from the lower cells.

Fig. 11. Young carpogonial branch, on which the carpogonium has produced a reflexed trichogyne and sterile laterals have arisen from most of the proximal cells. A jacket cell has also been initiated by the supporting cell.

Fig. 12. Dorsal view of a mature carpogonial branch, showing the zigzag arrangement of the cells and densely clustered nutritive cells borne on the hypogynous cell (cell #2).

Figs 13, 14. Lateral views of carpogonial branches bearing nutritive-cell clusters on the hypogenous cell and on cells #3, #4 (shaded), and lengthy sterile laterals on more proximal cells.

Fig. 15. Early carposporophyte development, showing the nutritive-cell clusters (shaded) and carposporangium initiation. The carpogonial branch cells and the basal cells of the sterile laterals inflate and pit connections widen. Cortical filaments arise from jacket cells.



Figs 16–20. *Reticulocaulis mucosissimus*. Cystocarpic and spermatangial features. (MAS 138). cfc = cortical filament cell; cp = carpogonium; cs = carposporangium; gc = gonimoblast cell; gi = gonimoblast initial; hy = hypogynous cell; nc = nutritive cell; sp = spermatangium; spm = spermatangial mother cell; tri = trichogyne. Scale bars = 10 µm.

Fig. 16. Division of the (presumably fertilized) carpogonium to produce the gonimoblast initial. Nutritive-cell filaments are borne on the hypogynous cell, and the trichogyne is still attached to the carpogonium.

Fig. 17. Fusion of the nutritive-cell clusters to the hypogynous cell through primary pit connections (arrowhead), in which the pit plugs progressively break down (arrows), resulting in broad open passageways. Gonimoblast cells are larger and more angular than nutritive cells and abut the clusters next to the remnant trychogyne.

Fig. 18. Ovoid terminal carposporangia borne on angular penultimate cells of branched gonimoblast filaments.

Fig. 19. Spermatangia forming in dendroid clusters on one of a pair of ultimate branches of a cortical filament, the cells of the second branch remaining sterile.

Fig. 20. Detail of a dendroid spermatangial cluster: the spermatangia are borne mostly in pairs on subterminal mother cells.

Cell #2 initiates a cluster of 4–6 branched filaments of tightly packed nutritive cells (Fig. 14), whereas cells #3 and #4 tend to bear a primary, slightly branched lateral, a second slightly more branched lateral, and 1–3 small clusters of ramified nutritive cells (Fig. 13). Primary laterals, 6–16 cells in length and branched to two orders, form adaxially on most of the remaining carpogonial branch cells, the longest occurring on the most proximal cells (Figs 13, 14). Any of the cells proximal to cell #4 may ultimately bear either an abaxial or an adaxial second sterile filament.

Upon presumed fertilization, the carpogonial branch cells and the basal cells of the sterile laterals inflate, and both the pit connections and the nuclei of these cells enlarge substantially (Fig. 15). The gonimoblast initial develops directly from the fertilized carpogonium (Fig. 16); at the same time, the nutritive cells fuse directly with the hypogynous cell through their pit connections, which retain their original size or expand only slightly as the pit plugs break down (Fig. 17). The passageways that are now open between the hypogynous cell and the nutritive cell clusters presumably become paths for direct nutrient transport to the developing gonimoblast. The carposporophyte remains compact, does not intermingle with vegetative tissue, and lacks a pericarp. Ovoid carposporangia (40 × 30 µm) terminate branches of the compact gonimoblast (Fig. 18); cystocarps at various stages of development are found scattered within the cortex and reach 330 µm in diameter.

Spermatangia are produced in terminal dendroid clusters on separate male gametophytes, the fertile axes often being accompanied by a sterile sibling cortical filament of one or two cells (Fig. 19). Spermatangial mother cells initiate 1–3 spermatangia (Fig. 20).

Tetrasporangial thalli were not collected in the course of this study and are unrecorded for the genus. In line with findings for other genera of the Naccariaceae (Jones & Smith 1970; Boillot & L'Hardy-Halos 1975), *Reticulocaulis* is presumed to have a heteromorphic life history involving a diminutive system of prostrate filaments bearing terminal tetrahedral tetrasporangia. Growth of Hawaiian *R. mucosissimus* in culture, reported by Abbott (1999, p. 123), resulted in a microscopic filamentous phase but no production of tetrasporangia.

Reticulocaulis obpyriformis* Schils, *sp. nov.

Affinis Reticulocaulis mucosissimis *Abbott (1985) sed differt characteribus pluribus. Gametophyta monoica; thallus pallido-roseolus pallidus, usque ad 15 cm altus, rami indeterminatis laxe et irregulatim ramificantibus. Cellulae corticis obpyriformes cylindricae; rami breves cellulis parvis sphaericis in filamento corticato, rarus evolutantes in axes indeterminatos; interdum trichomata in cellulis terminalibus rel subterminalibus corticis portata; cellulae axiales intra 1 mm sub apice latae ad 70(–80) µm. Spermatangia evoluta e filamenti corticalis cellulis distalibus. Praesentia duorum ramorum carpogonialium in cellula basali frequentior quam in* R. mucosissimo. *Filamenta lateralia secunda persaepe in cellulis proximis ramorum carpogonialium.*

Similar to *Reticulocaulis mucosissimus* Abbott (1985) but with the following distinguishing characters: gametophytes monoecious; thalli pale pink, to 15 cm high; branching of indeterminate axes loose and irregular. Cortical cells obpyriform and cylindrical; cortical filaments bearing short laterals consisting of small spherical cells and potentially developing into indeterminate axes; hairs occasional on terminal and subterminal cortical cells; axial cells broadening to 70(–80) µm within 1 mm of the apices. Spermatangia developing directly from catenate series of distal cortical cells. Supporting cells bearing two carpogonial branches occur more frequently than in *R. mucosissimus*. Secondary laterals common on proximal carpogonial branch cells.

HOLOTYPE: GENT, SMM 446 (Fig. 21)

TYPE LOCALITY: west of Bidholih, south coast of Socotra Island (Figs 1, 3). Sample site ALG-40 (12.303°N, 53.843°E): a rocky platform at –19 m covered with thin layers of sand and punctuated by deeper sand patches (*Schils*, 30.iv.2000).

ETYMOLOGY: *obpyriformis*, refers to the inverse pear shape of the cortical cells.

The thalli are terete, pale pink, and up to 15 cm in length (Fig. 21). Branching is irregularly radial, with a sparse development of up to four orders of indeterminate laterals. The dome-shaped apical cell divides obliquely, the immediate derivatives forming a sinusoidal pattern before the axial cells become aligned (Fig. 23).

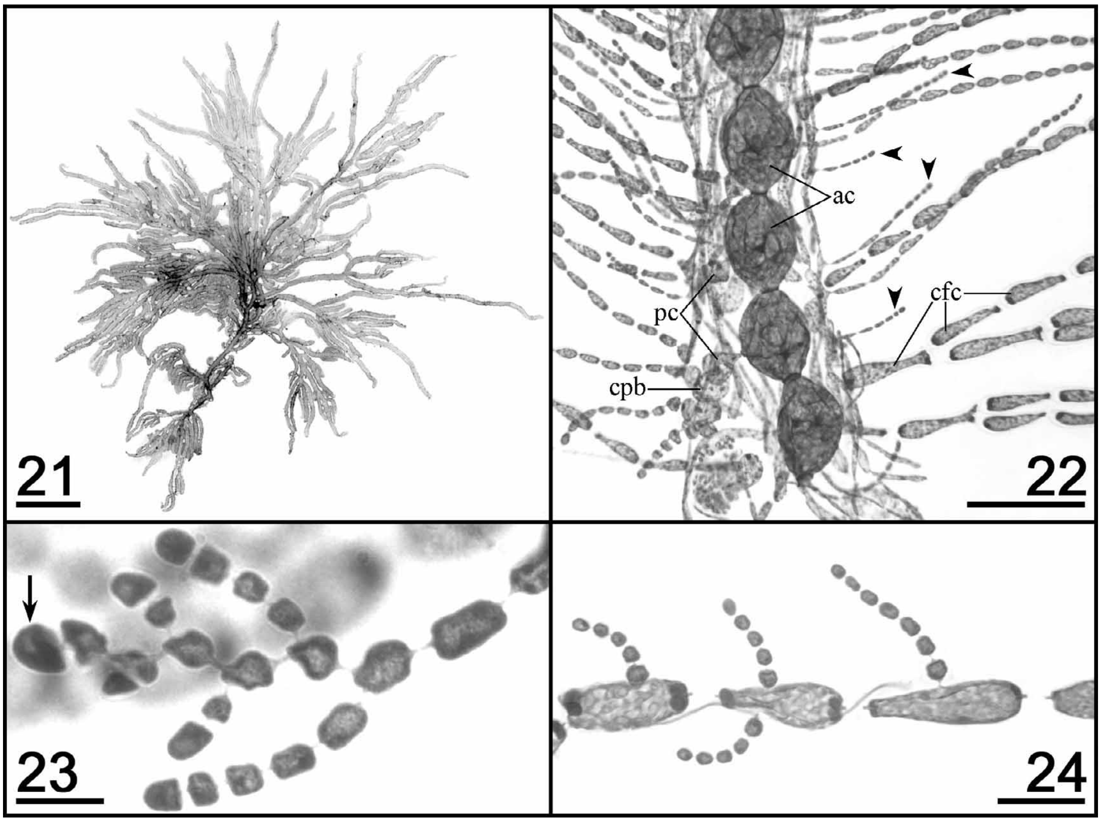
Within 1 mm of the apices, the axial cells broaden to attain length : width ratios of < 4 : 1 (Fig. 22). The superior periaxial cell is cut off at about the third axial cell behind the apex, the 'phyllotaxy' on successive segments being alternate (Fig. 23). Inferior periaxial cells, rhizoidal downgrowths and laterals develop from about the 40th axial cell downwards, at which time the phyllotaxy of the determinate laterals tends to become an irregular 1/4 spiral, because the inferior periaxials set in at a 90° angle to the superior periaxial cells. Derivatives of the inferior periaxial cells become more strongly developed than those of the superior cells and initiate the occasional indeterminate branch when the cortical filament continues growing and initiates periaxial cells. Third-order periaxial cells are very infrequently initiated in older parts of the thallus; they develop cortical filaments and jacket cells like the other periaxial cells.

The lower cells of the cortical filaments are predominantly obpyriform (Figs 22, 24), although cylindrical to barrel-shaped cells also occur (Fig. 24). The sizes and contours of the cortical cells change rather abruptly distally, from being elongated, obpyriform or cylindrical, and up to 90 µm long by 27 µm wide, to being small, spherical, and 4–6 µm in diameter. Hairs occasionally develop on terminal and subterminal cortical cells (Fig. 25), but propagules were not observed.

Certain cortical filaments bear short moniliform laterals of small spherical to ovoid cells (Fig. 24); these laterals can bear spermatangia, less often carpogonial branches, or may transform directly into indeterminate axes (the atypical way of indeterminate lateral formation: Fig. 23).

Several orders of rhizoidal downgrowths develop from the periaxial cells, the cells becoming inflated and linked by lateral secondary pit connections (Fig. 26) and forming a sheath around the axial strand (Fig. 27), in which the pit connections attenuate and become obscure. These jacket cells are spheroidal and may give rise to secondary cortical filaments. In older parts of the thallus, the jacket cells become densely covered by rhizoidal filaments. The rhizoidal filaments develop from periaxial cells and other jacket cells; they branch (Fig. 28) and some initiate secondary cortical filaments (Figs 22, 27, 28).

The rhodoplasts are discoid, have a distinctive 'erythrocyte' appearance (Fig. 29), and are 2–4 µm in diameter. As in *R. mucosissimus*, the rhizoidal and jacket cells contain fewer rhodoplasts than the cortical cells, and older axial cells virtually lack them altogether.



Figs 21–24. *Reticulocaulis obpyriformis*. Habit and vegetative features (SMM 446). ac = axial cell; cfc = cortical filament cell; cpb = carpogonial branch; pc = periaxial cell. Scale bars = 2 cm (Fig. 21); 100 µm (Fig. 22); 10 µm (Figs 23, 24).

Fig. 21. Holotype (a pressed monoecious specimen).

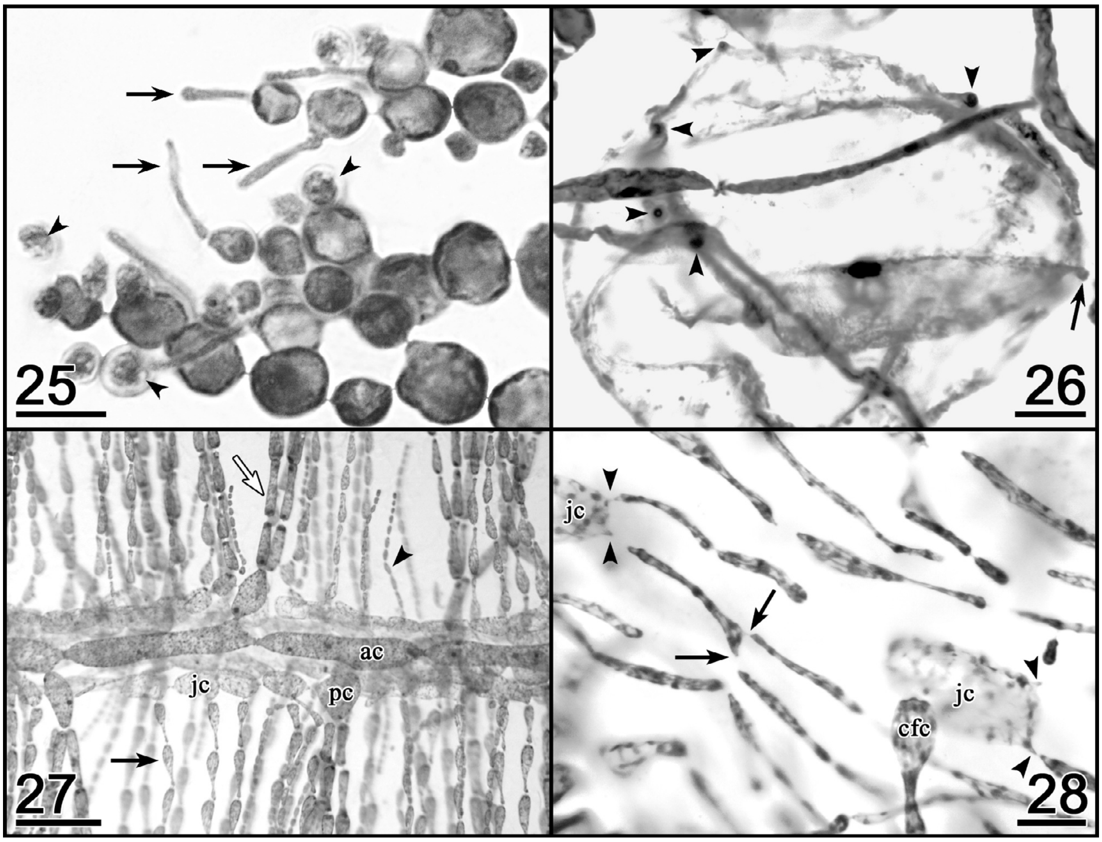
Fig. 22. Bead-like, inflated axial cells jacketed by derivatives of the periaxial cells and by rhizoids that give rise to unbranched secondary cortical filaments (arrowheads). Primary cortical filaments of obpyriform cells and a carpogonial branch are borne on the periaxial cells.

Fig. 23. Direct transformation of a short moniliform branch of a cortical filament into an indeterminate lateral, as indicated by the sinusoidal development of the axis behind the apical cell (arrow) and the alternate production of periaxial cells and cortical filaments.

Fig. 24. Obpyriform and cylindrical cortical cells bearing single or paired moniliform laterals of restricted growth.

The gametophytes are monoecious. Spermatangia develop on terminal (Fig. 25) and subterminal cortical cells, with up to nine fertile axial cells forming in series (Fig. 30). Unlike in *R. mucosissimus*, the spermatangia tend to be borne directly on fertile axial cells, rather than on terminal mother cells of dendroid cortical filaments. Carpogonial branches are scattered throughout the thallus in various states of development. The carpogonial branch is 7–13 cells long, the supporting cell being one of the periaxial cells, a jacket cell (rhizoidal filament cell), or a lower cortical filament cell. The presence of two carpogonial branches on a single supporting cell occurs more frequently than in *R. mucosissimus* (Fig. 31). The hypogynous cell produces 4–6 branched clusters of densely aggregated nutritive cells. Cells #3 and #4 generally each bear two longer branched laterals and 1–3 small nutritive-cell clusters. The carpogonial branch cells proximal to cell #4 bear a long primary sterile lateral and may ultimately come to bear an ab- or adaxial second sterile lateral. As the carpogonial branch matures, sterile laterals become progressively more branched. Upon fertilization, the carpogonial branch cells and the basal cells of the sterile laterals inflate, both the pit connections and nuclei of these cells enlarging substantially. The gonimoblast initial develops directly from the fertilized carpogonium. The nutritive cells did not stain, because their contents were rapidly emptied, and thickened strands between the nutritive cell clusters and the hypogynous cell were not seen. Mature carposporophytes were not observed and hence no measurements of cystocarpic structures (diameter of cystocarps and carposporangia) could be made.

Tetrasporophytes are unknown.



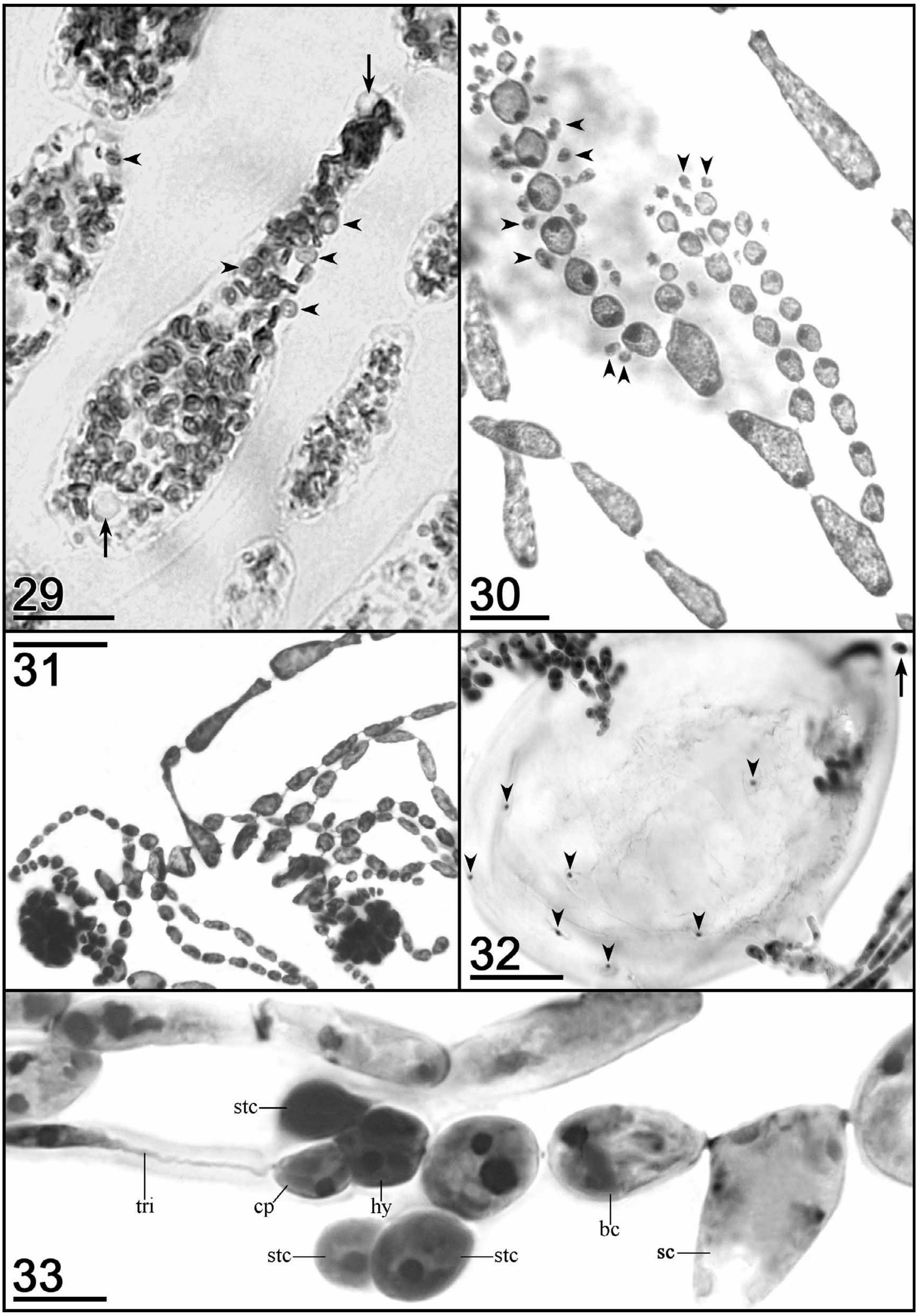
Figs 25–28. *Reticulocaulis obpyriformis*. Habit and vegetative features (SMM 446). ac = axial cell; cfc = cortical filament cell; jc = jacket cell; pc = periaxial cell. Scale bars = 10 μm (Fig. 25); 20 μm (Fig. 26); 100 μm (Fig. 27); 20 μm (Fig. 28).

Fig. 25. Hairs (arrows) and spermatangia (arrowheads) developing from terminal and subterminal cortical cells.

Fig. 26. Primary pit connection (arrow) and lateral secondary pit connections (arrowheads) of an inflated jacket cell covered by a narrow rhizoidal filament.

Fig. 27. Axial cells surrounded with a sheath of jacket cells, which develop branched (black arrow) and unbranched secondary cortical filaments (arrowhead). Primary cortical filaments (open arrow) are borne on the periaxial cells.

Fig. 28. Jacket cells that initiate multiple rhizoidal filaments (arrowheads), which branch (arrows), and secondary cortical filaments.



Figs 29–33. *Reticulocaulis obpyriformis* and *Naccaria wiggii*. bc = basal cell of carpogonial branch; cp = carpogonium; hy = hypogynous cell; sc = supporting cell of carpogonial branch; stc = sterile cell; tri = trichogyne. Scale bars = 10 µm (Fig. 29); 20 µm (Fig. 30); 50 µm (Figs 31, 32); 10 µm (Fig. 33).

Figs 29–31. *Reticulocaulis obpyriformis*, SMM 446.

Fig. 29. Discoid rhodoplasts (arrowheads) with thickened rims that give them an appearance similar to erythrocytes; the plastids densely fill an inner cortical cell and there are also surrounding reserve vacuoles (arrows).

Fig. 30. Spermatangia (arrowheads) developing on terminal and intercalary cortical mother cells.

Fig. 31. Two carpogonial branches borne on a single supporting cell of a cortical lateral.
Figs 32, 33. *Naccaria wiggii*, L 0276772.
Fig. 32. Primary pit connection (arrow) and lateral secondary pit connections (arrowheads) on a jacket cell.
Fig. 33. A four-celled carpogonial branch, on which sterile cells arise from cells #2 and #3 but which lacks nutritive-cell clusters.

DISCUSSION

The Arabian collections of *Reticulocaulis* extend the known distribution of the Naccariaceae from the Atlantic and the Pacific to the north-western Indian Ocean. Both species occur there in habitats similar to that occupied by *R. mucosissimus* in Hawaii, the Hawaiian populations forming part of a ‘spring flora’, which consists mainly of gelatinous species of *Acrosymphyton* L.G. Sjöstedt, *Dudresnaya*, *Gibsmithia* and *Schmitzia* P.C. Silva growing in areas scoured by waves 4–10 metres in height (I.A. Abbott, personal communication). The strong seasonality of members of the Naccariaceae has been documented previously (Dixon & Irvine 1977; Womersley 1996) and we suspect that seasonal growth in the northern Indian Ocean may be related to daylength changes and water temperature. The occurrence of *R. mucosissimus* in Hawaii and Oman corresponds to previous reports of a biogeographical affinity of certain Arabian Sea biota with distant regions in the Pacific (Coles 1995: Hawaii; Wynne 2000: Japan; Schils & Coppejans 2002: Australia). These disjunct distributions can be explained by (1) undersampling of subtidal habitats within the Indo-Pacific (Schils & Coppejans 2002) and (2) being relicts of Miocene distributions, which were altered as a result of changes in the current patterns (Hommersand 1986) that formerly connected these regions, separating the refugia that are subject to seasonal temperate water (Schils *et al.* 2001). However, because of the seasonal appearance of the Naccariaceae and their generally infrequent occurrence, few data are available and it is currently not possible to favour either of the two hypotheses.

The *Reticulocaulis* species, *R. mucosissimus* and *R. obpyriformis*, are easily distinguished by various anatomical and morphological features (Table 1). In erecting the genus, Abbott (1985) distinguished *Reticulocaulis* from the closely related *Naccaria* by the different developmental pattern of the ‘jacket cells’ (see below), the longer and more elaborately branched carpogonial branches, and the compact vs diffuse carposporophyte. However, Abbott (1985) was comparing *R. mucosissimus* with *N. naccarioides* (J. Agardh) Womersley & I.A. Abbott (previously regarded as the type species of *Neoardissonia* Kylin) and *Naccaria hawaiiana* I.A. Abbott, rather than with the generitype, *N. wiggii* (Turner) Endlicher. This becomes an important consideration when evaluating the contrast Abbott made between the axial sheath of *Reticulocaulis* and the ‘axial pseudoparenchyma’ of *Naccaria.* Abbott (1985) regarded the former as resulting from the cross-connection of enlarged periaxial- and rhizoidal-cell derivatives lying parallel to the central-axial filament in *Reticulocaulis*, whereas the multilayered axial sheath in *Naccaria* originates from several successive basal cells of the cortical filaments. Examination of material of *N. wiggii* (L 0276772: *leg.* P. & H. Huvé, 13.v.1963, Calanque de Sormiou, Marseilles, France; Fig. 32) and *N. corymbosa* (L 0276776: *leg.* A. J. Bernatowicz, 16.iii.1953, Gunners Bay, east end of St David’s Island, Bermuda) shows that both have similar secondary pit connections between axial-strand cells and that these become attenuate and obscure while maturing, as in *Reticulocaulis*. The sheath of jacket cells around the central axes of *N. wiggii* and *N. hawaiiana* is composed of inflated periaxial, rhizoidal and inner cortical cells (Boillot &

L'Hardy-Halos 1975: Figs 8, 13; Womersley & Abbott 1968). Millar (1990) notes that the degree of inflation of descending-filament cells in *N. naccarioides* varies in the few recorded specimens according to where in Australia they come from, thus perhaps undermining the absolute taxonomic value of the very criterion for which *Reticulocaulis* was named.

Table 1. Comparison of morphological and anatomical features in *Reticulocaulis mucosissimus* and *R. obpyriformis*.

Reticulocaulis mucosissimus	*Reticulocaulis obpyriformis*
dark rose	pale pink
thallus reaching 13 cm	thallus reaching 15 cm
densely branched; thallus contour tapers pyramidally at the apices due to the organisation of the short laterals	sparsely branched thallus, even the small indeterminate laterals do not branch densely
rather straight apices	sinusoidal apices
branching an irregular 1/4 spiral	branching initially alternate, later (from second periaxial cell formation onwards) an irregular 1/4 spiral
early (15–20th axial cell) appearance of second periaxial cell	late (> 40th axial cell) appearance of second periaxial cell
angular to globose jacket cells	spherical jacket cells
gradual acropetal transition of cortical cells from cylindrical to spherical; short moniliform branches of cortical filaments absent; terminal hairs lacking	abrupt acropetal transition of cortical cells from cylindrical or obpyriform to small and spherical or ovoid; short moniliform branches of cortical filaments present; terminal or subterminal hairs occasional
dioecious	monoecious
secondary laterals or rhizoidal filaments on proximal carpogonial branch cells relatively infrequent	secondary laterals or rhizoidal filaments on proximal carpogonial branch cells common
axial cells slender	axial cells broadly inflated
two-celled propagules occasional on outer cortical cells	two-celled propagules absent

Additional features separating *Reticulocaulis* and *Naccaria* include differences in which of the periaxial cells grows out into the dominant lateral on each axial cell: supposedly it is primarily the superior in *Naccaria* and the inferior in *Reticulocaulis*. However, this criterion may not be reliable, because Millar (1990) argues that the dominance of either determinate fascicle in *Naccaria* appears to be strongly affected by age or habitat.

Other characters, however, clearly distinguish *Reticulocaulis* from *Naccaria* (Table 2). The carpogonial branches are longer (7–13 cells vs 2–8 cells) in *Reticulocaulis* and develop from the periaxial cells, the jacket cells and the lower cells of the cortical fascicles, whereas in *Naccaria* species they can arise from the periaxial cells (in *N. hawaiiana*: Abbott 1985, fig. 11), from intercalary supporting cells at various levels in the cortex (in *N. wiggii*: specimen L 0276772), or from rhizoids (in *N. naccarioides*: Womersley 1996, p. 356). The degree to which sterile laterals arise and develop on carpogonial branch cells appears to be variable in *Naccaria* species such as *N. hawaiiana* (Abbott 1999), *N. naccarioides* (Millar

1990; Womersley 1996) and *N. wiggii* (Hommersand & Fredericq 1990; Fig. 33), but the sterile laterals in *Naccaria* never approach the degree of development seen in *Reticulocaulis*. The production of nutritive-cell clusters on the hypogynous cell is more consistent in *Reticulocaulis* than in *Naccaria* [e.g. observations of *N. wiggii*, L 0276772; *N. corymbosa* J. Agardh, L 0276776: *leg.* A.J. Bernatowicz, 16.iii.1953, Gunners Bay, east end of St David's Island, Bermuda; and *N. naccarioides*, Womersley & Abbott (1968)], in which their presence is variable even on single plants; at times they can be absent altogether (Fig. 33). The nutritive cell clusters on the two cells (carpogonial branch cells #3 and #4) proximal to the hypogynous cell in *Reticulocaulis* are lacking in *Naccaria*. Nutritive cell clusters are also more numerous and more densely packed in *Reticulocaulis* than in *Naccaria* (Abbott 1985).

Perhaps the greatest difference between *Naccaria* and *Reticulocaulis* lies in the structure of the cystocarp, which grows diffusely among cortical filaments in *Naccaria* (Dixon & Irvine 1977; Hommersand & Fredericq 1990; Millar 1990; Womersley 1996) but remains tightly compact in *Reticulocaulis*, although post-fertilization stages, such as the fusion of the fertilized carpogonium and hypogynous cell by widening of the pit connection, are similar in both genera (Millar 1990; Womersley 1996). Formation in *Naccaria* of a fusion cell that incorporates the fertile-axial cell (Hommersand & Fredericq 1990; Womersley 1996: Fig. 160 H), however, is not seen in *Reticulocaulis* and constitutes another major difference between the two genera. The difference in the sizes of the mature cystocarp structures of *R. mucosissimus* between those reported here (carposporangium and cystocarp diameter) and those reported in Abbott (1985: p. 557, Fig. 6), is probably the result of Abbott having made measurements on immature cystocarps. The specimens from Hawaii examined in this paper bore cystocarp structures covering the range reported found in the Omani specimens.

Spermatangial organization appears to differ between species of *Naccaria* to a degree equal to that seen between the two species of *Reticulocaulis*. In *R. mucosissimus*, the male gametophytes bear dense terminal clusters, in which branched laterals terminate in spermatangial mother cells (Abbott 1985, Fig. 4; our Figs 19, 20), whereas in *R. obpyriformis* they develop directly on outer cortical cells, as in *N. hawaiiana* (Abbott 1985, Fig. 7).

The *R. obpyriformis* type of spermatangial arrangement is also characteristic of the recently described *Liagorothamnion mucoides* Huisman, D.L. Ballantine & M.J. Wynne (2000), an enigmatic monotypic genus that the authors provisionally put in its own tribe (the Liagorothamnieae) within the family Ceramiaceae. The authors state that the post-fertilization process in *Liagorothamnion* is 'difficult to observe' and 'open to interpretation' but that it apparently involves fusion of the fertilized carpogonium by means of connecting cells or short filaments to the supporting cell, which is located at the base of a whorl-branchlet. This process is very similar to that reported for *Atractophora* (Millar 1990), to which *Liagorothamnion* thus shows a number of striking similarities. Both genera are mucilaginous, produce four whorl-laterals per axial cell, surround their central-axial filaments with a jacket of uninflated cells, have three- to four-celled recurved carpogonial branches bearing more than two sterile groups, and produce a carposporophyte that surrounds the axial strand and intermingles with vegetative filaments. *Liagorothamnion* may thus prove to have a closer alliance to the Naccariaceae than to the Ceramiaceae.

Table 2. Comparison of morphological and anatomical characteristics among the genera of the Naccariaceae (Zerlang 1889; Kylin 1928; Kylin 1956; Fan 1961; Womersley & Abbott 1968; Dixon & Irvine 1977; Abbott 1985; Hommersand & Fredericq 1990; Millar 1990; Womersley 1996; Abbott 1999; this paper).

Feature	*Atractophora*	*Naccaria*	*Reticulocaulis*
Branching pattern of determinate branches	whorls of four periaxial cells per axial cell	two periaxial cells per axial cell; branching on an irregular spiral of 1/4	two periaxial cells per axial cell; branching on an irregular spiral of 1/4
Sheath of inflated cells around axial strand	absent	present	present
Secondary pit connections	absent	present between jacket cells	present between jacket cells
Adventitious and rhizoidal filaments	present	present	present
Hairs on terminal cortical filament cells	present	present or absent	present or absent
Gametophytes	monoecious	monoecious or dioecious	monoecious or dioecious
Carpogonial branch (including carpogonium)	3- to 4-celled	2- to 8-celled	7- to 13-celled
Laterals on carpogonial branch cells	short	short	primary laterals lengthy, secondary sterile filaments present
Nutritive cells	present	absent or restricted to the hypogynous cell	always present on the hypogynous cell, small clusters on the carpogonial branch cells #3, #4
Immediate post-fertilization events	fusion of carpogonium with supporting cell via a short process	fusion of carpogonium with hypogynous cell by widening of pit-connection	fusion of carpogonium with hypogynous cell by widening of pit-connection
Gonimoblast composition	diffuse gonimoblast intermixed with vegetative filaments	diffuse gonimoblast intermixed with vegetative filaments	compact gonimoblast lacking vegetative filaments
Localized swelling of the branches by mature cystocarps	present	present	absent
Position of spermatangial mother cells	?	dendroid distal clusters or in catenate series	dendroid distal clusters or in catenate series

Abbott (1985) has suggested that *Reticulocaulis* ‘might be looked upon as reduced from *Acrosymphyton*-like forms in terms of the carpogonial branch ...’ and hence related to the Dumontiaceae, a family then placed in the order Cryptonemiales and now a member of the Gigartinales (Saunders & Kraft 1997). The proposed affinity between *Reticulocaulis* and *Acrosymphyton* is not supported by recent evidence. According to a phylogenetic analysis of the Dumontiaceae (Tai *et al.* 2001), *Acrosymphyton* (Acrosymphytaceae; Lindstrom 1987) is sister to the Gelidiales, whereas *Bonnemaisonia* is basal to the included Gigartinales and Gelidiales. Ongoing molecular research (G.W. Saunders & C.A. Maggs, personal communication) shows that the Naccariaceae is almost certainly not monophyletic (*Naccaria* groups weakly with the Bonnemaisoniaceae and may not belong in the Bonnemaisoniales, whereas *Atractophora* receives solid support as a member of the Bonnemaisoniaceae), and it clearly does not belong in either the Nemaliales or the Gigartinales. Saunders & Kraft (1997, p. 130) suggested that DNA studies of the Naccariaceae, to establish its ordinal affinities, should be a top priority for molecular systematists, and this recommendation still holds.

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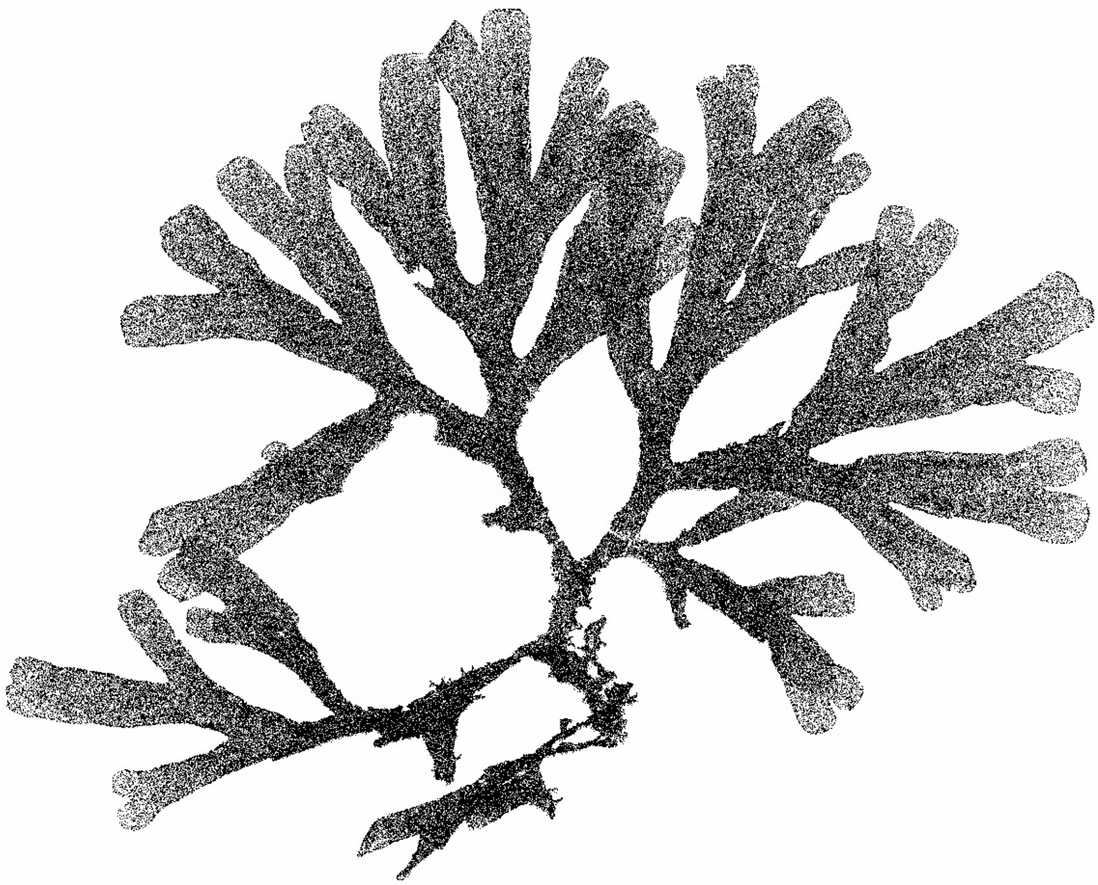

Stoechospermum polypodioides (Lamouroux) J. Agardh: a common brown alga of the Arabian Sea, which is frequently referred to by its synonym *Stoechospermum marginatum* (C. Agardh) Kützing.

CHAPTER 4

Chamaebotrys erectus sp. nov. (Rhodymeniales, Rhodophyta) from the Socotra Archipelago, Yemen

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ABSTRACT

A third species of *Chamaebotrys*, *C. erectus*, is described from an upwelling region off Socotra Island, Yemen. The new species clearly displays one of the defining features of the genus, viz. terminal tetrasporangia in nemathecial sori. The nemathecia become diffuse when mature and produce secondary tetrasporangia. Tetraspores can apparently germinate *in situ*, resulting in compound thalli with tetrasporic and cystocarpic parts. Carpogonial branches are four-celled and cystocarps are protuberant, both of which features illustrate the affinities of *Chamaebotrys* with the closely related *Coelarthrum*.

INTRODUCTION

The genus *Chamaebotrys* was recently erected by Huisman (1996) for *Coelarthrum boergesenii* Weber-van Bosse, the two features distinguishing it from the type species of *Coelarthrum*, *C. cliftonii* (Harvey) Kylin, being the terminal, rather than intercalary tetrasporangia and the nemathecial sori in which they occur (Huisman 1996). A second species of *Chamaebotrys* is *C. lomentariae* (Tanaka *et* K. Nozawa *in* Tanaka) Huisman, which is very imperfectly known only from the type collection. Both it and the type species have low-growing, decumbent thalli of small stature. It was therefore of interest when several relatively large, upright thalli referable to *Chamaebotrys* were collected from an upwelling area off Socotra (Fig. 1). These specimens are herein described as the new species *C. erectus*.

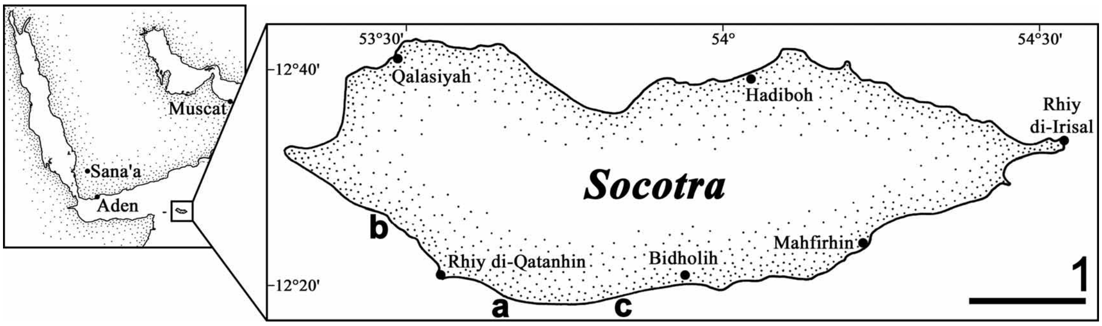


Fig. 1. Sampling stations around Socotra where *Chamaebotrys erectus* was collected: IT-059 (a); IT-103, type locality (b); Alg-40 (c). Scale bar: 20 km.

MATERIAL AND METHODS

Specimens were collected during two field trips to Socotra Island (Yemen; 12.47 N, 53.87 E) from 13 January–20 February 1999 and 26 March–7 May 2000, respectively. The subtidal habitats around the island were sampled while snorkelling or SCUBA diving. Specimens were pressed on herbarium sheets and preserved in a 5% Formalin-seawater solution. Herbarium sheets, liquid-preserved specimens and microscope slides are deposited in GENT. Material for microscopical examination was stained with aniline blue. The anatomical and reproductive characteristics were observed by studying transverse sections (made by hand or with a freezing microtome set at 40 µm) and squashed preparations (whole-mounts in a mixture of corn syrup and phenol, 50:1) under a standard light microscope (Leitz Diaplan, Wetzlar, Germany). Line drawings were prepared with a camera lucida, and photographs were taken with a digital camera (Olympus DP10, Melville, U.S.A.).

RESULTS

Chamaebotrys erectus Schils *et* Huisman, sp. nov.

Ad Chamaebotrydem boergesenii *(Weber-van Bosse) Huisman similis sed characteribus sequentibus distinguitur. Planta recta, ad 20 cm alta, sine anastomosibus inter ramos. Tetrasporangia decussate divisa, in nematheciis irregulariter formatis portata. Tetrasporae interdum in situ germinantes, thallum compositum facientes ex partis tetrasporicis gametophyticis et cystocarpicis constantes. Spermatangia ignota.*

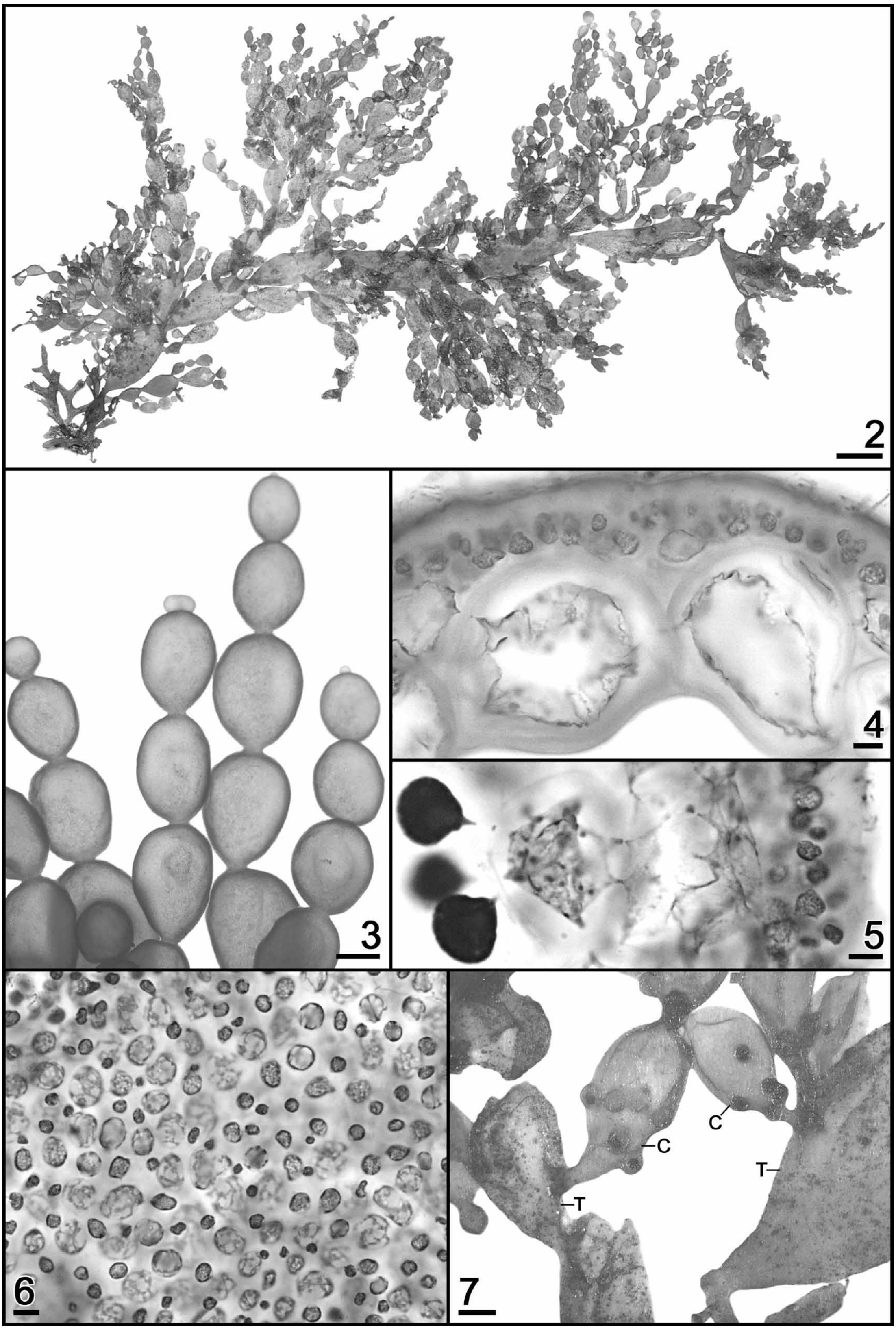
Similar to *Chamaebotrys boergesenii* (Weber-van Bosse) Huisman but with the following distinguishing characters: plants erect, to 20 cm tall, lacking anastomoses between branches. Tetrasporangia decussately divided, in irregularly shaped nemathecia. Tetraspores occasionally germinating *in situ*, resulting in a compound thallus comprised of tetrasporic, gametophytic and cystocarpic parts. Spermatangia unknown.

HOLOTYPE: SOC 265 (GENT).

ETYMOLOGY: The specific epithet (L. *erectus* = upright) alludes to the upright habit of the species.

TYPE LOCALITY AND SPECIMENS EXAMINED: Yemen, Socotra Island (Fig. 1): 5 February 1999, 10 km east of Rhiy di-Qatanhin (IT-059: 12.308 N, 53.658 E), shallow subtidal, leg. F. Leliaert (SOC 028: tetrasporophyte and female gametophyte); 3 March 1999, 1 km southeast of Ghubbah di-Net (IT-103: 12.425 N, 53.475 E; type locality), shallow subtidal, leg. F. Leliaert (SOC 265: tetrasporophyte and female gametophyte); 30 April 2000, west of Bidholih (ALG-40: 12.303 N, 53.843 E), subtidal: -20 m, leg. T. Schils (SMM 456: female gametophyte).

HABIT AND VEGETATIVE STRUCTURE: Plants are upright, to 20 cm tall (Fig. 2), segmented, and branch dichotomously or have a percurrent primary axis and verticillate laterals. Several thalli, each with a short solid stipe (to 7 mm long and 1.5 mm wide), can arise from a single discoid holdfast (to 3 mm diam.). Young branches and apical regions are bright red in colour and older parts of the thallus are brownish red. Thalli are soft in texture and composed of hollow, mucus-filled segments that are joined by narrow connections (Fig. 3). The shape of the segments varies from subcylindrical near the apex to thick, elongate and barrel-shaped in



Figs 2-7. *Chamaebotrys erectus* sp. nov.

Fig. 2. Habit of holotype.

Fig. 3. Apical region showing the narrow and short connections between the segments.

Fig. 4. Section of cortex.

Fig. 5. Cortical section showing gland cells attached to a medullary cell.

Fig. 6. Surface view of cortex.

Fig. 7. Compound thallus: cystocarpic axes (C) developing from tetrasporic segments (T). Scale bars: Fig. 2, 1 cm; Fig. 3, 1 mm; Figs 4-6, 10 μm; Fig. 7, 1 mm.

older thallus parts. The inner medulla is composed of 1 or 2 layers of large, colourless cells (22.5-125 μm [l] x 27-160 μm [w]; Fig. 4). Gland cells (6.5-20.5 μm in diam.) are borne singly or in pairs on the inner surface of medullary cells (Fig. 5) or on stellate cells attached to the medullary cells. Secondary internal filaments occasionally are initiated from the medullary cells. The cortex is composed of 2-3 layers of subspherical pigmented cells (4.5-18 μm in diam.), these gradually decreasing in size towards the thallus surface. Outer cortical cells regularly bear hairs. Cortical cells in surface view are irregularly arranged (Fig. 6) and variable in diameter.

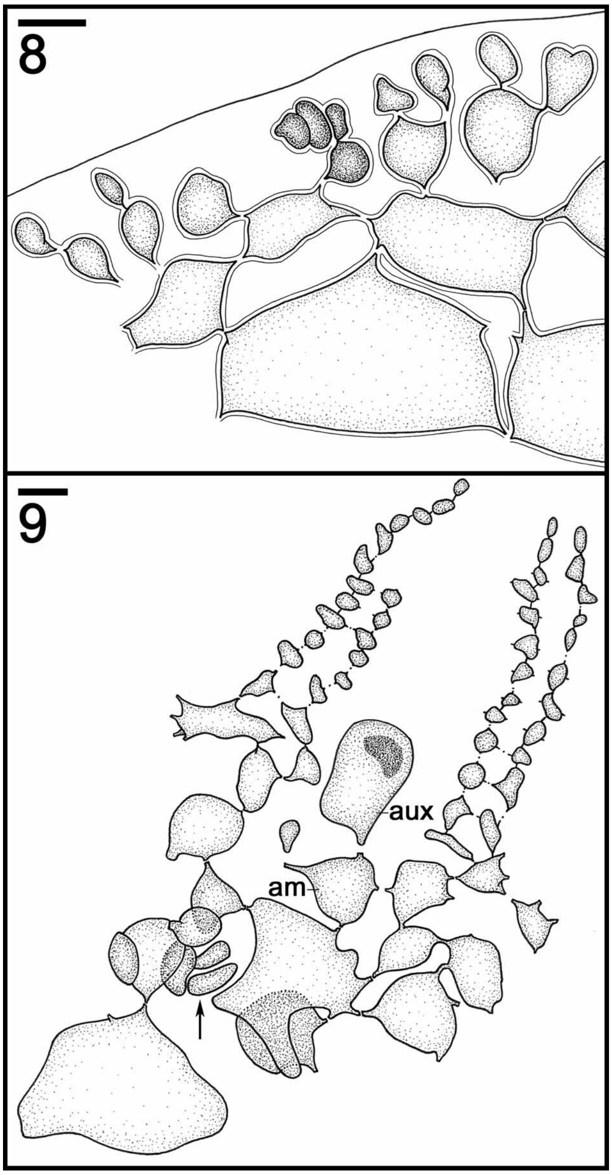
REPRODUCTIVE THALLI: The larger plants (e.g. SOC 265) are compound, composed of tetrasporic and gametophytic/cystocarpic individuals (Fig. 7), the latter occurring distally on the tetrasporophyte. Hence, it is suspected that the tetrasporangia germinate *in situ* and give rise to gametophytic thalli. The process of tetraspore germination, singly or syntagmatically, was not observed. Smaller, to 7 cm tall, entirely cystocarpic thalli also occur, indicating that the tetraspores can also disperse from the mother plant and produce free-living gametophytes.

CARPOGONIAL BRANCH AND CYSTOCARPS: Carpogonial branches are 4-celled and slightly curved (Fig. 8). A cortical cell, attached to the supporting cell and with secondary pit connections with adjacent cortical cells, acts as the auxiliary mother cell and initiates an obovoid auxiliary cell (Fig. 9). Immediate post-fertilisation events have not been observed. Upon presumed diploidisation of the auxiliary cell, the latter produces a stalked gonimoblast (Fig. 10). Basal to the gonimoblast, nutritive cells are formed from the cells that surround the supporting cell. Simultaneously, a protuberant pericarp surrounds the gonimoblast (Fig. 11).

SPERMATANGIA: Not observed.

TETRASPORANGIA: Tetrasporangia occur in nemathecial sori (Fig. 12). During maturation the sori spread into irregular diffuse patches that can cover the greater part of the thallus. The nemathecia are composed of slender filaments (Fig. 13) that arise from outer cortical cells and cut off distal tetrasporangia. Sterile filaments occur among the tetrasporangial filaments. After releasing the first order of tetrasporangia, secondary nemathecial filaments can be produced which give rise to secondary tetrasporangia in more elevated sori. Tetrasporangia develop from darkly staining elliptical initials 13.5-25 μm [l] x 6.5-14 μm [w] (Fig. 13). The first division is transverse and oblique, with subsequent divisions splitting the two halves longitudinally at right angles to one another, resulting in decussately divided tetrasporangia 27-41 μm x 20-25 μm.

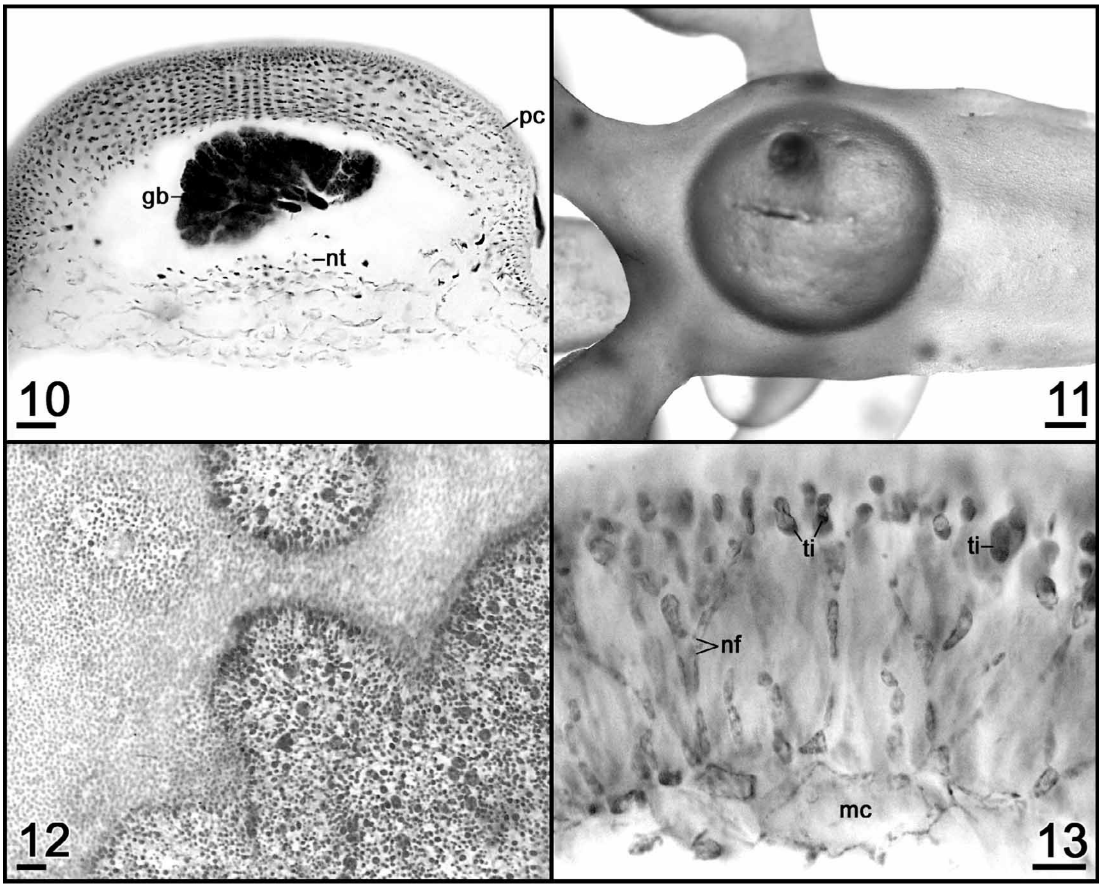
HABITAT: Plants are epilithic on bare or sand inundated rocks. The associated subtidal macroalgal flora is composed of *Asteromenia peltata* (W. R. Taylor) Huisman *et* Millar, *Botryocladia leptopoda* (J. Agardh) Kylin, *Carpopeltis maillardii* (Montagne *et* Millardet) Chiang, *Champia indica* Børgesen, *Chondria armata* (Kützing) Okamura, *Dictyota cervicornis* Kützing, *Euptilota fergusonii* Cotton, *Hypnea boergesenii* Tanaka, *Lobophora variegata* (Lamouroux) Womersley ex Oliveira, *Sarcodia montagneana* (J. Hooker *et* Harvey) J. Agardh, *Scinaia moniliformis* J. Agardh, *Sebdenia flabellata* (J. Agardh) Parkinson, and *Udotea indica* A. Gepp *et* E. Gepp.



Figs 8-9. *Chamaebotrys erectus* sp. nov.
Fig. 8. Four-celled carpogonial branch.
Fig. 9. Initiation of a cystocarp: auxiliary mother cell (am), auxiliary cell (aux) and carpogonial branch remnants (arrow).
Scale bars: 10 μm.

DISCUSSION

Chamaebotrys erectus clearly displays the key characteristic of the genus, viz. terminal tetrasporangia in nemathecial sori. The new species has morphological and anatomical features similar to the other *Chamaebotrys* species and also to species of the closely related *Coelarthrum* (Table 1). It can readily be distinguished from *Chamaebotrys boergesenii* and *C. lomentariae* by its erect thallus, large size and compound thalli comprising tetrasporic, gametophytic and cystocarpic parts (non-compound thalli also occur). In addition, *C. erectus* produces occasional internal filaments, these being secondarily produced and not comparable to longitudinal filaments of the Champiaceae (Ricker & Kraft 1979; Huisman 1995) and Lomentariaceae (Lee 1978). Adventitious filaments have also been observed in *Coelarthrum* species and not accorded taxonomic significance (Huisman 1996). The latter feature, however, might prove to be of taxonomic importance in other Rhodymeniaceae genera, viz. the absence of internal rhizoids in *Chrysymenia* and their presence in *Cryptarachne* (generally lumped in *Chrysymenia*, e.g. Abbott & Littler 1969) might support the molecular separation of both genera (Saunders *et al.* 1999, p. 38).



Figs 10-13. *Chamaebotrys erectus* sp. nov.

Fig. 10. Section of cystocarp: broken-off gonimoblast (gb), pericarp (pc), nutritive tissue (nt).

Fig. 11. Protuberant cystocarp with a prominent ostiole.

Fig. 12. Surface view of irregularly contoured tetrasporangial nemathecia.

Fig. 13. Section of tetrasporial nemathecium showing medullary cells (mc), nemathecial filaments (nf) and tetrasporangial initials (ti).

Scale bars: Fig. 10, 50 μm; Fig. 11, 0.5 mm; Fig. 12, 50 μm; Fig. 13, 20 μm.

In light of the recent molecular findings on the Rhodymeniales (Saunders *et al.* 1999), the observation of a 4-celled carpogonial branch in *Chamaebotrys erectus* supports maintaining the genus (which was not sequenced by Saunders *et al.* 1999) within the Rhodymeniaceae. The genus is unusual in the Rhodymeniaceae, however, in producing terminal tetrasporangia in nemathecia. This has been hypothesised as a reversion to the ancestral condition by Saunders *et al.* (1999). Further molecular studies may elucidate the phylogenetic placement of *Chamaebotrys* in relation to other Rhodymeniaceae.

Some tetrasporangia in *C. erectus* appear to be tetrahedrally divided, a result of the oblique first division in combination with the decussate arrangement of the tetraspores. Nevertheless, the divisions are always successive, a distinctive feature of cruciately (decussately) divided tetrasporangia (Guiry 1978, 1990).

Table 1. Comparison of *Chamaebotrys erectus* to other *Chamaebotrys* and *Coelarthrum* species (Mshigeni & Papenfuss 1981, Huisman 1996, Huisman 2000, Wynne 2001, this paper). *Chamaebotrys lomentariae* is excluded as the species is insufficiently known (Huisman 1996).

Feature	*Chamaebotrys erectus* Schils & Huisman, sp. nov.	*Chamaebotrys boergesenii* (Weber-van Bosse) Huisman	*Coelarthrum cliftonii* (Harvey) Kylin	*Coelarthrum decumbens* Huisman	*Coelarthrum opuntia* (Endlicher) Børgesen
Grouping of tetrasporangia	discrete nemathecial sori that diffuse while maturing and develop secondary tetrasporangia	discrete nemathecial sori that remain discrete	scattered, not in sori	indistinct sori	scattered, not in sori
Carpogonial branch	4-celled	?	4-celled	4-celled	4-celled
Tetrasporangia	terminal, decussately divided	terminal, cruciately divided	intercalary, cruciately divided	intercalary, cruciately divided	intercalary, cruciately to decussately divided
Habit	erect	decumbent	erect	decumbent	erect
Secondary lateral anastomoses	absent	present	present	present	absent
Constrictions between the segments	narrow	broad	broad	broad	stalk-like
Cystocarps	protuberant	protuberant	immersed	protuberant	protuberant
Additional peculiarities	*in situ* germination of tetraspores: female gametophytes epiphytic on tetrasporophytes. also free-living female gametophytes	elongate processes at apical regions of the thallus	monostromatic septa	outer cortex in a rosette-like formation in surface view	cartilaginous stipe
Size	to 20 cm	2-3 cm	to 20 cm	3-4 cm	to 30 cm
Distribution	upwelling area of Socotra Island, Yemen	warmer waters of the Indo-Pacific and upwelling area of Hallaniyat Islands, Oman	Indo-Pacific	Great Barrier Reef and Lord Howe Island, Australia	Indo-Pacific

In comparison to the reported sizes of the other *Chamaebotrys* species (Mshigeni & Papenfuss 1981; Huisman 1996), *C. erectus* is markedly larger. All material was collected from the south coast of Socotra, which is subject to upwelling of cold water. This phenomenon is beneficial for algal growth (constant nutrient flow and stable temperature regime), as the south coast harbours the most luxuriant and species-rich algal flora of the Island (Schils *et al.* 2001). Analogous discoveries of large representatives of certain genera from this upwelling region include *Champia gigantea* Wynne (1998), another member of the Rhodymeniales. These findings suggest that the Arabian Sea harbours a distinctive and interesting marine flora.

ACKNOWLEDGEMENTS

We appreciated constructive comments from Gerry Kraft and an anonymous reviewer. Sincere thanks are expressed to the Senckenberg Research Institute, Germany (Michael Apel, Uwe Zajonz and Fareed Krupp), for the excellent field trip preparations to the Socotra Archipelago. Frederik Leliaert is gratefully acknowledged for making his exquisite collection of Socotran algae available. Tom Schils is indebted to the Fund for Scientific Research Flanders (Belgium) for a research assistant grant and a travel grant to Murdoch University (Western Australia). John Huisman thanks Associate Professor Michael Borowitzka (Murdoch University) for hosting his research and Alex George (Four Gables, Barclay St., Kardinya) for kindly supplying the Latin translations. Financial support was provided by grants from the 'Australian Biological Resources Study' and the 'Western Australian Department of Commerce and Trade'.

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Coelarthrum opuntia (Endlicher) Børgesen: a Rhodymeniales species (Rhodophyta) from the Arabian Sea, which is closely related to the new species *Chamaebotrys erectus* Schils & Huisman (see *chapter 4*).

CHAPTER 5

A re-assessment of the genus *Izziella* Doty (Liagoraceae, Rhodophyta)

Published as: Huisman J.M. & Schils T. 2002. A re-assessment of the genus *Izziella* Doty (Liagoraceae, Rhodophyta). *Cryptogamie Algologie* 23(3): 237-249.

ABSTRACT

The genus *Izziella* Doty is reassessed based on an examination of a specimen of *Liagora orientalis* J. Agardh (the species into which *Izziella abbottiae* Doty has been subsumed) from the Socotra Archipelago, Yemen. This species shows marked differences from the type species of *Liagora* [*L. viscida* (Forsskål) C. Agardh], *Ganonema* [*G. farinosum* (Lamouroux) Fan & Wang], and *Trichogloea* [*T. requienii* (Montagne) Kützing] and we therefore propose that *Izziella* be restored as an independent genus. It is our contention that *Liagora*, as presently constituted, displays considerable variation in reproductive morphology and should probably be divided into several smaller genera.

INTRODUCTION

The genus *Izziella*, with the single species *I. abbottiae*, was described by Doty in 1978 for specimens collected from Oahu, Hawaiian Islands. The genus was thought to be closely related to *Liagora* but differing primarily in the cluster of sterile filaments radiating from the infra-supporting cell proximal to the developing gonimoblast. Doty (1978) gave a detailed description of the post-fertilization events in the new genus, which he felt were clearly unlike those of *Liagora viscida* (Forsskål) C. Agardh, the type of the genus *Liagora*. Subsequent to the description of *Izziella*, the genus was subsumed into *Liagora* (Abbott 1990), who regarded its type species as synonymous with *L. orientalis* J. Agardh. *Liagora orientalis*, originally described from Sri Lanka, is a widespread species that has been reported from numerous localities in the tropical Indian and Pacific Oceans and the Caribbean Sea (Abbott 1990).

Several authors have recently remarked on the variety of morphology and cystocarp types presently included in *Liagora* (Kraft 1989; Huisman & Kraft 1994; Huisman in press), suggesting that the differences are too great to be accommodated within a single genus. As a result, Huisman & Kraft (1994) resurrected the previously rejected (Abbott 1984) *Ganonema* for *Ganonema farinosum* (Lamouroux) Fan & Wang, and subsequent authors have made further combinations in the genus (Huisman in press).

The present paper re-assesses the genus *Izziella* (= *Liagora orientalis*) in light of these suggestions, concluding that the genus is worthy of recognition in a taxonomic scheme in which *Liagora* is more narrowly defined. The eventual further subdivision of the latter genus is also foreshadowed. This study is based primarily on a collection made by the second author from the Socotra Archipelago, Yemen, in addition to type and authentic specimens of *Izziella abbottiae* from Oahu, Hawaiian Islands.

MATERIAL AND METHODS

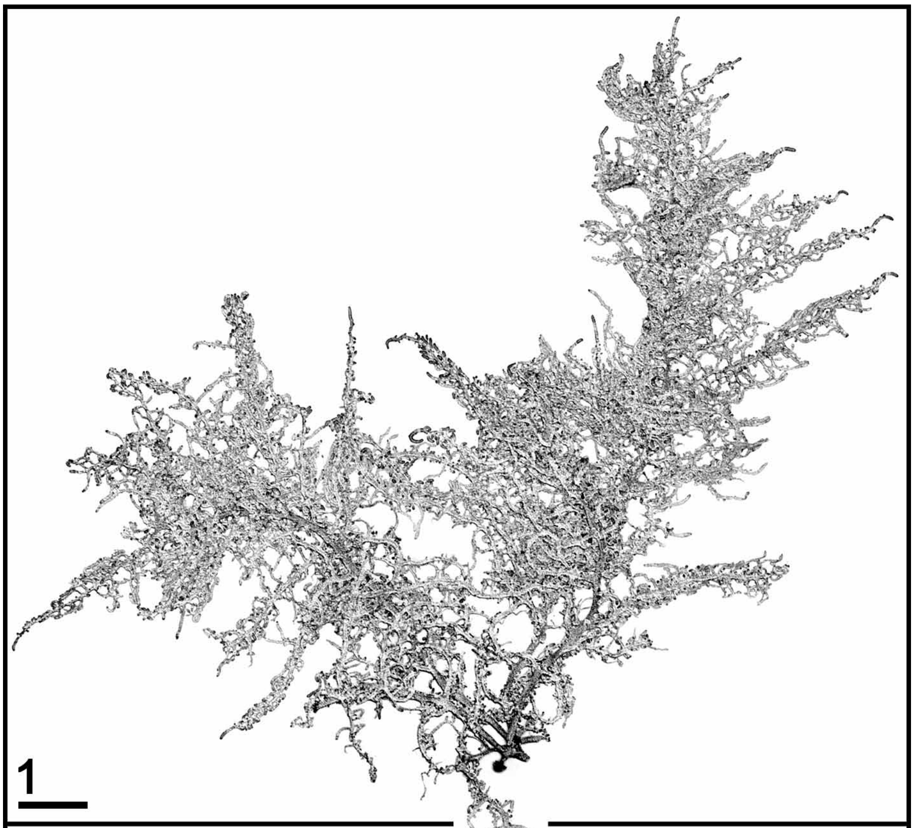
Specimens were collected while snorkeling and preserved in approximately 5% formalin/seawater. Portions of plants for microscopical examination were decalcified in 1N HCl under a fume hood, washed in seawater, stained in 1% aniline blue, washed again in seawater, then mounted in a 50% Karo (CPC International) corn syrup solution and macerated or lightly squashed to separate the filaments. Herbarium specimens and slide preparations are held in GENT (Ghent University Herbarium, Krijgslaan 281 - S8, 9000 Ghent, Belgium).

OBSERVATIONS

SPECIMENS EXAMINED: (1) *Liagora orientalis* - East Coast of Samha Island, Socotra Archipelago, Yemen (ALG-19: 12° 09.72 N, 35° 05.08 E), subtidal at 1.5 m depth, 7 April 2000, *T. Schils* (SMM 183) (Fig. 1). (2*). Izziella abbottiae* (isotypes) – Kahanahaiki, Waianae District, Oahu, Hawaiian Is., on surf zone sedimentary rock bench, 23 March, 1969, *M. Doty* (Doty 20591; MELU A037729, A037730). (3) *Izziella abbottiae* - Kahanahaiki, Waianae, Oahu, Hawaiian Is., lower littoral, 10 February 1962, *M. Doty & H.B.S. Womersley* (Doty 19630; AD A26006) (Fig. 2). (4) *Liagora viscida* - Banyuls, France 7 July 1937, *G. Mazoyer* (AD A24190). (5). *Liagora perennis* – Maili Beach, Waianae District, Oahu, Hawaiian Is., on intertidal bench, 26 April 2002, *J. Huisman & D. Spafford* (IA 28727). (6) *Ganonema farinosum* – Swanzy, Oahu, Hawaiian Is., 12 April 2002, *J. Huisman & D. Spafford*, (IA 28712). (7) *Ganonema farinosum* – Hanauma Bay, Oahu, Hawaiian Is. (IA 13871). (8) *Liagora orientalis* – Nanakuli, Oahu, Hawaiian Is., on intertidal limestone bench, 5 April 1985, *M. Cannon* (IA 17183). (9, 10) *Trichogloea requienii* - SSW tip of Rocher du Diamant (Diamond Rock), Martinique, (14º 26.94 N, 61º 02.41 W), 14 June 1995, *D.S. Littler, M.M. Littler & B.L. Brooks* (Littler 30916). E side of island on a steeply angled beach, attached to beach rock , Green Turtle Key, Bahamas, subtidal at 1 m depth, 28 March 1994, *D.S. Littler and M.M. Littler* (Littler 42001). (11). *Liagora ceranoides* – Swanzy, Oahu, Hawaiian Is., 12 April 2002, *J. Huisman & D. Spafford* (IA 28703).

HABIT: The Yemen plant (Fig. 1) is 22 cm in height, greyish/light green (when dried), mucilaginous, and arises from a discoid holdfast 3 mm in diam. Percurrent primary axes bear indeterminate lateral branches of similar form, both in turn bearing a further order of numerous short lateral branches. Primary axes and major lateral branches are 1-2.5 mm in diam., broader at the base and tapering gradually towards the apex. Secondary and short lateral branches are 0.5-1 mm in diam. Calcification is moderate and farinose.

VEGETATIVE STRUCTURE: The thallus structure is multiaxial, with a central medulla of hyaline longitudinal filaments 15-50 μm in diam. Assimilatory filaments are borne on medullary filaments and are sparsely dichotomously branched, often with lengthy unbranched sections. The filaments are 450-600 μm long, with cells 7-16 μm in diam., lower cells cylindrical, upper cells ellipsoidal or obovoid. Narrow rhizoidal filaments, 6-10 μm in diam., commonly arise from the lower cells of assimilatory filaments and course through the medulla, producing adventitious secondary assimilatory filaments that are generally simple or rarely branched. Cells of assimilatory filaments have a prominent central pyrenoid, 4-7 μm in diam.



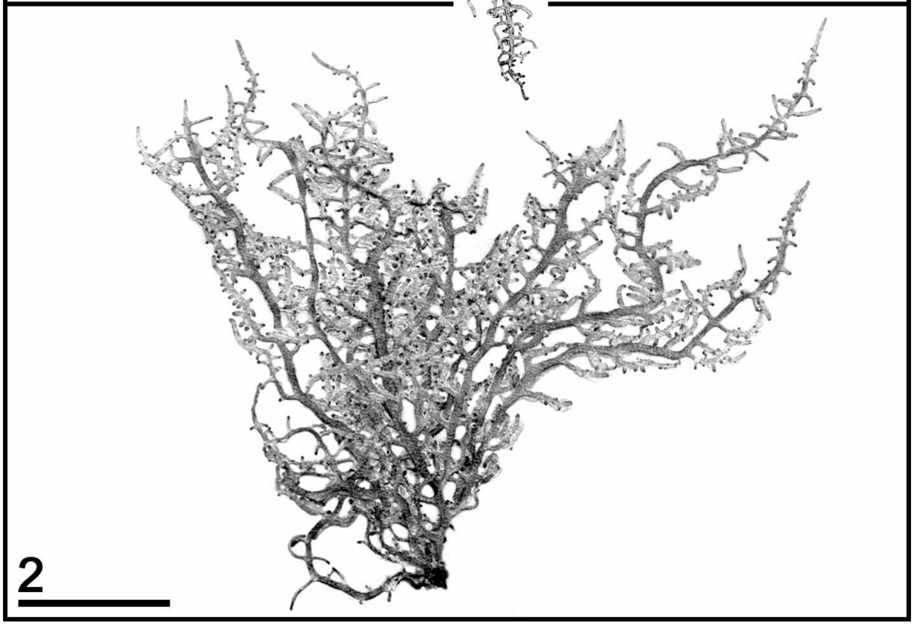
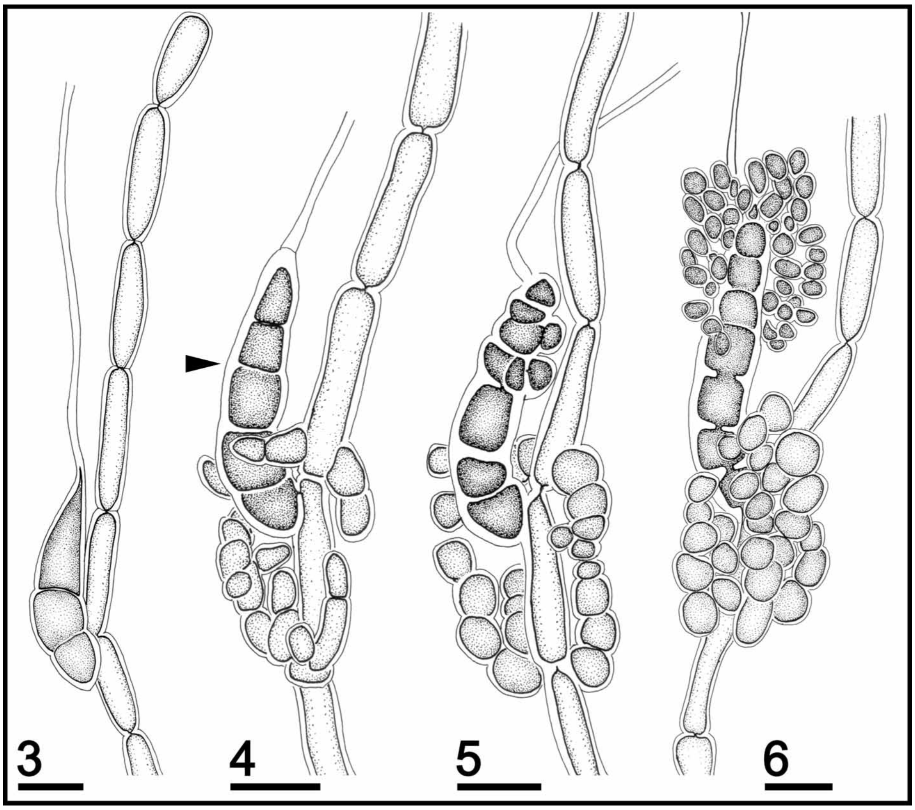


Fig. 1. Specimen of *Izziella orientalis* (J. Agardh) Huisman & Schils, comb. nov. from Yemen (SMM 183). Scale = 2 cm.

Fig. 2. Authentic specimen of *Izziella abbottiae* Doty (= *I. orientalis*) from Oahu, Hawaiian Is. (AD A26006). Scale = 2 cm.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Carpogonial branches are 3-4-celled (Fig. 3) and arise on the distal half of the supporting cell, which is a lower cell of an assimilatory filament. Following presumed fertilization the zygote (= post-fertilization carpogonium) divides transversely (Fig. 4). Of the two cells produced, the proximal remains undivided, while the distal cell undergoes several further transverse divisions (Fig. 5). Each of the resultant cells produces lateral gonimoblast filaments that are whorled around the central cells (Figs 5, 6). Gonimoblast filaments are very narrow, 2-3 μm in diam., with terminal carposporangia 5-7 µm long and 3-5 µm in diam. After release of carpospores, the sporangial walls persist and remain obvious. Mature gonimoblasts are spherical, 100-220 µm in diam., and are located primarily in the short lateral branches of the thallus (Fig. 7).



Figs 3-6. *Izziella orientalis* (J. Agardh) Huisman & Schils

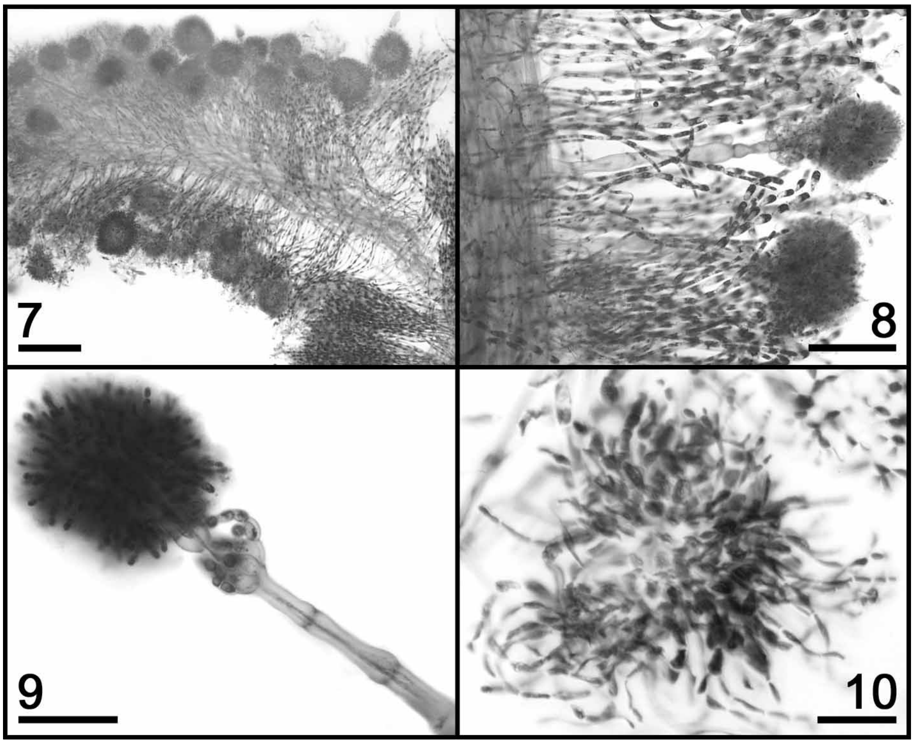
Fig. 3. Three-celled carpogonial branch borne on an assimilatory filament. (SMM 183). Scale = 20 µm.

Fig. 4. Post-fertilization division of the zygote. The first transverse division (arrowhead) is followed by subsequent divisions of the distal cell. Sterile filaments are present on the cells distal and proximal to the supporting cell (SMM 183). Scale = 20 µm.

Fig. 5. Later stage showing several divisions of the distal cell and initiation of lateral gonimoblast filaments. (SMM 183). Scale = 20 µm.

Fig. 6. Young gonimoblast. The sporangial mass is shown in optical section, demonstrating the presence of the longitudinal core arising from the cells of the divided zygote. The sterile filaments are forming a separate cluster below the gonimoblast (SMM 183). Scale = 20 µm.

Prior to fertilization, and perhaps independent to it, sterile filaments are produced from the cells to either side of the supporting cell (occasionally also from more distant cells) (Fig. 4). A whorl of sterile filaments arises from the distal end of the cell proximal to the supporting cell, and occasionally some additional, less branched, filaments arise from the mid-portion of the cell. These latter filaments are frequently reduced to only a single globose cell. The sterile filaments (from the cells distal and proximal to the supporting cell) grow towards each other and eventually envelop the supporting cell, producing a cluster of filaments that appear as a second cell mass below the gonimoblast (Figs 6, 9). After fertilization an extensive fusion cell is formed that encompasses the cells of the carpogonial branch, the supporting cell, and the majority of cells of the assimilatory filament subtending the supporting cell (Fig. 9). This fusion cell increases in length and girth and becomes hyaline, eventually appearing as a 'stalk' bearing the gonimoblast (Figs 8, 9). The fused cells of the carpogonial branch can be seen as a core within the gonimoblast. The lengthening stalk raises the gonimoblast to the level of the outer margin of the assimilatory filaments.



Figs 7-9. *Izziella orientalis* (J. Agardh) Huisman & Schils

Fig. 7. Decalcified squash preparation of a short lateral branch, showing the numerous cystocarps. (SMM 183). Scale = 200 µm.

Fig. 8. Closer view, showing gonimoblasts terminating elongate stalk cells. (SMM 183). Scale = 100 µm.

Fig. 9. Detail of mature cystocarp with distal gonimoblast mass, small cluster of sterile filaments, and elongate stalk cell. (SMM 183). Scale = 50 µm.

Fig. 10. *Liagora viscida* (Forsskål) C. Agardh. Mature cystocarp with somewhat diffuse gonimoblast and intermingled sterile filaments. (AD 24190). Scale = 20 µm.

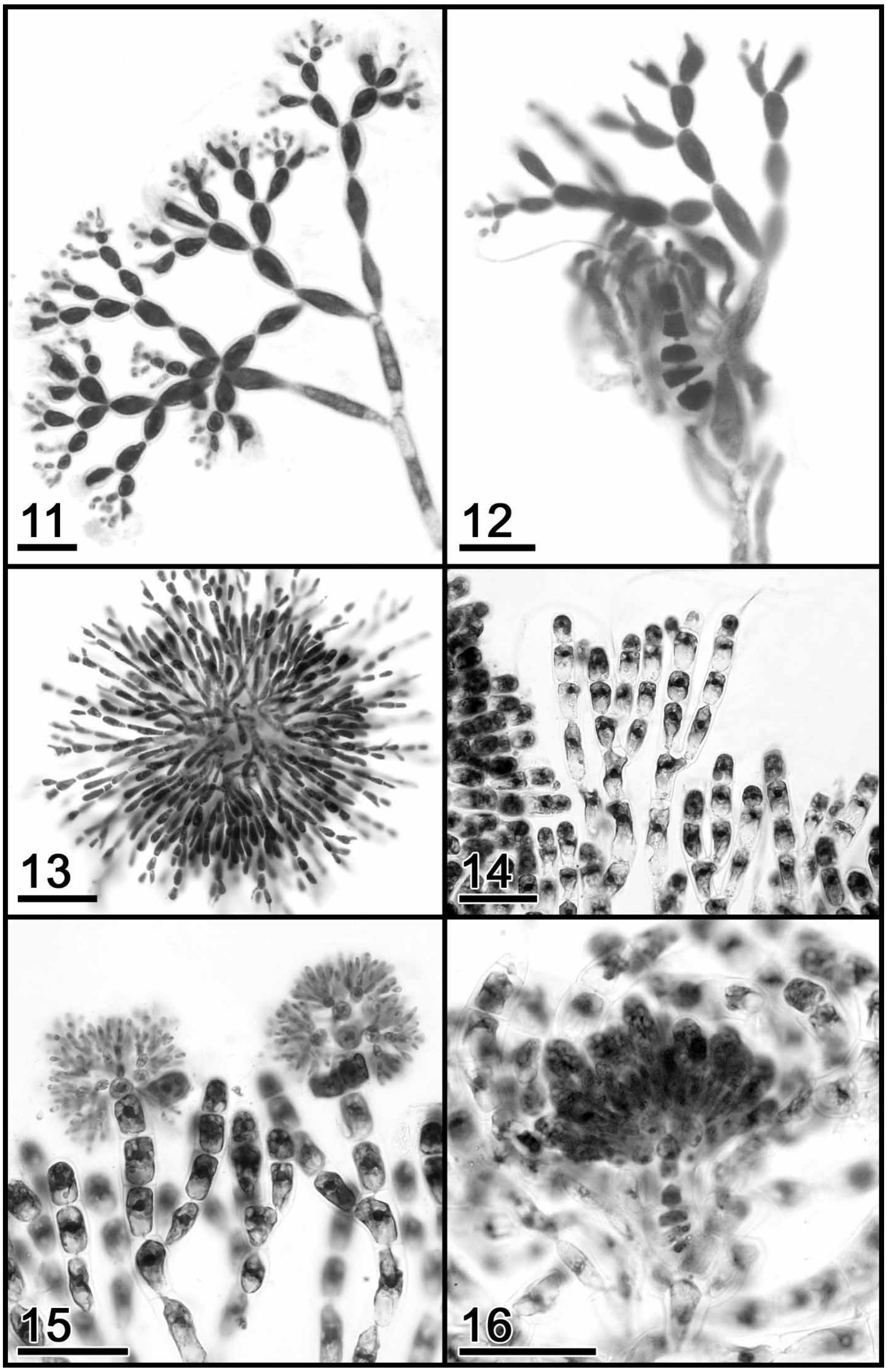
DISCUSSION

The vegetative morphology and reproductive development observed in the present specimen are entirely consistent with those described by Doty (1978, as *Izziella abbottiae*) and Abbott (1990, 1999, as *Liagora orientalis*) and as observed in type and other specimens recorded by Doty (1978) as *I. abbottiae* (MELU A037729, A037730; AD 26006). We have also examined a slide preparation of a type specimen of *Liagora orientalis*, held in the Botany Department, University of Hawaii, Manoa (see Abbott 1990 for details). We are therefore confident that our material is representative of that species as it conforms to the type and other specimens of *L. orientalis* examined by us and described in detail by Abbott (1990).

Based on observations of the type species of *Liagora*, *L. viscida* (Huisman, in press), we feel that *L. orientalis* is incorrectly placed in *Liagora* and we have undertaken a comparative morphological examination of potentially related genera. Four genera are considered: *Liagora* (type species *Liagora viscida*), *Izziella* (type species *I. abbottiae* = *Liagora orientalis*), *Ganonema* (type species *G. farinosum*), and *Trichogloea* (type species *T. requienii*). The latter is included as the appearance of the mature cystocarp is superficially similar to that of *L. orientalis*. Abbott (1995) included *Trichogloea javensis* Børgesen (1951: 22-26) as one of the synonyms of *L. orientalis*, but an examination of the type specimen shows it to be correctly placed in *Trichogloea*. *Trichogloea javensis* is therefore excluded from the synonymy of *L. orientalis*. Characteristics of the type species of these four genera are given in Table 1. Figures 11-22 show examples of these characteristics (*Liagora perennis* Abbott is used instead of *L. viscida* for illustrative purposes).

Table 1. Characteristics of the type species of *Ganonema*, *Izziella*, *Liagora* and *Trichogloea*.

	Ganonema	*Izziella*	*Liagora*	*Trichogloea*
Assimilatory filaments	dichotomously branched, often with unbranched periphery	dichotomously branched, often with unbranched periphery	di/tri/polychotomously branched, mostly near periphery	dichotomously branched, often with unbranched periphery
Medullary filaments	25-150 µm in diam.	15-50 µm in diam.	5-40 µm in diam.	15-45 µm in diam.
Carpogonial branch	4-5 celled, straight or slightly curved	3-4 celled, curved	3-6 celled, strongly to moderately curved.	6-9 celled, straight, basal 3-6 cells unmodified
Sterile (or involucral) filaments	surrounding gonimoblast	subtending gonimoblast, forming a separate cluster, derived from cells above and below the supporting cell	intermingling with gonimoblast filaments	subtending gonimoblast, forming a separate cluster, derived from mid-cells of carpogonial branch
Stalk cell (large elongate fusion cell subtending the gonimoblast)	absent	present	absent	present
Fusion cell	absent	present, involving the cells of the carpogonial branch and the subtending assimilatory filament.	present	present, involving the cells of the carpogonial branch and the subtending assimilatory filament.
Gonimoblast	compact, with radiating filaments	compact, with filaments whorled around a central spine	somewhat diffuse, with radiating filaments	compact, with radiating filaments
Spermatangia	on terminal, subterminal or lateral spermatangial branches, often forming heads	on spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments	on spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments	on spermatangial mother cells whorled on mid cells of assimilatory filaments



Figs 11-13. *Liagora perennis* Abbott (all IA 28727).

Fig. 11. Cortical filaments and spermatangia, showing much-divided filaments and apical/subapical spermatangial branches. Scale = 20 μm.

Fig. 12. Lateral carpogonial branch. Scale = 20 μm.

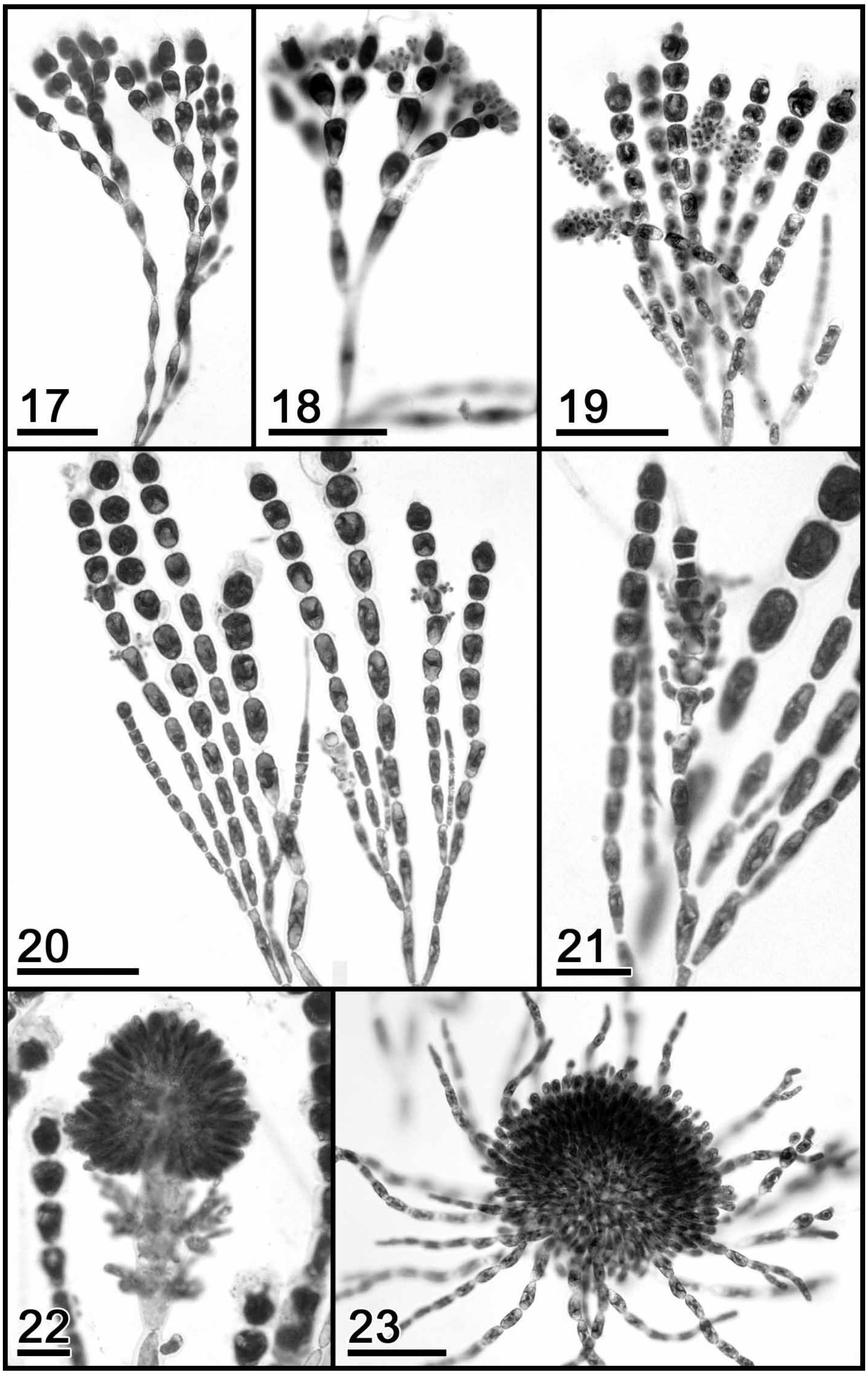
Fig. 13. Mature cystocarp with somewhat diffuse gonimoblast and intermingled sterile filaments. Scale = 50 μm.

Figs 14-16. *Ganonema farinosum* (Lamouroux) Fan & Wang

Fig. 14. Cortical filaments, showing undivided filaments of the outer cortex. (IA 28712). Scale = 100 μm.

Fig. 15. Spermatangial branches in dense heads. (IA 28712). Scale = 100 μm.

Fig. 16. Cystocarp with compact gonimoblast mass and sterile filaments forming an involucre. (IA 13871). Scale = 50 μm.



Figs 17, 18. *Izziella orientalis* (J. Agardh) Huisman & Schils

Fig. 17. Cortical filaments, showing sparsely branched filaments of the outer cortex. (IA 17183). Scale = 50 µm.

Fig. 18. Spermatangial branches formed on apical/subapical cells. (IA 17183). Scale = 50 µm.

Figs 19-22. *Trichogloea requienii* (Montagne) Kützing

Fig. 19. Cortical filaments with spermatangia borne in whorls on lower cells. (Littler 42001). Scale = 50 µm.

Fig. 20. Straight, many-celled, carpogonial branch and cortical filaments, showing undivided filaments of the outer cortex. (Littler 30916). Scale = 50 µm.

Fig. 21. Post-fertilization division of the carpogonium and production of sterile filaments from lower cells of the carpogonial branch. Scale = 20 µm.

Fig. 22. Mature cystocarp formed at the end of the carpogonial filament, with sterile filaments borne on the lower cells of the carpogonial filament. (Littler 30916). Scale = 20 µm.
Fig. 23. *Liagora ceranoides* Lamouroux. Showing compact gonimoblast and involucral filaments. (IA 28703). Scale = 50 µm.

This comparison suggests that, based on the type species, the four taxa are clearly separable. While several features are included in Table 1, those that we consider of primary importance are the cortical structure, the architecture of the carpogonial branch and mature cystocarp, and the derivation of spermatangia. Our observations indicate that *L. orientalis* should no longer be maintained in *Liagora*. A comparison of the mature cystocarps of *L. orientalis* (Fig. 9) and *L. viscida* (Fig. 10) shows differences in morphology sufficient to warrant placement in separate genera. The cystocarp of *Liagora viscida* has a somewhat diffuse gonimoblast in which sterile filaments are intermingled, whereas that of *L. orientalis* is compact and the sterile filaments form a discrete cluster below the gonimoblast. The presence of an elongate 'stalk cell' subtending the gonimoblast further distinguishes *L. orientalis*, as fusion cells in the genus *Liagora* only involve the cells of the carpogonial branch and are small in comparison.

We therefore conclude that *Liagora orientalis* is generically distinct from *Liagora.* Since *Izziella* Doty (1978) was based on this taxon (as *I. abbottiae*), we propose that the genus should be reinstated. We therefore make the following emendation and combination:

Izziella **Doty emend. Huisman & Schils**

Plants mucilaginous, moderately calcified, with percurrent primary and indeterminate lateral branches of similar form, or irregularly branched. Structure multiaxial; assimilatory filaments sparsely dichotomously branched, often with unbranched outer cortical filaments. Carpogonial branches lateral on supporting cells. Mature gonimoblasts spherical, compact. Sterile filaments arising from cells to either side of the supporting cell, growing towards each other and enveloping the supporting cell, eventually producing a cluster of filaments that appear as a second cell mass below the gonimoblast. Fusion cell formed encompassing the cells of the carpogonial branch, the supporting cell, and the majority of cells of the assimilatory filament subtending the supporting cell. Spermatangia borne on short spermatangial branches arising on apical or subapical cortical cells.

Izziella orientalis **(J. Agardh) Huisman & Schils, comb. nov.**

BASIONYM: *Liagora orientalis* J. Agardh. Analecta algologica, p. 99 (1896).

LECTOTYPE: From Sri Lanka, *W. Ferguson* (LD 32252). n.v., *fide* Abbott, 1990: fig. 7.

SYNONYMS (*fide* Abbott, 1990; Abbott, 1995; Abbott, 1999; excluding *Trichogloea javensis* Børgesen):

Liagora formosana Yamada, Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido Imperial University 2: 32-33 (1938).

Liagora tanakai I.A. Abbott, Bulletin of the Japanese Society of Phycology 15: 33 (1967).

Liagora visakhapatnamensis Umamaheswara Rao, Hydrobiologia 33: 201 (1969).

Izziella abbottiae Doty, Phycologia 17: 34 (1978).

As a further consequence of our observations, we feel that *Liagora* should be restricted to species with much-divided cortical filaments, lateral carpogonial branches, cystocarps with somewhat diffuse gonimoblasts wherein the sterile filaments intermingle or loosely envelop, and spermatangia borne on terminal or subterminal spermatangial branches. *Izziella*, in contrast, has cortical filaments that are often distally simple, compact gonimoblasts, and sterile filaments that form a separate cluster below the gonimoblast. This latter feature is superficially similar to that of *Trichogloea*, but the ontogeny of these structures is entirely different. Those of *Trichogloea* are derived from mid-cells of the elongate carpogonial branch, whereas the sterile filaments of *Izziella* arise from the cells to either side of the supporting cell.

Although the characteristics shown in Table 1 outline the differences between the four genera, consideration of other species of *Liagora* does demonstrate what could be regarded as a continuum of character states. Species such as *Liagora ceranoides* Lamouroux have close affinities with *Izziella*, as both display compact gonimoblasts (Fig. 22) and fusion cells. *Liagora ceranoides* differs from *Izziella*, however, in the production of in involucre that envelopes the gonimoblast (Huisman in press) and in lacking a large stalk cell. It is our contention that *Liagora*, as presently constituted, should be subdivided into several smaller genera. One of these segregate genera would include species with compact gonimoblasts, such as *L. ceranoides*. The subdivision of *Liagora* was also suggested by Huisman & Kraft (1994) and Huisman & Wynne (1999), although no generic boundaries were indicated. Preliminary DNA sequence studies (Huisman, Saunders & Harper in prep.) indicate that *Liagora* is indeed polyphyletic and support its subdivision into more precisely defined units. Further work on a range of species, however, is required before any additional taxonomic and nomenclatural revisions can be made.

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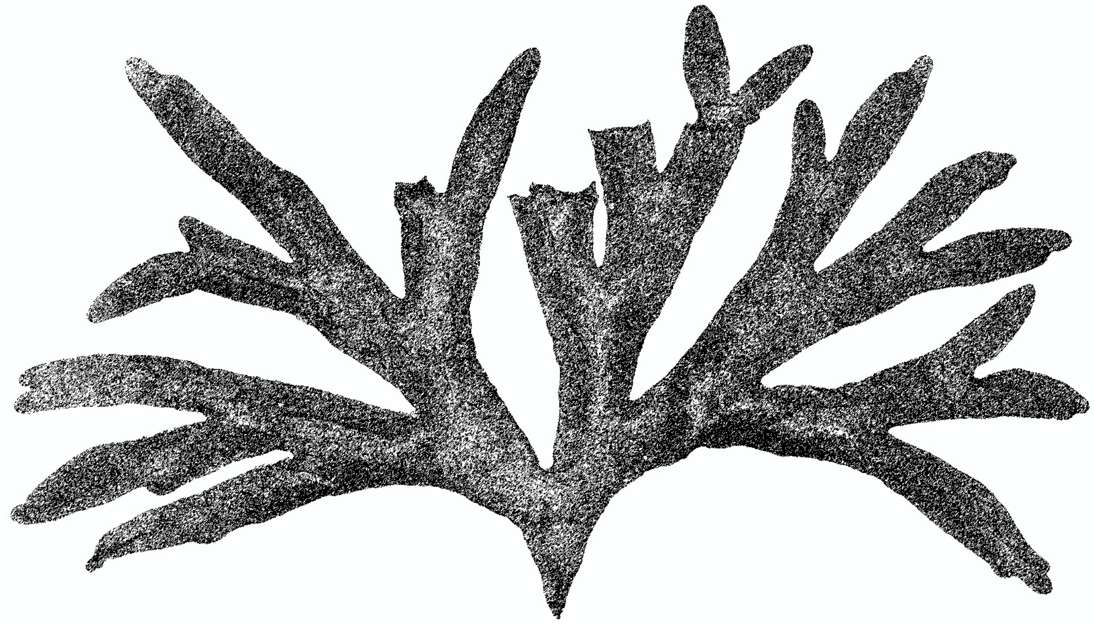

Sebdenia flabellata (J. Agardh) Parkinson: a red alga from the upwelling shores of Masirah Island and the Socotra Archipelago.

CHAPTER 6

Spatial variation in subtidal plant communities around the Socotra Archipelago and their biogeographic affinities within the Indian Ocean

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ABSTRACT

The subtidal plant communities of the Socotra Archipelago were studied by means of quadrat sampling. Ordination and statistic analyses reveal six distinct entities corresponding to the geographic location and the physico-chemical factors. The north coast of Socotra Island is composed of common Indian Ocean algae, with an intermediate species richness and alpha diversity for the archipelago. This entity also includes two species-poor sub-entities: the seagrass beds and the coral-dominated communities. The transition zone is an overlapping area between Socotra's north and south coast, showing the highest similarity in community structure with the upwelling flora of the south coast owing to similar environmental conditions. In addition, this zone is subject to intense current patterns favouring a pronounced diversity in red algae. The south coast totals the highest number of recorded species, a lower affinity with the (sub)tropical Indian Ocean flora and is marked by disjunctly distributed species. The plant communities of the outer islands comprise a mixture of the previous entities due to the drastically changing seasonal environmental conditions in a limited coastal area. The intermediate character of this entity, ongoing competition amongst biota without reaching a climax in the vegetation succession, is reflected in the vegetation analyses and the biogeographic comparison.

INTRODUCTION

The Socotra Archipelago (12.47°N, 53.87°E; Yemen) is situated in the southwestern part of the Arabian Sea (Fig. 1) and is affected by various gyres and eddies that result in upwelling during the SW monsoon in summer. The south coast of the main island is particularly influenced by the upwelling phenomenon, whereas the north coast is typified by warmer water with less temperature fluctuations. Biogeographic studies of Socotra's marine fauna (Kemp 1997, 1998b) show that many species are widespread throughout the Indo-Pacific and the Red Sea. In addition, the diverse habitats of the archipelago constitute an important refuge for closely related species from the Indian Ocean, Arabian Sea, Red Sea and Gulf of Aden (sympatry). Many species of the surrounding seas have their outermost distribution limits around Socotra, making it an important haven for larval stages and their dispersal throughout the Indian Ocean, the Red Sea and the Arabian Sea. Kemp (1998b) concluded that this southern Arabian region might be an extension of the upwelling region of Oman, characterized by a distinct species composition and a pronounced degree of endemism (Sheppard & Salm 1988, Randall & Hoover 1995).

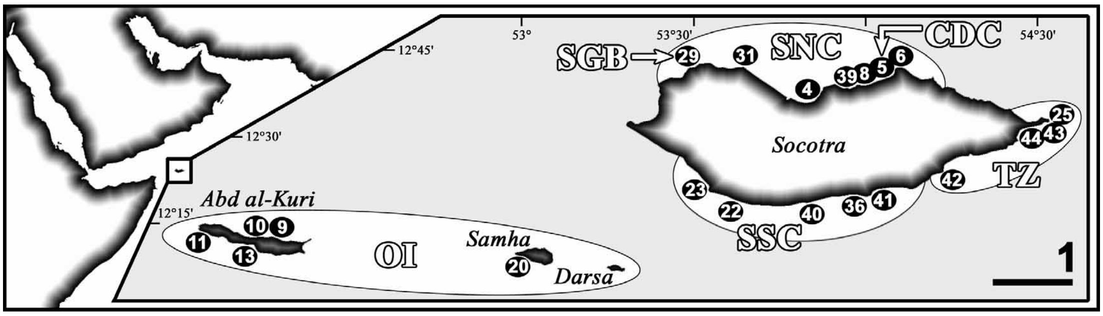


Fig. 1. Geographic position of the Socotra archipelago, with the indication of the sampling sites (black dots) and the DCA clusters: the seagrass beds (SGB), the coral dominated communities (CDC), Socotra's north coast (SNC), the transition zone (TZ), Socotra's south coast (SSC), and the outer islands (OI). Scale bar represents 25 km.

Despite limited studies on Arabian Sea macroalgae, Børgesen (1934) had already commented on the peculiar flora and its biogeographic affinities with distant regions. In the 1990's renewed interest in the marine biology of the region arose, including phycological studies. Ormond & Banaimoon (1994) studied the algal assemblages in relation to physico-chemical characteristics along the upwelling coast of Hadramout (Yemen). During the same period, numerous taxonomic studies on the seaweeds of upwelling areas in Oman were initiated by Wynne (Wynne & Banaimoon 1990, Wynne & Jupp 1998, Wynne 1998, Wynne 1999a, b, Wynne 2001). The large number of new records and newly described species in these studies illustrate the lack of knowledge of the Arabian Sea flora. Early phycological studies on the Socotra Archipelago are limited to Dickie (1888) and Holmes (1903), who reported 27 marine algae for Socotra Island and Abd al-Kuri. More recent studies focussed on specific taxonomic, systematic and ecological issues of Socotra's macroalgal flora (Kemp 1998a, Wynne & Leliaert 2001, Schils & Coppejans 2002, Schils *et al.* 2002). In an effort to protect the relatively pristine marine and terrestrial natural heritage of the Socotra Archipelago (United Nations Development Programme for the sustainable use and conservation of the Socotra Archipelago) an interdisciplinary team of scientists studied the vulnerable and endangered ecosystems and species around the archipelago. The resulting taxonomic and ecological studies highlighted the diversity and the pristine nature of the marine habitats. The present study is an ecological follow-up and aims at identifying the main plant communities around these islands, analysing their species composition and biogeographic affinities.

MATERIALS AND METHODS

Macroalgal and seagrass communities around the Socotra Archipelago were sampled in spring 2000 (26 March – 7 May). A total of 82 vegetation quadrats from 21 sites (Fig. 1; Appendix 1) were used to compare the different algal assemblages of the main island, Abd al-Kuri and Samha. At each site homogeneous macroalgal assemblages on subtidal platforms, ranging from –5 to –15 m depth, were selected, in which the quadrats (0.25 m^2) were randomly placed. Upon recording the species by means of Braun-Blanquet's combined estimation (Table 1), the quadrats were cleared and the algae were gathered in fine-meshed plastic bags. In the field laboratory, the mesh bags were sorted by species and fresh weight (including the rhizomes of the seagrasses) was measured with a dynamometer. Small and crustose algae are excluded from the analyses as their biomass is hard to determine and a meticulous investigation of the whole substratum and epiphytes is too time-consuming.

Representative specimens were pressed as herbarium specimens, preserved in a 5% formaldehyde-seawater solution or dried in silica gel for molecular purposes. The reference collection is lodged in GENT (Ghent University Herbarium, Krijgslaan 281 - S8, 9000 Ghent, Belgium).

Table 1. Braun-Blanquet's combined estimation and the transformed scale of Braun-Blanquet (van der Maarel 1979, Schaminée *et al.* 1995).

Braun-Blanquet's combined estimation			van der Maarel
No of individuals	**Cover**	**Code**	**Code**
rare	< 5%	r	1
few	< 5%	+	2
many	< 5%	1	3
abundant	< 5%	2	4
arbitrarily	5 - 25%	2	4
arbitrarily	25 - 50%	3	5
arbitrarily	50 - 75%	4	6
arbitrarily	> 75%	5	7

Ordination

The biomass data was selected as the most informative ordination input. Before ordination, the biomass data was log transformed and rare species were downweighted. Detrended Correspondance Analysis (DCA performed with CANOCO; ter Braak 1988) was chosen as an indirect gradient analysis as: (i) the data clearly represent a unimodal model (maximum gradient length: 7.615 SD; ter Braak & Šmilauer 1998) and (ii) the Correspondance Analysis (CA) showed a pronounced arch effect.

In an attempt to determine the species-environment correlation, environmental data around Socotra (latitude: 9.650°N – 14.383°N; longitude: 51.900°E – 57.067°E) were obtained from the Worldwide Ocean Optics Database (http://wood.jhuapl.edu, W.O.O.D. version 4.0). Chlorophyll a (CHL), nitrate (NO_3), nitrite (NO_2), oxygen (OX), phosphate (PO_4), salinity (SAL), silicate (SiO_4) and temperature (TEMP) parameters showed a good sample distribution for the area. All these parameters were sampled for the SW monsoon (Julian days 121-304) and the NE monsoon (Julian days 305-120) and the average of a parameter during one of both periods was calculated for 3 geographic areas around the archipelago (zone 1: > 12.335°N; zone 2: < 12.335°N and > 53.835°E; zone 3: < 12.335°N and < 53.835°E). The water masses of these 3 areas affect the greater part of the coastal waters in respect to their physico-chemical properties. Additional parameters were derived from the original data, i.e. the absolute difference of a parameter between the 2 monsoon periods (abbreviation of the environmental parameter + "_AD") and the average between the periods (parameter + "_AV"). Thus, this environmental data set has identical parameter values for all sites of a specific area (corresponding with the DCA clusters). To tackle this lack of resolution in the environmental data, a pseudo-environmental data set, composed of the latitude (LAT_N) and longitude (LON_E) coordinates of the quadrats, was used. The idea is that the species-GIS correlation might be indicative for environmental gradients that vary according to the geographic position around the archipelago. All parameters have been standardized to zero mean and unit variance.

Less informative ordination inputs, species records in a van der Maarel scale (deduced from the Braun-Blanquet cover data; Table 1) and species presence/absence, were tested against the ordination results of the biomass data for each species within a quadrat.

Statistics

Subsequent analyses of the DCA clusters (plant communities) include the calculation of species richness per quadrat, total biomass per quadrat, alpha diversity per quadrat (BioDiversity Professional Version 2: Fisher's log-series alpha; Fisher *et al.* 1943) and beta diversity (the Jaccard Coefficient as a qualitative index: $S_j = a\ (a+b+c)^{-1}$ a = # species shared between two clusters, b = # species restricted to the first cluster, c = # species restricted to the second cluster; and the Similarity Ratio as a quantative index: $SR_{ij} = S_k y_{ki} y_{kj} (S_k y_{ki}^2 + S_k y_{kj}^2 - S_k y_{ki} y_{kj})^{-1}$, y_{ki} = biomass of species k in cluster i, y_{kj} = biomass of species k in cluster j). The species richness was square root^{-1} transformed, total biomass and Fisher's alpha were natural log transformed prior to variance analysis in order to achieve normality and homogeneity of variances. Analyses of variance with the Tukey HSD test (Zar 1996) for post hoc multiple comparisons were performed with SPSS for Windows 11.0.1 (SPSS Inc. 2001).

Biogeography

The biogeographic affinity of Socotra's subtidal plant communities are analysed by comparing the species composition of the DCA clusters to species inventories of Indian Ocean countries. The latter data set is primarily based on Silva *et al.* (1996) and supplemented with records from recent papers. The floristic affinity of a cluster with a specific country is calculated as the Simpson Coefficient: $a\ (a+ \min (b, c))^{-1} \times 100$. In which a represents the number of shared species between a cluster and a country, b and c represent the number of species unique to the cluster and the country, respectively. The species inventories of the clusters are always smaller than those of the countries, so the equation does not include the floristic richness of a country as it is irrelevant in a study restricted to subtidal surveys, and it reduces the discrepancy of sampling efforts between the different countries. The countries are arranged from southeast Africa, over the Arabian Sea, to Western Australia. India was excluded from the series as its size and geographic position cover a wide diversity of floras within the Indian Ocean.

RESULTS

Species account

A total of 127 plant species [3 seagrasses, Magnoliophyta; 29 Chlorophyta; 26 Phaeophyta; 69 Rhodophyta] are recorded for the 82 subtidal quadrats (Appendix 2). This corresponds with a Cheney's ratio [(R+C)/P] of 3.8.

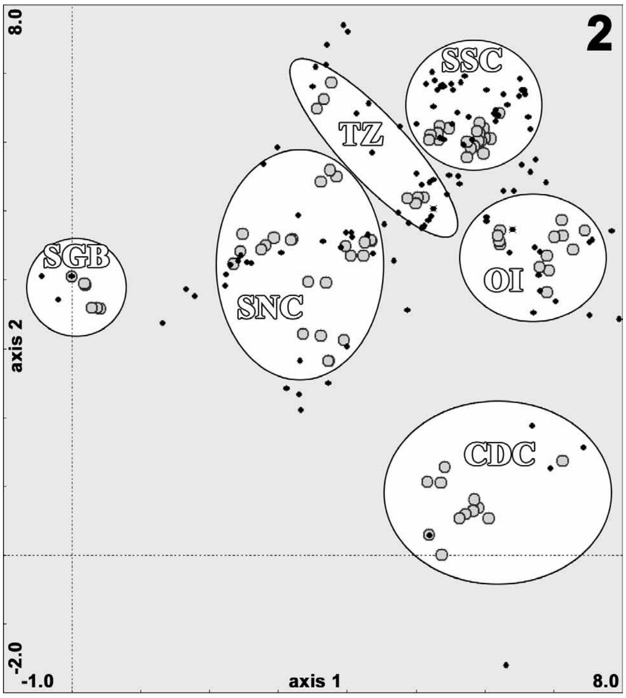


Fig. 2. First two ordination axes of a DCA based on the log transformed biomass data of the subtidal plants (black dots) in the different quadrats (grey circles), rare species are downweighted.

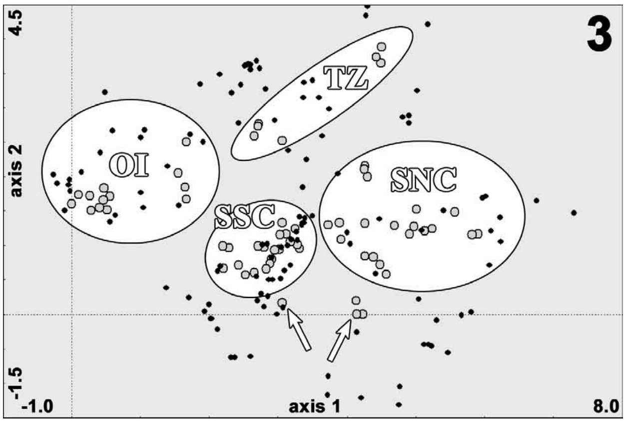


Fig. 3. First two ordination axes of the second DCA in which the quadrats of SGB and CDC are excluded (log transformed biomass data and downweighting of rare species). Cluster abbreviations as in Fig. 1. Arrows indicate the quadrats of ANC. Black dots represent plant species, grey circles represent quadrats.

Ordination

The DCA of the biomass data of the 82 quadrats shows 6 distinct site groupings (Fig. 2), which correspond well with their geographic position around the archipelago (Fig. 1). Both axes have high eigenvalues (0.781 and 0.688) and together they represent 14.8 % of the variation in species composition. The plot reflects the geographic position of the sample stations within the archipelago, presumably relating to the physico-chemical characteristics of the water mass. This is shown in the high correlation of the latitude coordinates (-0.7285) with the first and the longitude (0.4514) with the second DCA axis. Both axes have a large length of gradient (7.442 and 6.860), indicating the high ß-diversity between the quadrats of the different communities. The following clusters can be discerned (Fig. 2): the seagrass beds (SGB), the coral dominated communities (CDC), Socotra's north coast (SNC), the transition zone at the eastern extremity of Socotra Island (TZ), Socotra's south coast (SSC) and the outer islands (OI). The DCA shows a gradual change in species composition from SNC, over TZ, to SSC. The latter is characterized by a high number of species, many restricted to this zone for the archipelago (the aggregation of species around SSC in the biplot; Fig. 2). OI constitutes a distinct cluster, intermediately positioned along the gradient from SNC, over TZ to SSC. The quadrats of SGB and CDC also constitute 2 distinct clusters in the DCA. The plant communities of these two clusters differ substantially in species composition, biomass and species richness from the other DCA clusters (see below), potentially distorting the affinities of the remaining quadrats, hence their exclusion in the subsequent DCA.

The second DCA (axes 1 and 2, respectively: eigenvalues, 0.732 and 0.469; lengths of gradient, 5.513 and 3.876; cumulative % variance of species data, 9.6 and 15.7) revealed the same clusters as the previous analysis (Fig. 3). Though, the quadrat clusters are less geographically distributed in the biplot in comparison to the first DCA: high correlation of latitude (0.743) and longitude (0.490) coordinates with the first and less (0.199 and 0.291, respectively) with the second DCA axis. The difference between SNC, SSC and OI is principally determined by the first DCA axis. Perspective to the first axis, TZ and a few quadrats of the north coast of Abd al-Kuri (ANC; Fig. 3: arrows) are intermediate between SSC and SNC. The second axis mainly discerns SNC and SSC, from OI, and TZ. The second axis might be interpreted as the variability in current velocity and direction within a season: velocities are very high and the direction is rather irregular at TZ, somewhat less variable at OI, and more regular (although seasonally variable) at SSC and SNC. The low value of ANC for the second axis corresponds with the sheltered position of the site. This diversity in current patterns around the archipelago shapes the substratum (steep rocky shorelines with numerous microhabitats e.g. crevices, sand deposition, etc.), which in turn determines algal composition.

Table 2. Correlation coefficients of the environmental parameters with the first two axes of the second DCA of biomass data. Absolute coefficient values in decreasing order for the first axis. Abbreviations of parameters as in text.

Parameter	Axis 1	Axis 2	Parameter	Axis 1	Axis 2
PO4_SW	-0.7650	-0.0997	NO3_AD	-0.7146	-0.2765
PO4_AD	-0.7648	-0.0722	CHL_AD	-0.7135	-0.2784
SAL_SW	0.7628	0.1315	SAL_AD	-0.6893	0.1533
TMP_SW	0.7610	0.1452	NO3_SW	-0.6831	-0.3230
PO4_NE	0.7608	0.0313	CHL_NE	0.6440	0.3667
TMP_AD	-0.7567	-0.0085	NO3_AV	-0.5833	-0.4173
NO3_NE	0.7493	-0.0216	PO4_AV	-0.5770	-0.4218
OXY_AV	0.7473	-0.0283	SAL_AV	0.5351	0.4481
OXY_AD	0.7445	-0.0373	NO2_SW	-0.5046	0.3462
OXY_NE	0.7437	-0.0396	LON_E	0.4904	0.2910
LAT_N	0.7433	0.1990	SIO_AV	-0.4830	-0.4748
NO2_AD	0.7357	-0.0621	TMP_AV	0.4666	0.4820
CHL_SW	-0.7339	-0.2386	SAL_NE	-0.3112	0.4561
NO2_NE	0.7339	-0.0666	SIO_SW	-0.1278	-0.5466
NO2_AV	0.7330	-0.0688	SIO_AD	-0.1193	-0.5466
TMP_NE	-0.7293	0.0777	OXY_SW	0.0488	0.5438
CHL_AV	-0.7203	0.0975	SIO_NE	0.0136	0.5407

In Table 2 the parameters PO_4_SW to CHL_NE show that most variables have markedly higher (absolute) correlation values with the first DCA axis as opposed to the second axis. Certain parameters, however, correlate best with the second axis: SiO_4_SW (-0.547), SiO_4_AD (-0.547), OXY_SW (0.544), SiO_4_NE (-0.541). Most of the averages of both monsoon parameters (parameters with the "_AV" suffix) correlate well with both axes. The communities of SNC are separated from SSC along the first axis, which might result from the lower phosphate concentrations, the higher salinity and the higher temperatures of the former cluster during the SW monsoon. On the other hand, the PO_4 concentrations during the NE monsoon are higher at SNC than SSC. The difference between these clusters can also be explained by the lower PO_4, lower TMP and higher OXY fluctuations ("_AD" suffix) at SNC in comparison to SSC and OI. The separation along the second axis, e.g. TZ from SSC and SNC, might be caused by rather low SiO_4 and high OXY concentrations (intense current patterns) at TZ during the SW monsoon, and high SiO_4 concentrations at TZ during the NE monsoon. The fluctuations in SiO_4 concentrations are higher at SSC compared to TZ.

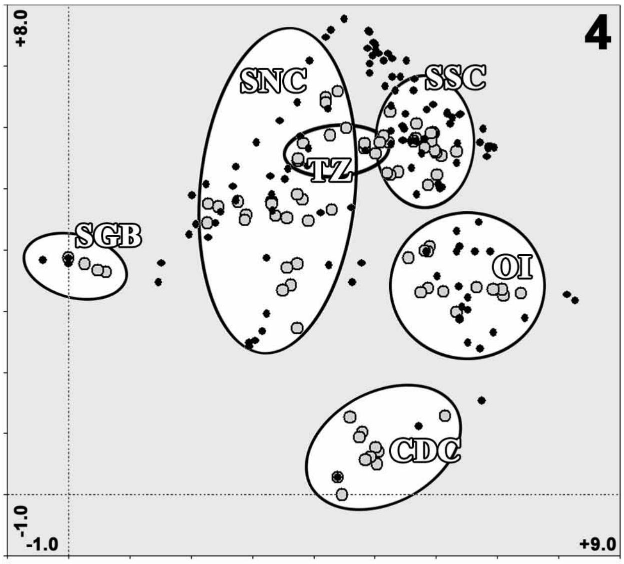


Fig. 4. First two ordination axes of a DCA based on cover data (van der Maarel scale) of the subtidal plants (black dots) in the different quadrats (grey circles), rare species are downweighted.

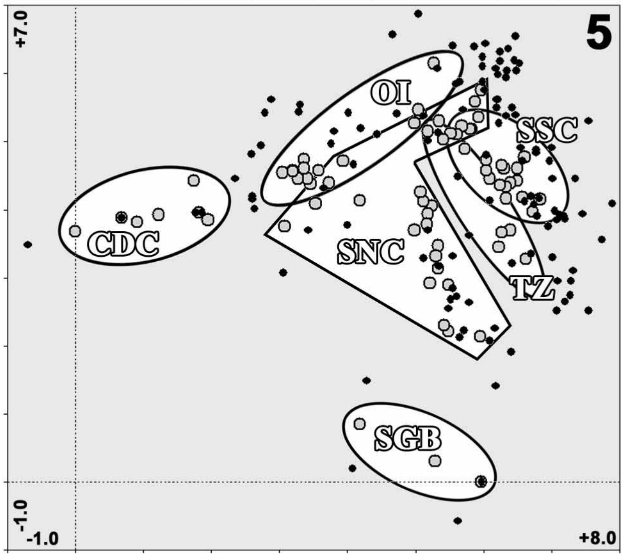
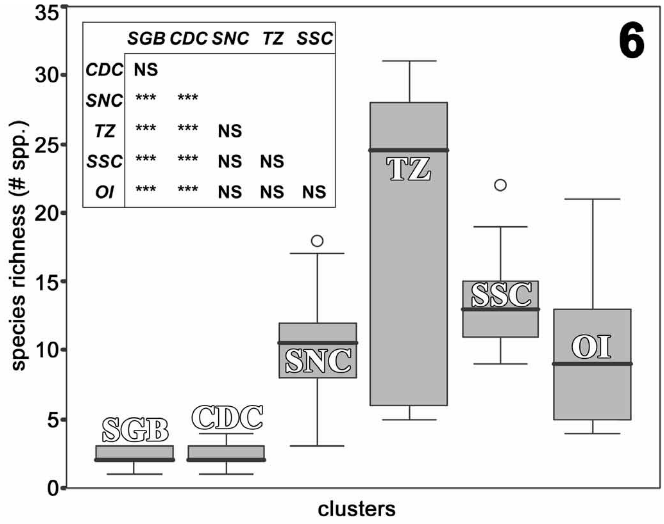
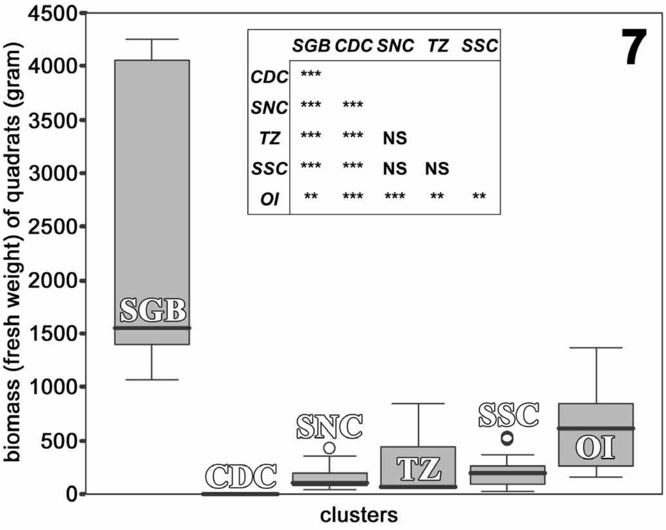


Fig. 5. First two ordination axes of a DCA based on presence/absence data. Cluster abbreviations as in Fig. 1. Black dots represent plant species, grey circles represent quadrats.

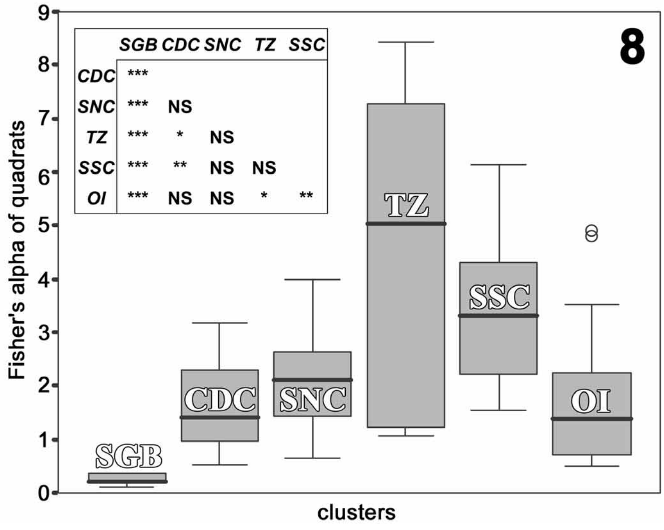
The DCA based on the van der Maarel data (Fig. 4), resulted in similar clusters but has less resolution as the quadrats of TZ are partly grouped in SSC and SNC, respectively. The first two axes of this ordination have high eigenvalues (0.743 and 0.689) and together they represent 15.7 % of the variation in species composition. The DCA of the nominal data (presence/absence) also shows a similar cluster pattern (Fig. 5), but the distinction between SNC, TZ, SSC and OI is less clear (intermingled quadrats) and the latter grouping of clusters constitutes a more homogeneous group in relation to CDC and SGB. The first two axes of the latter DCA have high eigenvalues (0.707 and 0.589) and together they represent 12.4 % of the variation in species composition.



	SGB	CDC	SNC	TZ	SSC
CDC	NS				
SNC	***	***			
TZ	***	***	NS		
SSC	***	***	NS	NS	
OI	***	***	NS	NS	NS



	SGB	CDC	SNC	TZ	SSC
CDC	***				
SNC	***	***			
TZ	***	***	NS		
SSC	***	***	NS	NS	
OI	**	***	***	**	**



	SGB	CDC	SNC	TZ	SSC
CDC	***				
SNC	***	NS			
TZ	***	*	NS		
SSC	***	**	NS	NS	
OI	***	NS	NS	*	**

Figs 6-8. Box plots of the variables (species richness, biomass and alpha diversity) showing the median, quartiles, and extreme values for each of the DCA clusters. Cluster abbreviations as in Fig. 1. Counts for categories: SGB (6), CDC (12), SNC (24), TZ (10), SSC (17), OI (13). ANOVA, Tukey HSD: NS, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Fig. 6. Species richness of the quadrats (untransformed) from the different DCA clusters. Inset: ANOVA, Tukey HSD, of square root^{-1} transformed data.

Fig. 7. Total biomass (fresh weight) of the quadrats (untransformed) from the different DCA clusters. Inset: ANOVA, Tukey HSD, of natural log transformed data.

Fig. 8. Fisher's alpha of the quadrats (untransformed) from the different DCA clusters. Inset: ANOVA, Tukey HSD, of natural log transformed data.

Species richness and biomass

The ANOVA of the transformed species richness per quadrat shows 2 groups of DCA clusters (Fig. 6). SGB and CDC are characterized by a low floristic species richness. The second group incorporates the remaining clusters. The range of the species richness per quadrat within this group varies highly, but the species richness of these clusters does not differ significantly. The highest number of species (31) per quadrat are reported for TZ.

The analysis of variance of the biomass data shows one group of clusters (SNC, TZ, SSC) with comparable biomasses (Fig. 7). Again, the interquartile range of TZ covers the widest range, encompassing those of SNC and SSC. The quadrats of the latter clusters have intermediate biomasses between those of SGB, expressing the highest biomass per quadrat, and those of CDC, characterized by a low biomass. OI differs significantly from the first group of clusters, but the quadrats of OI are also characterized by biomass values intermediate between, and differing substantially from, those of SGB and CDC.

Alpha and beta diversity

The log-series variable alpha, composite index of species richness and abundance, shows the highest species diversity per quadrat for the most species rich clusters with moderate biomass (high evenness), i.e. TZ and SSC (Fig. 8). A second group, consisting of CDC and OI, shows a significantly lower alpha diversity than the TZ-SSC-group. SNC has an intermediate alpha diversity between both groups, as it does not differ significantly from any of the four clusters. SGB is characterized by the lowest alpha diversity values.

The Jaccard coefficient, as a qualitative measurement for ß-diversity (Table 3), shows that SSC and TZ are the most similar DCA clusters (lowest degree of species turn-over). Both are somewhat less similar to the communities of SNC and OI. The quantitative similarity ratio is less resolving (Table 4). In addition to the high similarity in absolute species composition, the species occurring at TZ have a comparable biomass to those in SSC and SNC. The latter, however, show a low quantitative similarity to each other, illustrating the intermediate nature of TZ.

Table 3. The Jaccard coefficient (%) as a qualitative measurement for ß-diversity among the DCA clusters. Similarities higher than 10 are marked in bold.

	SGB	*CDC*	*SNC*	*TZ*	*SSC*
CDC	0.00				
SNC	3.57	3.45			
TZ	1.82	1.75	**24.71**		
SSC	1.16	2.30	**28.04**	**40.63**	
OI	0.00	**10.26**	**13.75**	**21.92**	**26.32**

Table 4. The similarity ratio as a quantative measurement for ß-diversity among the DCA clusters. The high similarity values of TZ with SSC and SNC, respectively, are marked in bold.

	SGB	*CDC*	*SNC*	*TZ*	*SSC*
CDC	0.00				
SNC	0.04	3.97			
TZ	0.01	0.01	**64.81**		
SSC	0.00	0.00	1.62	**80.76**	
OI	0.00	0.00	0.45	0.02	3.13

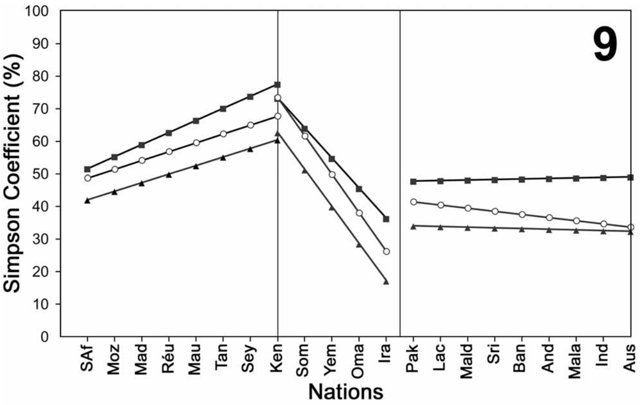
Biogeography

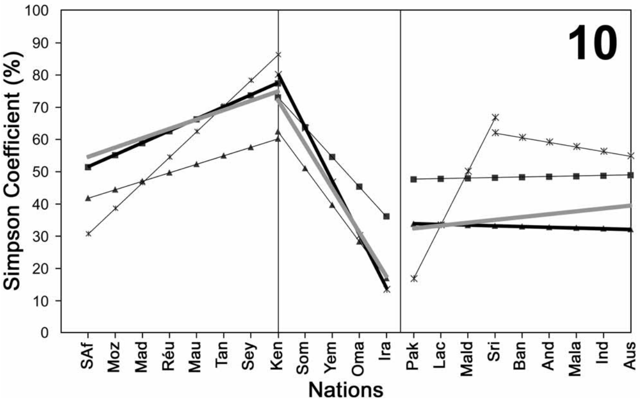
The graphs of the biogeographic affinity of the DCA clusters within the Indian Ocean show three general trends (Figs 7, 8), corresponding with the following coastal areas: (i) South Africa – Kenya (East African Coast); (ii) Kenya – Iran (Arabian Sea); and (iii) Iran - Western Australia (eastern Indian Ocean). CDC showed an additional trend for the eastern Indian Ocean, an increase in affinity for the region Pakistan – Sri Lanka and a plateau for Sri Lanka - Western Australia. For each of these coastal blocks the regression lines were calculated in order to compare the general trends of the different clusters (Schils *et al.* 2001). SGB and CDC are composed of common Indian Ocean taxa, visualized by an increasing affinity for the East African flora from South Africa to a peak in Kenya. Thereafter, the affinity decreases for the Arabian Sea, the result of a few unrecorded common Indian Ocean taxa for this area. These species [e.g. *Dictyosphaeria cavernosa* (Forsskål) Børgesen] are probably ubiquitous throughout the Arabian Sea as they already have been reported for the Arabian Gulf (De Clerck & Coppejans 1996). Similar patterns were obtained for SNC, TZ and SSC, however, with a decreasing overall affinity in this order (Fig. 9). OI behaved like a combination of the other clusters: having a relatively high affinity with the East African Coast (common Indian Ocean taxa) similar to SNC, a decreasing affinity with the Arabian Sea flora (an artefact of undersampling in the Arabian Sea) like CDC and a relatively low affinity with the Eastern Indian Ocean comparable to SSC (Fig. 10).

DISCUSSION

The Cheney ratio, the sum of the Rhodophyceae and Chlorophyceae divided by the number of Phaeophyceae, has been used to correlate macroalgal floras with seawater temperature (Cheney 1977, Bolton 1986). The overall ratio for the archipelago is 3.8, which is indicative for a warm temperate flora (Kapraun 1980). The Cheney ratios of the major quadrat clusters (SNC, TZ, SSC and OI) are comparable, due to similar proportions of Chloro-, Phaeo- and Rhodophyceae in these communities (Fig. 11).

The clusters obtained from the DCA can be grouped geographically, which is shown by the high correlation of the GIS coordinates to the first two DCA axes. The 6 clusters include distinct entities (SGB, CDC, SNC and SSC) and intermediate ones (TZ, OI). The characteristics of each of the subtidal plant communities are discussed below.





Figs 9, 10. Regression lines of the biogeographic affinities (y axis: Simpson Coefficient in %) between the DCA clusters of Socotra and check lists of Indian Ocean nations. The countries (x axis) are presented from the southwestern Indian Ocean, over the Arabian Sea, to the southeastern Indian Ocean (indicated by the vertical lines in the plot): South Africa (SAf), Mozambique (Moz), Madagascar (Mad), Réunion (Réu), Mauritius (Mau), Tanzania (Tan), Seychelles (Sey), Kenya (Ken), Somalia (Som), Yemen (Yem), Oman (Oma), Iran (Ira), Pakistan (Pak), Laccadive (Lac), Maldives (Mald), Sri Lanka (Sri), Bangladesh (Ban), Andaman (And), Malaysia (Mala), Indonesia (Ind), Australia (Aus).

Fig. 9. Biogeographic affinity of SNC (filled squares), TZ (open circles) and SSC (filled triangles).

Fig. 10. Biogeographic affinity of CDC (asterisks), SNC (filled squares) and SSC (filled triangles) in relation to that of OI (thick grey line). Similarities between the former clusters and OI, for a specific region (East Africa, Arabian Sea, western Indian Ocean), are indicated with a thickened line.

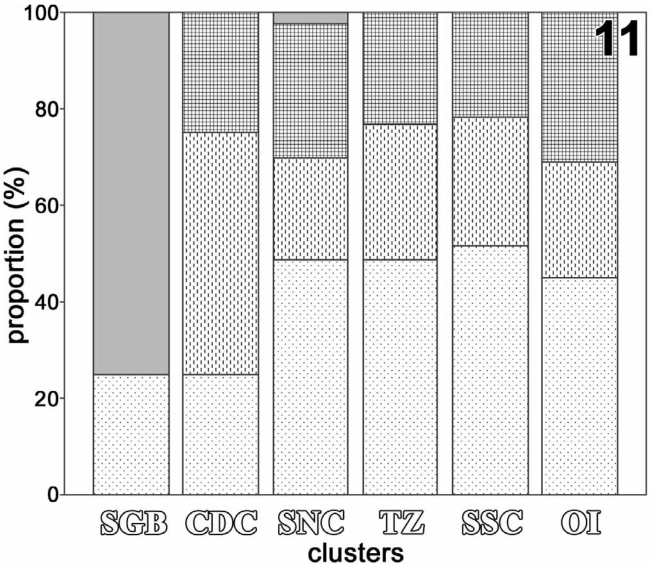


Fig. 11. Percentage of Rhodophyta (dotted), Phaeophyta (hatched), Chlorophyta (vertically striped) and seagrasses (grey shaded) in the DCA cluster. Cluster abbreviations as in Fig. 1.

Seagrass beds (SGB) and coral dominated communities (CDC)

SGB and CDC are characterized by a low floristic richness. Both clusters, however, can be regarded as sub-entities of Socotra’s north coast as they occur in specialized habitats within SNC. The communities of these two biotopes differ substantially in species composition, biomass and species richness from the other DCA clusters and were excluded from the second DCA, in which the environmental variables were tested. Extensive seagrass beds are rather rare around the archipelago: patches of *Halodule uninervis* (Forsskål) Ascherson are scattered around the north coast (sandy substrate), well-developed *Thalassodendron ciliatum* (Forsskål) den Hartog beds occur in Mahfirhin Bay (Fig. 1: close to site 42; no quadrats available) and extensive seagrass beds, composed of *Halodule uninervis*, *Halophila ovalis* (R. Brown) Hooker and *Thalassia hemprichii* (Ehrenberg) Ascherson are found in Qalansiyah lagoon (Fig. 1: site 29). Owing to the exclusion of small epiphytes in this study, SGB is species-poor but shows the greatest standing stock of all community types. With respect to other seagrass communities, generally consisting of one or two seagrass species (Duarte 2000), Qalansiyah lagoon, however, contains plant communities with a moderate seagrass richness (three species).

CDC is typified by a predominant coral cover (> 90%), complemented with some common Indian Ocean algae characteristic for this habitat [e.g. *Chlorodesmis fastigiata* (C. Agardh) Ducker and *Dictyota friabilis* Setchell]. Coral reef development is restricted to small patches around the archipelago. As a rule, coral reef formation is rare within the Arabian Sea and the phenomenon of large monotypic reefs (e.g. the *Montipora* reefs at Masirah Island, Oman) shows that the environmental conditions are generally too harsh and unfavourable for many corals species (Coles 1995, Paulay 1999, Wilson 2001). Recent field studies have, however, demonstrated that the area hosts more coral species and endemics than previously thought (Paulay & Meyer 2001).

Socotra's north coast (SNC)

The north coast of Socotra is typified by a mixture of well-developed coral assemblages (e.g. CDC at Hawlaf; Fig. 1: site 5) and algal communities (e.g. Diham; Fig. 1: site 4). The marine macroflora of this area consists mainly of common East African/Indian Ocean taxa (Fig. 9), reflected in the high general affinity with the Indian Ocean flora. The environmental correlations show that this cluster is characterized by the highest water temperatures and salinities of the archipelago during the SW monsoon. SNC has the highest values of the low phosphate concentrations during the NE monsoon. During the SW monsoon, the phosphate concentrations are higher with the lowest values for SNC. Consequently, this entity is characterized by the smallest changes in phosphate concentrations and temperature, the lowest average chlorophyll a concentrations, and the highest average oxygen concentrations. A total of 43 species were collected in the subtidal quadrats of this area. The species richness per quadrat does not differ from SSC, TZ and OI, and the alpha diversity is intermediate of all communities around the archipelago. The biomass of the quadrats equals those of TZ and SSC. The communities of SNC have a high similarity in structural composition (quantitative ß-diversity) with TZ (64.81), and show a high qualitative similarity with SSC (28.04) and TZ (24.71). SNC and SSC thus share a relatively high number of species, partly due to the high number of recorded species for SSC, but these occur throughout both clusters in low abundances.

Socotra's south coast (SSC)

During the SW monsoon, the Great Whirl, extending northwards along the Somali Coast, spins off towards Socotra's south coast (http://www.nioz.nl/en/facilities/dmg/niop/themes/theme-c/thmchydr). This cold and nutrient rich surface water (~ 22°C) shapes the southern coast of Socotra. The impact of upwelling hampers coral development (e.g. bioerosion;

Paulay 1999) and promotes macroalgal growth in an ongoing competition with the coral communities due to the favouring environmental parameters during the SW monsoon (e.g. high phosphate concentrations and low temperature). Consequently, the SSC vegetation is relatively high in biomass and rich in species, resulting in high alpha diversity values. In addition, SSC contains the largest number of species per cluster (64). The flora comprises a large number of red algal species that generally contribute little to the total biomass in understory layers (e.g. *Zellera tawallina* G. Martens), and more to the primary layer [e.g. large plants of *Botryocladia leptopoda* (J. Agardh) Kylin]. In addition, a remarkable number of gelatinous red algae (Schils & Coppejans 2002) has been reported for this area. Despite the relatively high number of species recorded for the quadrats, the biogeographic affinity within the Indian Ocean is low. This is the result of a number of disjunctly distributed and endemic species (Schils *et al.* 2002; Schils & Huisman 2003), reflecting biogeographic affinities with distant areas (Australia, Hawaii, Japan and South Africa). Børgesen (1934) and Wynne (2000) noted similar distribution patterns for certain species within the Pakistani and Omani flora, respectively. The disjunct distribution pattern of these algae could result from: (i) the upwelling phenomenon and the resulting peculiar environmental conditions; (ii) refugia where algae could persist subtidally over a long time (e.g. *Reticulocaulis*; Schils *et al.* 2002; Millar and Kraft 1984); or (iii) the lack of subtidal studies in the Indian Ocean. Similar disjunct distribution patterns have also been reported for coral species from the Arabian Sea (Coles 1995).

Transition zone (TZ)

The algal communities at the eastern extremity of Socotra Island are characterized by high biomass stands, being rich in species (species richness of the quadrats). This results in the highest alpha diversity values of all surveyed sites around the archipelago. The total amount of recorded species in this cluster (39) is somewhat lower than those of SSC and SNC, most probably a result of the low number of quadrats (10) included in TZ. The communities are composed of a mixture of primarily south coast species (highest qualitative and quantative similarities) and north coast species. The macroalgal stand (biomass) is similar to those of SNC and SSC. We can conclude that the transition zone, hence its name, is a gradual overlapping zone between the communities of Socotra's north and south coast. This cluster is, however, also characterized by certain algae (e.g. *Gibsmithia larkumii* Kraft and *Sympodothamnion* sp.; Schils & Coppejans 2002; pers. obs.), displaying a disjunct distribution pattern within the Indo-Pacific. This is reflected in the biogeographic graph (Fig. 9), in which TZ, compared to SNC, shows a decline in the general affinity with Indian Ocean taxa. The floristic peculiarity of this cluster is most probably related to the prevailing environmental conditions. The eastern tip of Socotra Island is subject to upwelling and in addition there seems to be a pronounced effect of the Socotra Eddy evolving east from the island, contiguous with the other anticyclonic circulation the "Great Whirl" (http://www.ssc.erc.msstate.edu/Altimetry/north_indian_ocean.html). Complex and intense current patterns were noted in this area, and local fisherman cannot access this area during the greater part of the SW monsoon (pers. obs.). Presumably, these intense currents favour the luxuriant and particular red algal flora due to the constant flow of nutrients and the temperature regulation of these subtidal habitats (corresponding to its position along the first DCA axis, in between SSC and SNC). Unfortunately, data of current patterns and velocities were not available for inclusion in the analysis.

Outer islands (OI)

The outer islands of this study include Abd al-Kuri and Samha Island. There were no quadrat data from Darsa Island available, but based on its geographic position the communities are likely to be similar to those of OI. Certain quadrats of the north coast of Abd al-Kuri (ANC) group with SNC in the first DCA, but less pronounced so in the second (arrows in Fig. 3). This supports the hypothesis for a drive towards the development of macroalgal communities comparable to those of the main island (SNC and SSC), but this climax stage is not reached due to the drastically changing chemical characteristics and water dynamics around a small coastal area (area effect). Support for these speculations can be found in the second DCA, where OI is positioned close to the origin of the first axis, which is highly negatively correlated with the fluxes in phosphate concentrations and temperature. This is backed by the statement of van Bennekom J., de Bruin T., Nieuwenhuis J. (http://www.nioz.nl/en/facilities/dmg/niop/themes/theme-c/thmchydr) that the region between Socotra and Ras Fartak shows alternating patches of relatively warm and cold surface water. Likewise, van Ooijen J.C., van Weerlee E (http://www.nioz.nl/en/facilities/dmg/niop/themes/theme-c/thmchydr) note that between Cap Guardafui and Socotra the entire water column is seasonally renewed to a depth of 1100 m. The importance of the high environmental dynamics at OI has major ecological implications: Turner (http://www.cordio.org/Repstatus10) observed that the islands Samha and Darsa were barely affected by the coral bleaching that hit main Socotra severely in 1998. The mixed species composition is also reflected in the biogeographic trend, being composed of different biogeographic affinities characteristic for the other communities. Accordingly, OI is characterized by the high abundances and diversity in coastal fish, soft corals and scleractinian corals, counting for a large proportion of the archipelago's total diversity (DeVantier 2000, Reinicke *et al.* 2000, Zajonz *et al.* 2000).

CONCLUSIONS

The DCA of the van der Maarel data, a less time consuming method, reveals similar results to the biomass DCA. Using this methodology, it is still needed to clear the quadrats in order to note the smaller and uncommon species that prove to be important in the analyses [e.g. *Chauviniella coriifolia* (Harvey) Papenfuss and *Claudea elegans* Lamouroux]. The presence/absence data, on the other hand, obscure the patterns in community structure and more elaborate data sets (checklists of larger areas, more samples, more zonation belts) are required to discriminate among the community types.

The relationship of the SiO_4 concentration and the second DCA axis seems to be odd, as this indicator for upwelling does not differentiate between SNC and SSC. There are several possibilities to explain this anomaly: (i) upwelling is a coastal phenomenon but the included environmental data are averages of a broader area and the cycle in which the parameter varies from highs to lows might happen considerably more frequent than the two periods for which the data were averaged, so the resolution of the data set might be too low; (ii) the SiO_4 concentrations vary likewise in the different coastal waters and correspond to a lesser extent with the vegetation differences around the archipelago; (iii) a synergy of environmental variables might be important in shaping the macroalgal assemblages, obscuring the importance of SiO_4 as an indicator for upwelling. Altogether, the oceanic data around the archipelago correspond well to the seasonal changes in environmental parameters reported for the southern Arabian shores and the resulting influence on its biotic communities (e.g.

Ormond & Banaimoon 1994). Besides these abiotic factors, biotic interactions or complex cascade effects are suspected to be important in shaping the subtidal communities, especially so for the species-rich outer islands with a limited coastal area.

Although the Socotra archipelago harbours a diversity of well-characterized subtidal communities, showing high affinities with a common Indian Ocean flora, its similarity with other communities within the upwelling-influenced Arabian Sea remains unclear as ecological macroalgal studies in this area are lacking. Another question that remains is the quantification of the relationship between the upwelling flora (disjunct species of SSC, TZ and OI) with distant regions as Australia, Hawaii, Japan and South Africa.

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APPENDICES

Appendix 1. Coordinates of the 21 sample sites around the Socotra Archipelago.

site 4: 12.630°N, 53.869°E	site 13: 12.173°N, 52.226°E	site 36: 12.321°N, 53.919°E
site 5: 12.681°N, 54.077°E	site 20: 12.157°N, 52.985°E	site 39: 12.639°N, 53.944°E
site 6: 12.693°N, 54.085°E	site 22: 12.315°N, 53.623°E	site 40: 12.303°N, 53.843°E
site 8: 12.664°N, 54.045°E	site 23: 12.355°N, 53.544°E	site 41: 12.322°N, 54.034°E
site 9: 12.204°N, 52.259°E	site 25: 12.528°N, 54.540°E	site 42: 12.403°N, 54.243°E
site 10: 12.204°N, 52.273°E	site 29: 12.701°N, 53.500°E	site 43: 12.535°N, 54.513°E
site 11: 12.226°N, 52.073°E	site 31: 12.700°N, 53.654°E	site 44: 12.532°N, 54.520°E

Appendix 2. Species recorded in the quadrats, with mention of their cluster occurrence. Cluster abbreviations as in Fig. 1.

RHODOPHYCEAE - FLORIDEOPHYCIDAE

BONNEMAISONIALES

BONNEMAISONIACEAE

Asparagopsis taxiformis (Delile) Trevisan - SSC

CERAMIALES

CERAMIACEAE

Balliella repens Huisman & Kraft - TZ - SSC

Centroceras clavulatum (C. Agardh) Montagne - SNC

Euptilota fergusonii Cotton - SSC

Haloplegma duperreyi Montagne - SSC

DASYACEAE

Dictyurus purpurascens Bory de Saint-Vincent - SSC

DELESSERIACEAE

Chauviniella coriifolia (Harvey) Papenfuss - SSC

Claudea elegans Lamouroux - SSC

Duckerella ferlusii (Hariot) Wynne - SSC

Martensia elegans Hering - SSC

RHODOMELACEAE

Acanthophora dendroides Harvey - SNC - TZ - SSC

Acanthophora spicifera (Vahl) Børgesen - SNC

Amansia rhodantha (Harvey) J. Agardh - OI

Chondria armata (Kützing) Okamura - TZ - SSC

Chondrophycus papillosus (C. Agardh) Garbary & Harper - SNC

Chondrophycus parvipapillatus (C.K.Tseng) Garbary & Harper - TZ

Herposiphonia nuda Hollenberg - SNC - SSC

Laurencia majuscula (Harvey) Lucas - SNC - SSC

Laurencia pedicularioides Børgesen - TZ - SSC - OI

Leveillea jungermannioides (Hering & G. Martens) Harvey - OI

Osmundaria melvillii (J. Agardh) R. Norris - TZ - SSC

CORALLINALES

CORALLINACEAE

Amphiroa anceps (Lamarck) Decaisne - TZ - SSC

Amphiroa fragilissima (Linnaeus) Lamouroux - SNC

Amphiroa rigida Lamouroux - SNC - TZ - SSC - OI

GELIDIALES

GELIDIACEAE

Pterocladiella caerulescens (Kützing) Santelices & Hommersand - SNC - SSC – OI

Pterocladia cf. *caloglossoides* (Howe) Dawson - SNC

GELIDIELLACEAE

Gelidiella pannosa (Feldmann) Feldmann & Hamel - CDC – SNC

GIGARTINALES

HYPNEACEAE

Hypnea charoides Lamouroux / *valentiae* (Turner) Montagne complex - SGB - SNC - TZ

Hypnea musciformis (Wulfen) Lamouroux - SNC - TZ

Hypnea pannosa J. Agardh - TZ - OI

Hypnea spinella (C. Agardh) Kützing - SNC - TZ - SSC

RHIZOPHYLLIDACEAE

Portieria hornemannii (Lyngbye) P. Silva - SNC - SSC - OI

SARCODIACEAE

Sarcodia montagneana (J. Hooker & Harvey) J. Agardh - SSC

SCHIZYMENIACEAE

Titanophora pikeana (Dickie) J. Feldmann - SSC

SOLIERIACEAE

Sarconema filiforme (Sonder) Kylin - SNC

Solieria robusta (Greville) Kylin - TZ - SSC

GRACILARIALES

GRACILARIACEAE

Gracilaria debilis (Forsskål) Børgesen - SNC

Gracilaria millardetii (Montagne) J. Agardh - SNC - SSC - OI

HALYMENIALES

HALYMENIACEAE

Carpopeltis maillardii (Montagne & Millardet) Chiang - SSC - OI

NEMALIALES

GALAXAURACEAE

Galaxaura marginata (Ellis & Solander) Lamouroux - SSC - OI

Scinaia moniliformis J. Agardh - TZ - SSC

Scinaia tsinglanensis Tseng - SNC

Tricleocarpa fragilis (Linnaeus) Huisman & Townsend - SSC

RHODYMENIALES

CHAMPIACEAE

Champia compressa Harvey - TZ - SSC - OI

Champia indica Børgesen - TZ

Champia parvula (C. Agardh) Harvey - SNC

LOMENTARIACEAE

Gelidiopsis variabilis J. Agardh (Schmitz) - SNC - TZ - SSC

RHODYMENIACEAE

Botryocladia leptopoda (J. Agardh) Kylin - TZ - SSC - OI

Botryocladia skottsbergii (Børgesen) Levring - TZ - SSC - OI

PHAEOPHYCEAE

DICTYOTALES

DICTYOTACEAE

Dictyopteris delicatula Lamouroux - TZ - SSC - OI

Dictyopteris macrocarpa (Areschoug) O. Schmidt - SSC - OI

Dictyopteris polypodioides (De Candolle) Lamouroux - SNC - SSC

Dictyota bartayresiana Lamouroux - SNC

Dictyota cervicornis Kützing - SNC - TZ - SSC - OI

Dictyota ceylanica Kützing - SSC

Dictyota crispata Lamouroux - TZ - SSC

Dictyota friabilis Setchell - CDC - OI

Dictyota grossedentata De Clerck & Coppejans - TZ - SSC

Dictyota stolonifera Dawson - OI

Lobophora variegata (Lamouroux) Womersley ex Oliveira - SNC - TZ - SSC - OI

Padina australis Hauck - SNC - TZ

Padina boergesenii Allender & Kraft - SNC - SSC

Padina elegans Koh ex Womersley - SSC

Spatoglossum asperum J. Agardh - SNC - TZ - SSC

Stoechospermum polypodioides (Lamouroux) J. Agardh - SNC

FUCALES

SARGASSACEAE

Nizamuddinia zanardinii (Schiffner) P. Silva - SNC

Sargassum angustifolium C. Agardh - SNC - SSC

Sargassum decurrens (R. Brown ex Turner) C. Agardh - OI

Sargassum latifolium (Turner) C. Agardh - TZ - SSC

Sargassum cf. *linearifolium* (Turner) C. Agardh - SNC - OI

Turbinaria ornata (Turner) J. Agardh - OI

SCYTOSIPHONALES

SCYTOSIPHONACEAE

Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier - SNC - TZ

Rosenvingea intricata (J. Agardh) Børgesen - SSC

CHLOROPHYCEAE

BRYOPSIDALES

CAULERPACEAE

Caulerpa brachypus Harvey - TZ - OI

Caulerpa lanuginosa J. Agardh - SNC - TZ - SSC

Caulerpa mexicana Sonder ex Kützing - SNC - TZ - SSC

Caulerpa peltata Lamouroux - OI

Caulerpa racemosa (Forsskål) J. Agardh - TZ - SSC

Caulerpa scalpelliformis (R. Brown ex Turner) C. Agardh - SSC

CODIACEAE

Codium dwarkense Børgesen - SNC - SSC - OI

UDOTEACEAE

Avrainvillea lacerata Harvey ex J. Agardh - SSC

Chlorodesmis fastigiata (C. Agardh) Ducker - CDC - OI

Halimeda copiosa Goreau & Graham / *minima* (W.R. Taylor) Colinvaux - TZ - SSC - OI

Halimeda cuneata Hering - SNC - SSC

Halimeda discoidea Decaisne - SNC - SSC

Halimeda tuna (Ellis & Solander) Lamouroux - SNC - TZ - SSC

Udotea indica A. Gepp & E. Gepp - SNC - TZ - SSC

CLADOPHORALES

CLADOPHORACEAE

Cladophora coelothrix Kützing - TZ - SSC

Cladophora prolifera (Roth) Kützing - SNC

Cladophora vagabunda (Linnaeus) van den Hoek - SNC - SSC

SIPHONOCLADACEAE

Boergesenia forbesii (Harvey) J. Feldmann - SSC - OI

Chamaedoris auriculata Børgesen - TZ - SSC

Dictyosphaeria cavernosa (Forsskål) Børgesen - CDC

Siphonocladus tropicus (P. Crouan & H. Crouan) J. Agardh - TZ

Struveopsis siamensis (Egerod) P. Silva - SSC

Ventricaria ventricosa (J. Agardh) Olsen & J. West - OI

DASYCLADALES

DASYCLADACEAE

Neomeris van-bosseae Howe - TZ - SSC

MAGNOLIOPHYTA - LILIOPSIDA

ALISMATALES

CYMODOCEACEAE

Halodule uninervis (Forsskål) Ascherson - SGB - SNC

HYDROCHARITACEAE

Halophila ovalis (R. Brown) Hooker - SGB

Thalassia hemprichii (Ehrenberg) Ascherson - SGB

CHAPTER 7

Phytogeography of upwelling areas in the Arabian Sea

Submitted as: Schils T. & Coppejans E. Phytogeography of upwelling areas in the Arabian Sea.

ABSTRACT

Aim Comparing the marine plant communities of two islands, with a similar diversity in biotopes, in two different upwelling areas of the Arabian Sea.

Location Arabian Sea: (1) the Socotra Archipelago (Yemen; 12.47°N, 53.87°E) in the Somali upwelling area, (2) Masirah Island (Oman; 20.42°N, 58.79°E) in the upwelling area of the southern Arabian Peninsula.

Methods The marine flora of different biotopes around both islands were examined by means of qualitative assessments. Ordination analysis (DCA) was used to identify the different plant communities and to correlate these with environmental parameters. The species composition of the identified communities were compared (tripartite similarity index) and their biogeographic affinity with nations bordering the Indian Ocean was determined. Indicator species analyses were performed to identify the characteristic species of the different plant communities and their biotopes.

Results The DCA analysis shows a clustering of sites (plant communities) corresponding with their geographic position, linked in turn to the prevailing environmental conditions of the different coastal areas. The combined interpretation of the ordination, similarity and biogeographic analyses results in the aggregation of similar plant communities of both upwelling areas into four biotopes.

Main Conclusions The north coast communities of Socotra and the west coast communities of Masirah can be grouped into 3 biotopes related to the degree of exposure and sedimentation. These biotopes are typified by indicator species, characteristic for specific substrata, and have a high biogeographic affinity with the East African coast. The plant communities of Socotra's south coast and Masirah's east coast constitute a fourth biotope, being diverse and species rich, typified by a large proportion of red macroalgae including the characteristic species of the unique Arabian Sea flora. This biotope has a pronounced biogeographic affinity with distant regions (disjunctly distributed taxa). Within the different biotopes, the communities of Masirah are more divergent from an East African flora in comparison to Socotra, the latter being a stepping stone between the East African and Arabian Sea flora.

INTRODUCTION

The Arabian Sea is regarded as a biogeographic sub-region of the Indian Ocean (Sheppard *et al.* 1992). Seasonal upwelling, maximal in strength during the southwest monsoon (summer), influences the greater part of the Arabian Sea coasts and is considered as the main regulating phenomenon for a biogeographic barrier in the area (Wilson 2000).

Case studies on the macroalgae of confined areas within the Arabian Sea (Wynne & Banaimoon 1990; Ormond & Banaimoon 1994; Wynne & Jupp 1998; Schils 1999; Wynne 1999a, b, 2000, 2001; Leliaert 2000; Wynne & Leliaert 2001; Schils 2002; Schils & Coppejans 2002; Schils *et al.* 2003a, b) indicate that the region harbours a species rich and diverse marine flora. The upwelling area along the Hadramout (Yemen) and Dhofar (Oman) coasts on the southern Arabian Peninsula is a centre of high endemism within the Arabian Sea (Sheppard & Salm 1988; Randall & Hoover 1995). Within this area, Masirah Island has been comparatively well investigated as the island harbours a wide diversity of biotopes (from upwelling affected shores to large monotypic reefs) within a limited geographic area (de Vaugelas 2001). The Socotra Archipelago, located within the Somali upwelling area, is likewise identified as the "Galapagos of the Indian Ocean" (Wilson & Klaus 2000) due to its diversity in biota and biotopes. The archipelago recently received scientific interest owing to the comparatively pristine state of its natural environment. The marine ecosystems of Socotra also vary from coral dominated communities to upwelling influenced shores, with clearly defined subtidal plant communities (T. Schils & E. Coppejans submitted). The Socotra Archipelago is located at the boundary of many species distributions (sympatry of sister taxa; Kemp 1998b) and it serves as a stepping stone for genetic exchange, by means of larval and spore dispersal, between the Indian Ocean, the Red Sea (Gulf of Aden) and the Arabian Sea. Besides being located on the crossroads of these biogeographic regions, the Arabian Sea flora shows pronounced biogeographic affinities with distant marine floras (Børgesen 1934; Wynne 2000; Schils & Coppejans 2002; Schils *et al.* 2003a). Despite these anecdotic observations, no quantitative research has been performed in order to characterize the different plant communities of the Arabian Sea and to determine their similarity, diversity and biogeography. This study attempts to provide insight into the diversity and unicity of the region by comparing detailed species inventories of different sampling sites within the Somali and southern Arabian upwelling areas. Biomass analyses of vegetation quadrats around the Socotra Archipelago (T. Schils & E. Coppejans submitted) showed that a qualitative comparison (presence/absence of taxon data) returns reliable results if the sites are intensively sampled in a relatively wide vertical (different zones) and horizontal range (large sample area).

MATERIAL AND METHODS

The field trips to Masirah Island and the Socotra Archipelago were conducted by the first author in the period between two successive SW monsoons, from 2 to 30 November 1999 and from 26 March to 7 May 2000, respectively. During the qualitative surveys, samples were collected from intertidal and subtidal habitats to 20 m depth. Plants were gathered in fine-meshed plastic bags and sorted in a field laboratory. Small and crustose algae were excluded from the dataset as they can easily be overlooked from one survey to another and a meticulous investigation of the whole substratum and epiphytes is very time-consuming. Reference specimens were selected and pressed as herbarium specimens, preserved in a 5%

formaldehyde-seawater solution or dried in silica gel for molecular purposes. This collection is housed in GENT (Ghent University Herbarium, Krijgslaan 281 - S8, 9000 Ghent, Belgium).

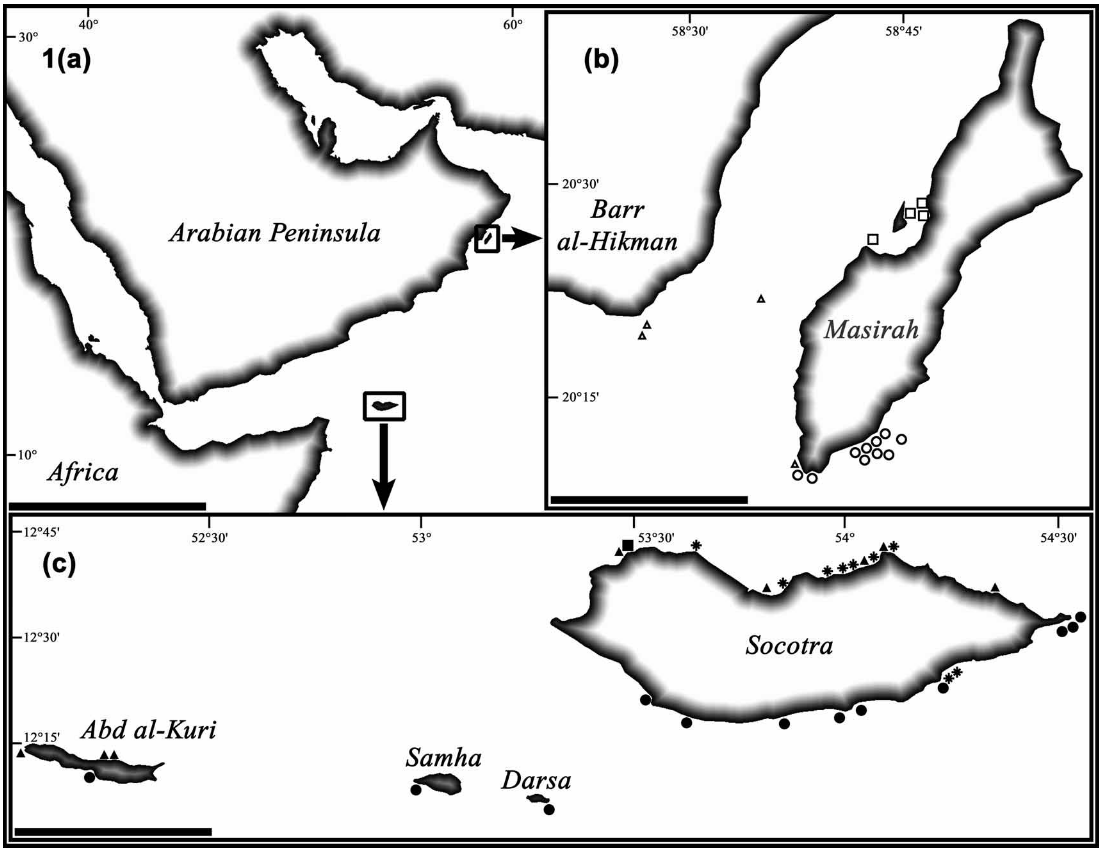

Figure 1. Map of the Arabian Sea **(a)** with Masirah Island **(b)** and the Socotra Archipelago **(c)** as insets. The sample sites are indicated according to their clustering in the DCA plot: east coast of Masirah (MAS EC, open circles), seagrass beds of Masirah (MAS SG, open boxes), west coast of Masirah (MAS WC, open triangles), north coast of Socotra and two sheltered sites in Mahfirhin Bay (SOC NC, stars), north coast of Socotra and outer islands (S&O NC, filled triangles), seagrass beds of Socotra (SOC SG, filled box) and south coast of Socotra and outer islands (S&O SC, filled circles). The scale bar represents 1000 km (a), 25 km (b) and 50 km (c), respectively.

Ordination

The 48 sample sites (Fig. 1) of which complete species inventories were recorded (1048 species records) served as the ordination input. Detrended Correspondance Analysis (DCA performed with CANOCO; ter Braak 1988) was chosen as an indirect gradient analysis as the data clearly represent a unimodal model (maximum gradient length: 5.227 SD; ter Braak & Šmilauer 1998).

In an attempt to determine the species-environment correlation, environmental data around Socotra (latitude: 9.650°N – 14.383°N; longitude: 51.900°E – 57.067°E) and Masirah (latitude: 18.080°N – 22.500°N; longitude: 57.850°E – 61.950°E) were obtained from the Worldwide Ocean Optics Database (http://wood.jhuapl.edu, W.O.O.D version 4.0). Chlorophyll a (CHL), salinity (SAL) and temperature (TEMP) parameters (i) showed a good sample distribution and (ii) were sampled during the SW monsoon (Julian days 121-304; abbreviated as "parameter" + "_SW") and the NE monsoon (Julian days 305-120; "parameter" + "_NE") for both islands. The average of these parameters during one of the monsoons was calculated for 2 geographic areas (water masses) around the islands: (i) Socotra's north coast, > 12.550°N; (ii) Socotra's south coast, < 12.550°N; (iii) Masirah's west coast, < 58.637°E; (iv) Masirah's east coast, > 58.637°E. The south coast of Socotra and the east coast of Masirah are the main upwelling areas of the islands. Socotra's north coast and Masirah's west coast are on the lee side of the major current patterns and less influenced by the upwelling phenomenon. Whereas SAL and TEMP are directly related to upwelling and are influential for algal growth, CHL represents the overall productivity of the phytoplankton, linked to the changes in dissolved nutrients and hence is indirectly related to upwelling. Additional parameters were derived from the original data, i.e. the absolute difference of a parameter between the 2 monsoon periods (abbreviation of the environmental parameter + "_AD") and the average of both monsoon periods (parameter + "_AV"). The complete environmental data set had identical parameter values for all sites of a specific area.

Indicator analysis

Indicator species analysis was used to examine the characteristic species, showing significant indicator values (IV), for each of the marine plant communities (DCA clusters) and biotopes (grouping of similar communities of Socotra and Masirah). The indicator analyses were conducted with PC-ORD (McCune & Mefford 1999), using 1000 Monte Carlo random permutations to test the statistical significance of the indicator values.

Species richness and similarity

Subsequent analyses of the plant communities included the calculation of species richness (specified per Phylum/Class) for each DCA cluster, and the tripartite similarity index (Tulloss 1997) as a qualitative index of beta diversity.

Biogeography

The biogeographic affinity of the plant communities are analysed by comparing the species composition of the DCA clusters to species inventories of Indian Ocean nations. The latter data set is primarily based on Silva *et al.* (1996) and supplemented with records from omitted and recent sources: Dickie (1888), Holmes (1903), Nizamuddin & Campbell (1995), De Clerck & Coppejans (1996; 1999), Critchley *et al.* (1997), Kemp (1998a), Wynne & Jupp (1998), cd-rom "Mangroves and seagrasses of the Indian Ocean" (R. Phillips and M. Spalding; Indian Ocean Guides, Department of Biological Sciences, University of Warwick, 1998), De Clerck (1999), Wynne (1999a, b, 2000, 2001), Coppejans *et al.* (2000), Huisman (2000), Wynne & Leliaert (2001), De Clerck *et al.* (2002). The floristic affinity of a cluster with a specific country is calculated as the Simpson Coefficient: $a\ (a + min\ (b, c))^{-1}\ x\ 100$. In which a represents the number of shared species between a cluster and a country, b and c represent the number of species unique to the cluster and the country, respectively. The species inventories of the clusters are always smaller than those of the countries, so the equation does not include the floristic richness of a country which reduces the discrepancy of sampling efforts between the different countries. The countries are arranged from southeastern Africa, over the Arabian Sea, to Western Australia. India was excluded from the series as its size and geographic position cover a wide diversity of floras within the Indian Ocean. In order to visualize the main biogeographic trends of the site clusters, based on both species and generic inventories, the plots are best represented as polynomial trend lines of a fourth order.

RESULTS

Species account

A total of 236 plant species were recorded for the 48 sites (Appendix 1): 6 seagrasses (Magnoliophyta), 53 Chlorophyta, 43 Phaeophyta and 134 Rhodophyta. Certain species of the same genus with a similar ecology could not be discerned in the field, therefore the 236 taxa are lumped into 204 species abbreviations (Appendix 1), which are used in the subsequent analyses. The number of recorded genera totals 128: 5 seagrasses (Magnoliophyta), 26 Chlorophyta, 17 Phaeophyta and 80 Rhodophyta.

Ordination

A DCA of the species data of the 48 sites showed 6 site groupings (Fig. 2), corresponding with coastal areas around both islands. Both axes have high eigenvalues (0.525 and 0.406) and high lengths of gradient (5.226 and 3.531), indicating a high beta diversity within the samples. The 6 DCA clusters are identified as (Fig. 2, counter clock-wise starting from the left): (i) the seagrass beds of Socotra (SOC SG) and Masirah (MAS SG); (ii) a distinct entity of Socotra's north coast sites (SOC NC); (iii) the south coast sites of Socotra and the outer islands (Abd al-Kuri, Samha, Darsa; S&O SC); (iv) the east coast of Masirah (MAS EC); (v) the west coast sites of Masirah (MAS WC); and (vi) the north coast sites of Socotra and the outer islands (S&O NC). Fig. 3 shows the proportion of seagrasses, Rhodophyta, Phaeophyta and Chlorophyta in the total number of species and genera recorded for each cluster. The DCA plot of the first two axes shows an overlap in sites belonging to S&O NC and MAS WC; and a partial overlap between S&O SC and MAS EC.

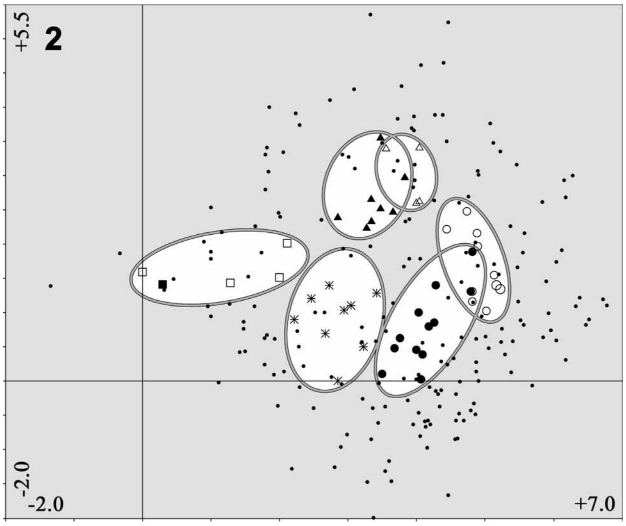

Figure 2. First two ordination axes of a DCA based on the qualitative site data (species records, represented as small dots). The six DCA clusters indicative for the different plant communities are encircled. Sample site symbols as in Fig. 1.

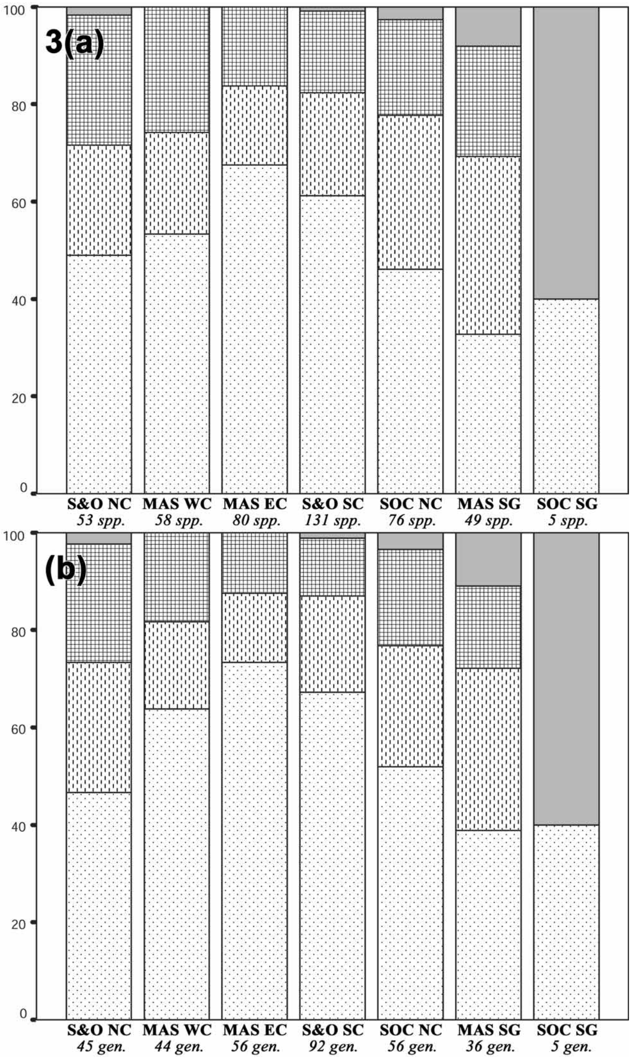

Figure 3. Percentage of Rhodophyta (dotted), Phaeophyta (hatched), Chlorophyta (vertical stripes) and seagrasses (grey shaded) in the total account of genera and species for each DCA cluster. Cluster abbreviations as in Fig. 1. **(a)** Number of species per cluster. **(b)** Number of genera per cluster.

Table 1 lists the correlation coefficients of the environmental parameters with the first two DCA axes. The salinity parameters SAL_AD, SAL_AV and SAL_NE have high correlation values with the first DCA axis (the latter two being negatively correlated) and lower ones with the second axis (all negatively correlated). SAL_SW has very low correlation coefficients with both axes. The average temperature and the chlorophyll a concentrations show relatively high correlations with both DCA axes. Since these parameters are positively correlated with both axes, they represent the difference in environmental variables between the Socotra clusters and the Masirah clusters, which are plotted in the upper right-hand corner of the DCA, following the resultant of both axes. High chlorophyll a concentrations are indicative of upwelling, the effect of this phenomenon thus being stronger at Masirah in comparison to Socotra. The average chlorophyll a concentration at Masirah (1.55 $\mu g\ l^{-1}$) is almost 4 times as high compared to that of the Socotra clusters (0.40 $\mu g\ l^{-1}$). Similarly, TMP_AV differs between Socotra and Masirah. The average yearly temperature turns out to be higher around Masirah Island (24.9°C) in comparison to the Socotra Archipelago (24.5°C) due to the higher winter temperatures of the upwelling sheltered sites (26.1°C vs 24.9°C). The remaining temperature parameters (TMP_NE, TMP_AD, TMP_SW) and SAL_SW have low correlation coefficients with both axes, pointing out the slight differences of the seasonal temperature between both islands, the small differences in temperature changes between both monsoon periods, and the similar salinities for both islands during the SW monsoon.

Table 1. Correlation coefficients of the environmental parameters in decreasing order (absolute values) with the first two axes of the DCA, respectively. Abbreviations of parameters as in text.

Parameter	Axis 1	Axis 2	Parameter	Axis 1	Axis 2
SAL_AD	0.689	-0.239	CHL_SW	0.402	0.428
SAL_AV	-0.588	-0.284	CHL_AV	0.397	0.427
SAL_NE	-0.470	-0.277	CHL_NE	0.384	0.420
TMP_AV	0.453	0.306	CHL_AD	0.397	0.402
CHL_SW	0.402	0.428	TMP_AV	0.453	0.306
CHL_AD	0.397	0.402	SAL_AV	-0.588	-0.284
CHL_AV	0.397	0.427	SAL_NE	-0.470	-0.277
CHL_NE	0.384	0.420	SAL_AD	0.689	-0.239
TMP_NE	0.241	0.042	TMP_SW	0.076	0.226
TMP_AD	0.118	-0.072	TMP_AD	0.118	-0.072
TMP_SW	0.076	0.226	TMP_NE	0.241	0.042
SAL_SW	0.066	0.030	SAL_SW	0.066	0.030

Tripartite similarity

The tripartite similarity indices are shown in Table 2, in which the sites are ordered so that the highest indices adjoin the diagonal. This results in a linear representation of sites that are most similar to one another. MAS WC and MAS EC have the highest similarity index with one another (0.51), but the former also has a high similarity index with S&O NC (0.48) and the latter with S&O SC (0.47). S&O SC has equal similarity indices for MAS EC and SOC NC. MAS SG has the highest index with SOC NC (0.47). All similarity indices with SOC SG are very low due to the low species richness of this cluster. SOC SG has its highest similarity index with MAS SG (0.08).

Table 2. Tripartite similarity indices of DCA cluster couples. Clusters are ordered in a way that their highest similarities adjoin the diagonal position. Similarities > 0.40 are marked in bold. Cluster abbreviations as in Fig. 1.

	S&O NC	MAS WC	MAS EC	S&O SC	SOC NC	MAS SG	SOC SG
S&O NC	-	**0.48**	0.40	0.34	0.38	0.36	0.03
MAS WC	**0.48**	-	**0.51**	0.31	0.28	0.34	0.02
MAS EC	0.40	**0.51**	-	**0.47**	0.35	0.17	0.02
S&O SC	0.34	0.31	**0.47**	-	**0.47**	0.20	0.02
SOC NC	0.38	0.28	0.35	**0.47**	-	0.39	0.04
MAS SG	0.36	0.34	0.17	0.20	0.39	-	0.08
SOC SG	0.03	0.02	0.02	0.02	0.04	0.08	-

Biogeography

SOC SG was omitted from the analysis, as this site only contained 5 species. The dominant factors that determine species occurrence at SOC SG are the harsh and variable ecological conditions characteristic of lagoons, as opposed to the biogeographic distribution patterns of species.

The biogeographic trends of the DCA clusters based on the species inventories (Fig. 4a) shows a decreasing affinity with the Indian Ocean from the seagrass beds to the upwelling zones: MAS SG (47.8%) > S&O NC (46.5%) > MAS WC (42.6%) > SOC NC (40.2%) > S&O SC (33.6%), MAS EC (33.5%). In general, the biogeographic affinities increase from South Africa to Kenya, decrease from Somalia to Malaysia and increase again towards Indonesia and Western Australia.

In addition to the biogeographic comparison based on species lists, affinities at a generic level were also calculated (Fig. 4b) as certain Indian Ocean taxa have been identified by a plethora of names (to some extent corrected for in the analyses) dependent on the author or the phycological school. The identifications at genus level, however, are more rigid. The generic affinities of the clusters with the Indian Ocean nations are markedly higher than those based on the species lists. The decreasing order of general affinity with the Indian Ocean are similar to the results of the species analysis: highest affinity for MAS SG (77.4%); high affinities for SOC NC (74.7%), S&O NC (73.3%) and MAS WC (71.4%); and lower affinities for MAS EC (58.3%) and S&O SC (57.4%).

All clusters have high affinities with both ends of the graphs (Figs 4a, b), corresponding with South Africa and Western Australia, respectively. Parts of these nations are subjected to temperate waters and other parts to (sub)tropical waters, resulting in high affinities with all plant communities of the Arabian Sea defined here. The overall biogeographic affinities are highest with the East African coast and surprisingly lower with the Arabian Sea. The affinities of the SOC (S&O) and MAS communities with Yemen and Oman respectively, are by definition 100%. This result is, however, not obtained from the analysis because the species lists of the Indian Ocean nations are based on literature reports. Consequently, many of the species reported here are new records for Yemen and Oman.

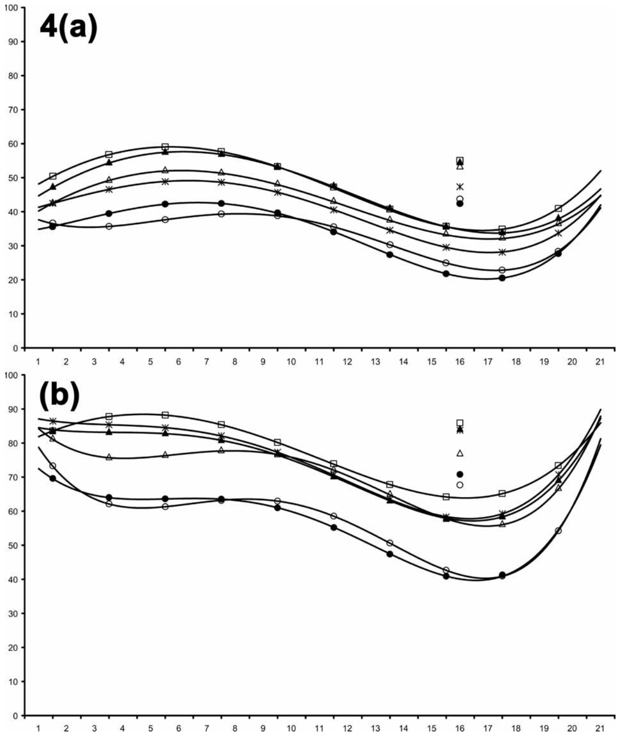

Figure 4. Biogeographic affinities (Simpson Coefficient in %, y-axis) between the species lists of the DCA clusters and those of the Indian Ocean nations. The countries are ordered on the x-axis from the southwestern Indian Ocean, over the Arabian Sea, to the southeastern Indian Ocean: South Africa (1), Mozambique (2), Madagascar (3), Réunion (4), Mauritius (5), Tanzania (6), Seychelles (7), Kenya (8), Somalia (9), Yemen (10), Oman (11), Iran (12), Pakistan (13), Laccadive (14), Maldives (15), Sri Lanka (16), Bangladesh (17), Andaman (18), Malaysia (19), Indonesia (20), Australia (21). DCA cluster symbols as in Fig. 1: MAS WC (open triangles), MAS SG (open boxes), MAS EC (open circles), S&O NC (filled triangles), SOC NC (stars), and S&O SC (filled circles). **(a)** Quartic polynomial trend lines of the biogeographic affinity of the DCA clusters based on the species records. **(b)** Quartic polynomial trend lines of the biogeographic affinity of the DCA clusters based on the generic records. The biogeographic affinities of Sri Lanka behave as outliers for all polynomial trend lines, hence their separate representation in both graphs.

In both biogeographic analyses, Sri Lanka is an outlier (Figs 4a, b). To date, no other reports of strong affinities between the marine communities of the Arabian Sea and Sri Lanka are known. Being on the crossroads of the Arabian Sea, the Bay of Bengal and the Indian Ocean, the high similarities can be attributed to common Indian Ocean taxa that also occur in the tropical regions of the East African Coast (e.g. Kenya and Tanzania). Calculations support this statement: out of the 83 species that the Arabian Sea (ordination data) and Sri Lanka share, 76 and 73 species have also been reported for Kenya and Tanzania, respectively. Of the 85 genera found in the Arabian Sea and Sri Lanka, 80 and 83 genera are also known for Kenya and Tanzania, respectively.

Indicator species

The species, with a significant indicator value ($P < 0.05$), listed in Table 3 prove to be characteristic for the identified DCA clusters. S&O NC contains only three indicator species, being common Indian Ocean taxa. The indicator species of MAS WC are predominantly composed of Phaeophyta (6/9). The indicator species *Nizamuddinia zanardinii* and *Lomentaria strumosa* are endemic for the Arabian Sea and ecologically associated to the upwelling phenomenon (Kemp, 1998a). The other large Phaeophyta (*Dictyota bartayresiana*, *Sargassum* spp., *Stoechospermum polypodioides*, *Turbinaria ornata*) are generally linked to increased nutrient levels in (sub)tropical seas (Schaffelke & Klumpp, 1998). MAS EC is typified by indicator species predominantly belonging to the Rhodophyta. Many of these species are indicative of colder water, e.g. *Calliblepharis fimbriata*, *Kallymenia crassiuscula*, *Plocamium telfairiae* and *Rhodymenia* spp., and show a disjunct distribution pattern within the Indo-Pacific. Similar observations to those of MAS EC apply for the indicator species of S&O SC. Despite the high number of species records for SOC NC, the majority of species found in this cluster also occur in other clusters. This results in only three species with significant indicator values, being common Indian Ocean species. The species-rich seagrass beds of MAS WC are characterized by plants typically associated with these habitats. SOC SG was excluded from the analysis because of its extremely low species richness.

In a second analysis, the plant communities of both islands (DCA clusters) are united in biotopes, based on similarities in species composition and biogeographic trends. This results in 3 clusters that are composed of Socotra and Masirah sites, and a single Socotra cluster. S&O NC and MAS WC are united in a cluster composed of upwelling sheltered sites, S&M SS. S&O SC and MAS EC are combined in a cluster composed of upwelling affected sites, S&M US. SOC SG and MAS SG are joined in the cluster of seagrass communities, S&M SG. SOC NC shows the highest similarity in species composition with S&O SC though its biogeographic affinity more closely resembles that of S&O NC. Because of its mixed behaviour, SOC NC was retained from aggregation with other clusters. The sites of these cluster groupings correspond with the areas of both islands that are subject to similar seasonal environmental conditions. A subsequent species indicator analysis revealed the species that are characteristic for each of the four biotopes in the Arabian Sea (Table 4).

Table 3. Species with significant probabilities ($P < 0.05$) and indicator values (IV, % perfect indication) for each of the plant communities (DCA clusters). High indicator values are marked in bold and grouped according to cluster preference. Probabilities are based on 1000 Monte Carlo permutations. Cluster abbreviations as in Fig. 1. The species abbreviations correspond to the species listed in appendix 1.

Species	S&O NC	MAS WC	MAS EC	S&O SC	SOC NC	MAS SG	*P*
Sar_lin	**38**	0	0	0	0	0	0.027
Dic_fri	**37**	0	1	1	0	0	0.008
Gel_pan	**25**	0	0	0	0	0	0.039
Niz_zan	2	**64**	0	0	0	0	0.002
Sar_sp1	0	**56**	0	0	0	6	0.002
Sto_pol	3	**52**	5	0	1	3	0.004
Lom_stru	0	**50**	0	0	0	0	0.010
Bry_spe	1	**49**	1	2	0	0	0.003
Pte_cae	**15**	**38**	2	4	2	2	0.017
Tur_orn	2	**35**	0	1	0	0	0.030
Dic_bar	0	**35**	1	0	2	0	0.035
Sar_pil	0	**33**	0	0	0	8	0.039
Plo_tel	0	**21**	**41**	0	0	0	0.018
Rho_sp2	0	0	**70**	0	0	0	0.001
Rho_sp1	0	7	**52**	0	0	0	0.001
Dic_cri	0	6	**44**	2	0	0	0.006
Kal_spe	0	0	**43**	1	0	0	0.011
Cal_fim	0	0	**40**	0	0	0	0.007
Sci_tsi	0	0	**37**	7	1	0	0.035
Gra_tex	0	0	**33**	1	0	0	0.022
Amp_anc	0	4	**32**	**22**	0	0	0.020
Hal_com	0	0	0	**67**	0	0	0.001
Bot_lep	0	0	0	**50**	0	0	0.012
Hal_dup	0	0	0	**50**	0	0	0.005
Zel_spe	0	0	0	**42**	0	0	0.007
Cry_spe	0	0	0	**33**	2	0	0.012
Cha_ind	0	0	0	**33**	0	0	0.049
Ast_pel	3	0	0	**32**	0	0	0.021
Cau_lan	0	0	0	3	**64**	0	0.002
Gra_deb	0	0	2	0	**47**	0	0.006
Amp_fra	5	0	0	8	**44**	0	0.010
Hal_uni	0	0	0	0	1	**90**	0.001
Hal_ova	0	0	0	0	0	**75**	0.001
Cho_pap	0	0	0	0	1	**65**	0.004
Gra_sal	0	0	0	0	0	**50**	0.014
Sar_fil	0	0	0	0	2	**41**	0.023
Boe_for	0	0	0	4	0	**38**	0.008
Cau_len	0	0	0	1	2	**36**	0.032
Cau_sca	0	0	0	1	2	**36**	0.028

Nizamuddinia zanardinii and *Sargassum linearifolium* are indicator species of S&M SS that make up the largest biomass stands of the studied macroalgal communities (excl. the seagrass communities; T. Schils pers. obs.). Besides *N. zanardinii*, the indicator species of S&M SS have a wide (sub)tropical distribution within the Indian Ocean. As a consequence of uniting S&O SC and MAS EC, the indicator species of S&M US are predominantly Rhodophyta, composing very diverse algal communities. Again, species indicative for colder water characterize this biotope, e.g. *Kallymenia crassiuscula* and *Rhodymenia* sp. 2. More indicator species were found for SOC NC in the second analysis, this however, being characteristic for similar habitats as those examined in the first analysis. The indicator species of S&M SG are also identical to those of MAS SG in the previous species indicator analysis.

Table 4. Species with significant probabilities (*P* < 0.05) and indicator values (IV, % perfect indication) for each of the biotopes (groups of DCA clusters). Biotope 1, upwelling sheltered areas (S&M SS): MAS WC, S&O NC; biotope 2, upwelling exposed area (S&M US): MAS EC, S&O SC; biotope 3, distinct north coast entity of Socotra: SOC NC; biotope 4, seagrass beds (S&M SG): MAS SG, SOC SG. High indicator values are marked in bold and grouped according to biotope preference. Probabilities are based on 1000 Monte Carlo permutations. The species abbreviations correspond to the species listed in appendix 1.

Species	S&M SS	S&M US	SOC NC	S&M SG	*P*
Pte_cae	**39**	5	3	3	0.018
Niz_zan	**33**	0	0	0	0.009
Val_pac	**29**	1	0	0	0.018
Dic_fri	**26**	2	0	0	0.032
Sar_lin	**25**	0	0	0	0.047
Amp_anc	1	**56**	0	0	0.001
Lau_ped	1	**40**	2	0	0.016
Car_mai	4	**38**	0	0	0.018
Gal_mar	0	**36**	0	0	0.024
Hal_com	0	**36**	0	0	0.019
Seb_fla	0	**36**	0	0	0.028
Dic_cri	1	**34**	0	0	0.037
Rho_sp2	0	**32**	0	0	0.030
Sci_tsi	0	**32**	2	0	0.049
Sch_spe	2	**30**	0	0	0.047
Bot_lep	0	**27**	0	0	0.027
Hal_dup	0	**27**	0	0	0.035
Hyp_spe	0	**27**	0	0	0.032
Kal_spe	0	**27**	0	0	0.029
Hal_dct	0	**23**	**38**	8	0.045
Cau_lan	0	1	**70**	0	0.001
Amp_fra	2	3	**54**	0	0.002
Gra_deb	0	0	**51**	0	0.004
Pad_aus	0	1	**29**	0	0.048
Cho_sp2	0	0	**22**	0	0.040
Cla_lon	0	0	**22**	0	0.040
Hlp_spe	0	0	**22**	0	0.040
Hal_uni	0	0	1	**90**	0.001
Hal_ova	0	0	0	**80**	0.001
Cho_pap	0	0	2	**51**	0.002
Gra_sal	0	0	0	**40**	0.008
Boe_for	0	2	0	**33**	0.015
Sar_fil	0	0	2	**31**	0.030

DISCUSSION

The plant communities defined in this study cover a larger geographic area compared to those derived from a biomass analysis of quadrat data around the Socotra archipelago (T. Schils & E. Coppejans submitted). The transition zone between Socotra's south and north coast, and the outer island communities (both with a pronounced south coast affinity) are in the present study included in S&O SC. The analysis of species inventories hence results in a substantial loss of resolution because the species structure (biomass data) of the different communities is excluded from the information input. However, in a comparison between the plant communities of different geographic locations (both islands), analogies among the communities of both islands can satisfactorily be assessed by a holistic approach incorporating analyses of site data (ordination), species data (similarity indices) and biogeographic distribution patterns. The environmental parameters show two types of correlation with respect to the plant communities. The first one includes the parameters with high correlations for the first DCA axis. SAL_AV and SAL_NE are negatively correlated with the first axis, corresponding with the high salinity concentrations recorded for the seagrass communities (MAS SG and SOC SG), SOC NC and S&O NC. The absolute difference in salinity values, however, is the largest for the upwelling areas (MAS EC and S&O SC) where the changes in salinity between both monsoons are greatest. The second type of correlation is related to the differences between the Socotra and Masirah clusters, following the resultant of both DCA axes. All chlorophyll a parameters have relatively high (positive) correlations with both axes, showing overall higher chlorophyll a concentrations for Masirah. The latter environmental variable is indicative of primary production, dependent on increased nutrient levels and thus related to the intensity of upwelling. Table 1 shows that the resultant of both axes has the highest positive correlation with CHL_SW, which corresponds to the chlorophyll a concentrations for Masirah during the SW monsoon, being the highest observed values (2.20 $\mu g\ l^{-1}$). The chlorophyll a concentrations thus show that the effect of upwelling is more pronounced at Masirah Island.

Plant communities and biotopes

Upwelling sheltered sites (S&M SS): S&O NC and MAS WC

S&O NC has the highest similarity (0.48) in species composition with MAS WC. The ordination also shows an overlap between the sites of these clusters. MAS WC, on the other hand, has the highest tripartite similarity values with MAS EC (0.51), but the biogeographic affinities within the Indian Ocean are quite different between both. The biogeographic affinity of S&O NC, on a species level, is higher for the East African coast and the Arabian Sea compared to that of MAS WC. Based on the generic records, S&O NC and MAS WC also have similar Indian Ocean affinities, however, MAS WC again has a lower affinity for the East African coast. This shows that the Socotra community has a higher transient character from the Western Indian Ocean to the Arabian Sea, and the Masirah community comprises a higher proportion of typical Arabian Sea taxa. The biotope of upwelling sheltered sites has 85 species records in total. The indicator species of the plant communities, and the biotope in general, reflect the seasonally high biomass stands for this area. These communities have a macroalgal cover up to 100% and their species are indicative of seasonally high nutrient levels. Besides common Indian Ocean taxa, the endemic *Nizamuddinia zanardinii* grows abundantly at these partly sheltered sites.

Upwelling affected sites (S&M US): S&O SC and MAS EC

The ordination plot (Fig. 2) shows a gradual spread of the S&O SC sites towards MAS EC. The tripartite similarity (Table 2) of the complete species list is high between both clusters (0.47), although both clusters have a comparably high similarity with other biotopes from their islands, i.e. MAS EC-MAS WC (0.51) and S&M SC-SOC NC (0.47). This is a result of the high number of species recorded for the S&M US clusters (80 spp. and 131 spp.) and the inclusion of transition sites between the sheltered and upwelling biotopes. In fact, a detailed analysis of vegetation quadrats of the Socotra archipelago revealed that the southeastern tip of Socotra is a diverse, intermediate cluster between the north and south communities (T. Schils & E. Coppejans submitted). This low scale resolution has not been detected in the analyses of the species inventories, which is reflected in the high number of species recorded for S&M US: 158 species. The indicator species of this biotope are largely Rhodophyta. These red algae are common elements of species rich communities, often associated with a well-developed understory flora.

Distinct entity of Socotra's north coast (SOC NC)

This cluster was retained from grouping, it is characterized by a high species richness (76 spp.) and its affinities with other clusters differ between the analyses. In the DCA, the sites of SOC NC are plotted in between those of S&M SG and S&O SC. Its tripartite similarity is highest with S&O SC (0.47), the cluster with the highest species richness. As discussed under S&M US, S&O SC comprises transition zones between Socotra's north and south coast, increasing the affinity between SOC NC and S&O SC. The biogeographic analyses of SOC NC, however, shows a similar trend as the communities of S&M SS, most pronounced in the generic analysis. The indicator species analysis provides an insight into the characteristic species of this cluster: these species are common Indian Ocean algae growing in sheltered environments, often associated with fine sediment (sandy patches or hard substratum covered by a fine sand layer). Although typified by different habitat specific species, this biotope is regarded as a sub-entity of the upwelling sheltered shores (S&M SS). The macroalgal stands of the SOC NC sites are governed by high physical stress (bioerosion due to sand scouring) and, hence, characterized by a much lower biomass and substratum cover in comparison to S&M SS sites.

Seagrass communities (S&M SG): MAS SG and SOC SG

In the DCA plot, the sites of both islands cluster together. SOC SG has the greatest similarity with MAS SG, the tripartite similarity between the seagrass communities of both islands being low, however. This results from the species-poor (5 spp.) seagrass beds at Qalansiyah lagoon (Socotra), predominantly comprised of the seagrasses *Halodule uninervis*, *Halophila ovalis* and *Thalassia hemprichii*. The indicator species of this biotope as a whole are well known to occur in seagrass beds. Analogous to the discussion of SOC NC, this entity can be regarded as a sub-entity of S&M SS, constituting a specific biotope within the sheltered coasts of both islands. This is reflected in the rather high similarity values of the species rich seagrass communities of MAS SG with SOC NC, S&O NC and MAS WC.

CONCLUSIONS

The analysis of two upwelling areas within the Arabian Sea presented here shows (i) the identification of similar plant communities (upwelling affected areas, upwelling sheltered areas, seagrass communities) at both islands, based on their taxon (species and genera) composition, and (ii) an increased divergence of the East African flora from Socotra towards Masirah. In this respect the Socotra Archipelago is a stepping stone between marine plant communities of the East African coast and the Arabian Sea. The plant communities of the upwelling sheltered sites can be grouped in 3 distinct biotopes depending on the degree of exposure (reflected in the degree of sedimentation): (i) the seagrass beds in the protected embayments (MAS SG and SOC SG), (ii) a floristic entity related to a sand covered substratum (SOC NC, including a few seagrass communities of protected sites on Socotra's south coast), and (iii) the macroalgal communities of more exposed sites (often associated with well-developed coral communities; S&O NC and MAS WC). The peculiar marine floristics that characterize the uniqueness of the Arabian Sea predominantly occur at the upwelling affected shores. The plant communities of these areas show a marked biogeographic affinity with distant areas (South Africa and Western Australia; Figs 4a, b) due to the disjunct distribution pattern of certain taxa (Wynne 2000; Schils & Coppejans 2002; Schils *et al.* 2003a). The species richness of the upwelling affected communities is the highest, with a large proportion of red algae (comprising most of the indicator species of this biotope) in the total species composition (Figs 3a, b). This biotope also includes species-rich overlap communities towards the upwelling sheltered sites being, however, clearly characterized as upwelling communities.

In comparison to faunistic studies of the area (Apel 2000), it is important to note that the characteristic plant communities of the Arabian Sea are situated at opposing biotopes where faunistic (e.g. corals, decapods, etc.) diversity, species richness and endemism thrive. The evolution towards distinct biogeographic entities (e.g. centre of endemism along the southern Arabian Peninsula) at these favourable biotopes within the Indian Ocean is most likely the result of vicariation events. The environmental barriers (warmer and less nutrient-enriched waters) isolating the macroalgal communities are the favourable biotopes of the faunistic communities, and vice versa. The occurrence of these opposing biotopes in a restricted geographic area, make both islands a haven for both the characteristic floristic and faunistic communities of the Arabian Sea. Consequently, these islands can be reasonably well managed from a logistical and financial point of view, serving as ideal subjects of intended conservation efforts (e.g. Socotra Biodiversity Project, GEF/Ned/UNDP) to preserve the unique biotic communities of the Arabian Sea.

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APPENDIX

Appendix 1. Species recorded for Masirah Island and the Socotra Archipelago, including the abbreviations used in the analyses and the cluster occurrences of each species. Cluster abbreviations as in Fig. 1.

RHODOPHYTA

AHNFELTIALES

AHNFELTIACEAE

Schottera sp. (Sch_spe) - MAS EC - MAS WC - S&O SC

BONNEMAISONIALES

BONNEMAISONIACEAE

Asparagopsis taxiformis (Delile) Trevisan (Asp_tax) - MAS EC - MAS WC - S&O SC

NACCARIACEAE

Reticulocaulis mucosissimus I.A. Abbott (Ret_muc) - MAS EC

Reticulocaulis obpyriformis Schils, De Clerck & Coppejans (Ret_obp) - S&O SC

CERAMIALES

CERAMIACEAE

Antithamnion sp. (Ant_spe) - MAS EC - SOC NC - S&O SC

Balliella repens Huisman & Kraft (Bal_spe) - S&O NC - S&O SC

Balliella subcorticata (Itono) Itono & Tanaka (Bal_spe) - S&O SC

Balliella sp. (Bal_spe) - MAS EC - MAS WC

Centroceras clavulatum (C. Agardh) Montagne (Cen_cla) - SOC NC - S&O NC

Centroceras sp. (Cen_cla) - MAS SG

Ceramium sp. (Cer_spe) - MAS EC - MAS WC - SOC NC - S&O SC

Euptilota fergusonii Cotton (Eup_fer) - MAS EC - MAS WC - S&O SC

Griffithsia sp. (Gri_spe) - SOC NC - S&O SC

Haloplegma duperreyi Montagne (Hal_dup) - S&O SC

Spyridia hypnoides (Bory de Saint-Vincent) Papenfuss (Spy_spe) - SOC NC - S&O NC

Spyridia sp. (Spy_spe) - MAS EC - SOC NC - S&O SC

Sympodothamnion leptophyllum (Tanaka) Itono (Sym_lep) - S&O SC

DASYACEAE

Amphisbetema indica (J. Agardh) Weber-van Bosse (Amp_ind) - S&O SC

Dasya flagellifera Børgesen (Das_spe) - S&O SC

Dasya sp. (Das_spe) - MAS EC - SOC NC - S&O SC

Dictyurus purpurascens Bory de Saint-Vincent (Dic_pur) - S&O SC

Heterosiphonia sp. (Het_spe) - S&O SC

DELESSERIACEAE

Acrosorium venulosum (Zanardini) Kylin (Acr_spe) - MAS EC

Acrosorium sp. (Acr_spe) - MAS EC - S&O NC - S&O SC

Chauviniella coriifolia (Harvey) Papenfuss (Cha_cor) - S&O SC

Chauviniella jadinii (Børgesen) Papenfuss (Cha_jad) - MAS EC

Claudea elegans Lamouroux (Cla_ele) - MAS EC - S&O SC

Cryptopleura sp. (Crp_spe) - MAS EC

Duckerella ferlusii (Hariot) Wynne (Duc_fer) - S&O SC

Hypoglossum heterocystideum (J. Agardh) J. Agardh (Hyp_spe) - MAS EC

Hypoglossum sp. (Hyp_spe) - MAS EC - S&O SC

Martensia elegans Hering (Mar_ele) - S&O SC

Zellera sp. (Zel_spe) - S&O SC

RHODOMELACEAE

Acanthophora dendroides Harvey (Aca_den) - MAS SG - SOC NC - S&O SC

Acanthophora spicifera (Vahl) Børgesen (Aca_spi) - SOC NC

Amansia rhodantha (Harvey) J. Agardh (Ama_rho) - S&O SC

Chondria armata (Kützing) Okamura (Cho_arm) - S&O SC

Chondria dangeardii Dawson (Cho_dan) - MAS EC - S&O SC

Chondria sp. 1 (Cho_sp1) - MAS EC - SOC NC - S&O NC - S&O SC

Chondria sp. 2 (Cho_sp2) - SOC NC

Chondrophycus papillosus (C. Agardh) Garbary & Harper (Cho_pap) - MAS SG - SOC NC

Digenea simplex (Wulfen) C. Agardh (Dig_sim) - MAS SG

Herposiphonia nuda Hollenberg (Her_spe) - SOC NC - S&O SC

Herposiphonia parca Setchell (Her_spe) - SOC NC

Herposiphonia sp. (Her_spe) - SOC NC - S&O SC

Laurencia columellaris Børgesen (Lau_col) - SOC NC - S&O SC

Laurencia majuscula (Harvey) Lucas (Lau_maj) - MAS SG - SOC NC - S&O NC - S&O SC

Laurencia parvipapillata Tseng (Lau_par) - S&O SC

Laurencia pedicularioides Børgesen (Lau_ped) - MAS EC - SOC NC - S&O NC - S&O SC

Laurencia perforata (Bory de Saint-Vincent) Montagne (Lau_per) - MAS WC - S&O SC - SOC SG

Leveillea jungermannioides (Hering & G. Martens) Harvey (Lev_jun) - MAS WC - MAS SG - S&O NC

Lophocladia sp. (Lop_spe) - S&O SC

Melanamansia sp. (Mel_spe) - MAS EC - SOC NC

Melanothamnus somalensis Bornet & Falkenberg (Mel_som) - MAS WC

Osmundaria melvillii (J. Agardh) R. Norris (Osm_mel) - SOC NC - S&O SC

Polysiphonia sp. (Pol_spe) - MAS WC - S&O SC

Tolypiocladia glomerulata (C. Agardh) Schmitz (Tol_glo) - MAS WC

CORALLINALES

CORALLINACEAE

Amphiroa anceps (Lamarck) Decaisne (Amp_anc) - MAS EC - MAS WC - S&O SC

Amphiroa beauvoisii Lamouroux (Amp_bea) - MAS EC - MAS WC - S&O NC - S&O SC

Amphiroa fragilissima (Linnaeus) Lamouroux (Amp_fra) - SOC NC - S&O NC - S&O SC

Amphiroa misakiensis Yendo (Amp_bea) - MAS EC - S&O NC

Amphiroa rigida Lamouroux (Amp_fra) - SOC NC - S&O NC - S&O SC

Amphiroa sp. (Amp_bea) - MAS SG

Haliptilon sp. (Hlp_spe) - SOC NC

Jania sp. (Jan_spe) - MAS WC - MAS SG - SOC NC - S&O NC - S&O SC

SPOROLITHACEAE

Sporolithon sp. (Spo_spe) - MAS SG - S&O NC

GELIDIALES

GELIDIACEAE

Pterocladia cf. *caloglossoides* (Howe) Dawson (Pte_cfe) - MAS EC - MAS WC - S&O NC - S&O SC

Pterocladiella caerulescens (Kützing) Santelices & Hommersand (Pte_cae) - MAS EC - MAS WC - MAS SG - SOC NC - S&O NC - S&O SC

GELIDIELLACEAE

Gelidiella acerosa (Forsskål) J. Feldmann & G. Hamel (Gel_ace) - MAS WC - MAS SG - S&O NC

Gelidiella pannosa (Feldmann) Feldmann & Hamel (Gel_pan) - S&O NC

GIGARTINALES

CYSTOCLONIACEAE

Calliblepharis fimbriata (Greville) Kützing (Cal_fim) - MAS EC

DUMONTIACEAE

Dudresnaya capricornica Robins & Kraft (Dud_cap) - S&O SC

Gibsmithia larkumii Kraft (Gib_lar) - S&O SC

HYPNEACEAE

Hypnea charoides Lamouroux / *valentiae* (Turner) Montagne complex (Hyp_cha) - MAS SG - SOC NC - S&O NC - S&O SC - SOC SG

Hypnea musciformis (Wulfen) Lamouroux (Hyp_mus) - MAS EC - S&O NC - S&O SC

Hypnea pannosa J. Agardh (Hyp_pan) - MAS WC - S&O NC - S&O SC

Hypnea spinella (C. Agardh) Kützing (Hyp_cha) - MAS EC - MAS SG - SOC NC - S&O NC - S&O SC - SOC SG

KALLYMENIACEAE

Kallymenia crassiuscula Okamura 1934 (Kal_spe) - MAS EC

Kallymenia sp. (Kal_spe) - MAS EC - S&O SC

NEMASTOMATACEAE

Predaea laciniosa Kraft (Pre_lac) - MAS EC - S&O SC

Predaea weldii Kraft & I.A. Abbott (Pre_wel) - MAS EC - MAS WC

RHIZOPHYLLIDACEAE

Portieria hornemannii (Lyngbye) P. Silva (Por_hor) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

SARCODIACEAE

Sarcodia montagneana (J. Hooker & Harvey) J. Agardh (Sar_mon) - MAS EC - MAS WC - S&O SC

SCHIZYMENIACEAE

Platoma heteromorphum Schils (Pla_het) - MAS EC

Titanophora pikeana (Dickie) J. Feldmann (Tit_pik) - S&O SC

SOLIERIACEAE

Callophycus serratus (Harvey ex Kützing) P.C. Silva (Cal_ser) - S&O SC

Sarconema filiforme (Sonder) Kylin (Sar_fil) - MAS SG - SOC NC

Sarconema sp. (Sar_fil) - SOC NC

Solieria robusta (Greville) Kylin (Sol_rob) - MAS EC - S&O SC

GRACILARIALES

GRACILARIACEAE

Gracilaria corticata (J. Agardh) J. Agardh (Gra_mil) - MAS WC - MAS SG - SOC NC - S&O SC

Gracilaria debilis (Forsskål) Børgesen (Gra_deb) - MAS EC - SOC NC

Gracilaria millardetii (Montagne) J. Agardh (Gra_mil) - MAS EC - SOC NC - S&O NC - S&O SC

Gracilaria salicornia (C. Agardh) Dawson (Gra_sal) - MAS SG

Gracilaria textorii (Suringar) De Toni (Gra_tex) - MAS EC - S&O SC

HALYMENIALES

HALYMENIACEAE

Carpopeltis maillardii (Montagne & Millardet) Chiang (Car_mai) - MAS EC - MAS WC - S&O NC - S&O SC

Carpopeltis sp. (Car_mai) - MAS EC

Cryptonemia sp. (Cry_spe) - SOC NC - S&O SC

Halymenia durvillei Bory de Saint-Vincent (Hal_por) - SOC NC - S&O SC

Halymenia porphyraeformis Parkinson (Hal_por) - MAS EC - MAS WC

PEYSSONNELIACEAE

Peyssonnelia sp. (Pey_spe) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

SEBDENIACEAE

Sebdenia flabellata (J. Agardh) Parkinson (Seb_fla) - MAS EC - S&O SC

NEMALIALES

GALAXAURACEAE

Galaxaura marginata (Ellis & Solander) Lamouroux (Gal_mar) - MAS EC - S&O SC

Galaxaura obtusata (Ellis & Solander) Lamouroux (Gal_obt) - MAS EC - S&O SC

Galaxaura rugosa (Ellis & Solander) Lamouroux (Gal_rug) - S&O SC

Scinaia complanata (Collins) Cotton (Sci_com) - MAS EC

Scinaia hormoides Setchell (Sci_mon) - MAS EC

Scinaia moniliformis J. Agardh (Sci_mon) - S&O SC

Scinaia tsinglanensis Tseng (Sci_tsi) - MAS EC - SOC NC - S&O SC

Tricleocarpa cylindrica (Ellis & Solander) Huisman & Borowitzka (Tri_cyl) - SOC NC - S&O SC

Tricleocarpa fragilis (Linnaeus) Huisman & Townsend (Tri_fra) - S&O SC

LIAGORACEAE

Liagora ceranoides Lamouroux (Lia_spe) - SOC NC

Liagora sp. (Lia_spe) - MAS WC - SOC NC

PLOCAMIALES

PLOCAMIACEAE

Plocamium fimbriatum Wynne (Plo_fim) - MAS EC - MAS WC

Plocamium microcladioides South & N.M. Adams (Plo_mic) - MAS EC - MAS WC

Plocamium telfairiae (J. D. Hooker et Harvey) Harvey ex Kützing (Plo_tel) - MAS EC - MAS WC

Plocamium telfairiae (J. D. Hooker et Harvey) Harvey ex Kützing var. *uncinatum* (Plo_tel) - MAS EC - MAS WC

RHODYMENIALES

CHAMPIACEAE

Champia compressa Harvey (Cha_com) - MAS EC - MAS WC - SOC NC - S&O SC

Champia indica Børgesen (Cha_ind) - S&O SC

Champia parvula (C. Agardh) Harvey (Cha_com) - MAS SG - SOC NC - S&O NC - S&O SC

FAUCHEACEAE

Fauchea sp. (Fau_spe) - MAS EC

Gloiocladia sp. (Glo_spe) - S&O SC

LOMENTARIACEAE

Gelidiopsis sp. (Gel_var) - MAS EC - SOC NC - S&O NC - S&O SC

Gelidiopsis variabilis J. Agardh (Schmitz) (Gel_var) - MAS EC - SOC NC - S&O SC

Lomentaria strumosa Wynne (Lom_stru) - MAS WC

RHODYMENIACEAE

Asteromenia peltata (W.R. Taylor) Huisman & Millar (Ast_pel) - S&O NC - S&O SC

Botryocladia leptopoda (J. Agardh) Kylin (Bot_lep) - S&O SC

Botryocladia skottsbergii (Børgesen) Levring (Bot_sko) - S&O SC

Chamaebotrys sp. (Chm_spe) - S&O SC

Chrysymenia grandis Okamura (Chr_gra) - MAS EC - S&O SC

Chrysymenia sp. (Chr_spe) - MAS EC - S&O SC

Coelarthrum opuntia (Endlicher) Børgesen (Coe_opu) - SOC NC - S&O SC

Erythrocolon podagricum J. Agardh (Ery_pod) - S&O SC

Rhodymenia sp. 1 (Rho_sp1) - MAS EC - MAS WC

Rhodymenia sp. 2 (Rho_sp2) - MAS EC

PHAEOPHYTA

DICTYOTALES

DICTYOTACEAE

Dictyopteris delicatula Lamouroux (Dic_del) - S&O SC

Dictyopteris macrocarpa (Areschoug) O. Schmidt (Dic_mac) - MAS EC - S&O SC

Dictyopteris membranacea (Stackhouse) Batters (Dic_pol) - SOC NC

Dictyopteris polypodioides (De Candolle) Lamouroux (Dic_pol) - SOC NC - S&O NC - S&O SC

Dictyota bartayresiana Lamouroux (Dic_bar) - MAS EC - MAS WC - SOC NC

Dictyota cervicornis Kützing (Dic_cer) - MAS SG - SOC NC - S&O NC - S&O SC

Dictyota ceylanica Kützing (Dic_cey) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

Dictyota ciliolata Kützing (Dic_cil) - MAS EC - MAS WC

Dictyota crispata Lamouroux (Dic_cri) - MAS EC - MAS WC - S&O SC

Dictyota dichotoma (Hudson) Lamouroux var. *intricata* (C. Agardh) Greville (Dic_cer) - S&O SC

Dictyota friabilis Setchell (Dic_fri) - MAS EC - S&O NC - S&O SC

Dictyota grossedentata De Clerck & Coppejans (Dic_gro) - S&O SC

Dictyota stolonifera Dawson (Dic_sto) - S&O SC

Lobophora variegata (Lamouroux) Womersley ex Oliveira (Lob_var) - MAS EC - MAS WC - MAS SG - S&O NC - S&O SC

Padina antillarum (Kützing) Piccone (Pad_ant) - MAS EC

Padina australis Hauck (Pad_aus) - SOC NC - S&O SC

Padina boergesenii Allender & Kraft (Pad_boe) - MAS SG - SOC NC - S&O NC - S&O SC

Padina dubia Hauck (Pad_gym) - MAS EC - MAS WC

Padina elegans Koh ex Womersley (Pad_ele) - MAS EC - S&O SC

Padina glabra Gaillard (Pad_gym) - MAS EC - MAS WC

Padina gymnospora (Kützing) Sonder (Pad_gym) - SOC NC - S&O NC

Padina minor Yamada (Pad_min) - MAS SG

Spatoglossum asperum J. Agardh (Spa_asp) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

Stoechospermum polypodioides (Lamouroux) J. Agardh (Sto_pol) - MAS EC - MAS WC - MAS SG - SOC NC - S&O NC

Stypopodium sp. (Sty_spe) - SOC NC - S&O SC

ECTOCARPALES

ECTOCARPACEAE

Ectocarpus sp. (Ect_spe) - SOC NC - S&O SC

FUCALES

CYSTOSEIRACEAE

Cystoseira indica (Thivy & Doshi) Mairh (Cys_ind) - MAS SG

Cystoseira myrica (S. Gmelin) C. Agardh (Cys_myr) - MAS SG

Hormophysa cuneiformis (J. Gmelin) P. Silva (Hor_cun) - SOC NC

SARGASSACEAE

Nizamuddinia zanardinii (Schiffner) P. Silva (Niz_zan) - MAS WC - S&O NC

Sargassum angustifolium C. Agardh (Sar_ang) - SOC NC - S&O SC

Sargassum decurrens (R. Brown ex Turner) C. Agardh (Sar_dec) - MAS WC - S&O SC

Sargassum latifolium (Turner) C. Agardh (Sar_lat) - MAS EC - MAS WC - S&O SC

Sargassum linearifolium (Turner) C. Agardh (Sar_lin) - S&O NC

Sargassum oligocystum Montagne (Sar_oli) - MAS WC - MAS SG

Sargassum piluliferum (Turner) C. Agardh (Sar_pil) - MAS WC - MAS SG

Sargassum sp. (Sar_sp1) - MAS WC - MAS SG

Turbinaria ornata (Turner) J. Agardh (Tur_orn) - MAS WC - S&O NC - S&O SC

SCYTOSIPHONALES

CHNOOSPORACEAE

Chnoospora implexa J. Agardh (Chn_imp) - S&O NC

SCYTOSIPHONACEAE

Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier (Col_sin) - SOC NC - S&O SC

Hydroclathrus clathratus (C. Agardh) Howe (Hyd_cla) - SOC NC

Rosenvingea intricata (J. Agardh) Børgesen (Ros_int) - S&O NC - S&O SC

CHLOROPHYTA

BRYOPSIDALES

BRYOPSIDACEAE

Bryopsis hypnoides Lamouroux (Bry_spe) - S&O SC

Bryopsis indica A. Gepp & E. Gepp (Bry_spe) - MAS EC - MAS WC - S&O SC

Bryopsis pennata Lamouroux (Bry_spe) - MAS WC

Bryopsis sp. (Bry_spe) - S&O NC

Pseudobryopsis hainanensis Tseng (Pse_spe) - MAS EC - MAS SG

CAULERPACEAE

Caulerpa brachypus Harvey (Cau_bra) - S&O SC

Caulerpa cupressoides (Vahl) C. Agardh (Cau_cup) - SOC NC

Caulerpa lanuginosa J. Agardh (Cau_lan) - SOC NC - S&O SC

Caulerpa lentillifera J. Agardh (Cau_len) - MAS SG - SOC NC - S&O SC

Caulerpa mexicana Sonder ex Kützing (Cau_mex) - MAS EC - MAS SG - SOC NC - S&O SC

Caulerpa peltata Lamouroux (Cau_pel) - MAS EC - MAS WC - S&O NC - S&O SC

Caulerpa racemosa (Forsskål) J. Agardh (Cau_rac) - MAS EC - MAS WC - MAS SG - S&O SC

Caulerpa scalpelliformis (R. Brown ex Turner) C. Agardh (Cau_sca) - MAS SG - SOC NC - S&O SC

Caulerpa serrulata (Forsskål) J. Agardh (Cau_ser) - MAS WC - MAS SG

Caulerpa sertularioides (S. Gmelin) Howe (Cau_set) - MAS SG - SOC NC - S&O SC

CODIACEAE

Codium arabicum Kützing (Cod_ara) - MAS WC - MAS SG - SOC NC

Codium dwarkense Børgesen (Cod_dwa) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

Codium ovale Zanardini (Cod_ova) - MAS EC

Codium tenue (Kützing) Kützing (Cod_ten) - MAS EC

DERBESIACEAE

Pedobesia simplex (Kützing) M.J. Wynne & Leliaert (Ped_sim) - S&O SC

UDOTEACEAE

Avrainvillea lacerata Harvey ex J. Agardh (Avr_lac) - SOC NC - S&O SC

Chlorodesmis fastigiata (C. Agardh) Ducker (Chl_fas) - S&O NC

Chlorodesmis sp. (Chl_fas) - MAS EC - MAS SG

Halimeda copiosa Goreau & Graham / *minima* (W.R. Taylor) Colinvaux (Hal_com) - S&O SC

Halimeda cuneata Hering (Hal_dct) - SOC NC - S&O SC

Halimeda discoidea Decaisne (Hal_dct) - MAS SG - SOC NC - S&O SC

Halimeda stuposa W.R. Taylor (Hal_stu) - SOC NC - S&O SC

Halimeda tuna (Ellis & Solander) Lamouroux (Hal_dct) - MAS EC - MAS WC - MAS SG - SOC NC - S&O SC

Udotea indica A. Gepp & E. Gepp (Udo_ind) - MAS SG - SOC NC - S&O SC

CLADOPHORALES

ANADYOMENACEAE

Microdictyon sp. (Mic_spe) - S&O SC

CLADOPHORACEAE

Chaetomorpha sp. (Cht_spe) - MAS SG - SOC NC - S&O SC

Cladophora catenata (Linnaeus) Kützing (Cla_cat) - MAS EC

Cladophora coelothrix Kützing (Cla_coe) - MAS SG - SOC NC - S&O SC

Cladophora prolifera (Roth) Kützing (Cla_pro) - SOC NC

Cladophora sericea (Hudson) Kützing (Cla_ser) - MAS WC

Cladophora vagabunda (Linnaeus) van den Hoek (Cla_vag) - MAS EC - MAS WC - SOC NC - S&O NC - S&O SC

Cladophora sp., section Longi-articulatae (Cla_lon) - SOC NC

SIPHONOCLADACEAE

Boergesenia forbesii (Harvey) J. Feldmann (Boe_for) - MAS SG - S&O SC

Boodlea composita (Harvey) Brand (Boo_com) - SOC NC

Chamaedoris auriculata Børgesen (Cha_aur) - SOC NC - S&O SC

Chamaedoris delphinii (Hariot) J. Feldmann & Børgesen (Cha_del) - S&O NC

Cladophoropsis herpestica (Montagne) Howe (Cla_her) - MAS WC - MAS SG

Cladophoropsis sundanensis Reinbold (Cla_sun) - MAS SG

Dictyosphaeria cavernosa (Forsskål) Børgesen (Dic_cav) - S&O NC

Phyllodictyon anastomosans (Harvey) Kraft & M.J. Wynne (Phy_spe) - S&O NC - S&O SC

Siphonocladus tropicus (P. Crouan & H. Crouan) J. Agardh (Sip_tro) - SOC NC - S&O SC

Struveopsis siamensis (Egerod) P. Silva (Str_sia) - S&O SC

Ventricaria ventricosa (J. Agardh) Olsen & J. West (Ven_ven) - S&O NC

VALONIACEAE

Valoniopsis pachynema (G. Martens) Børgesen (Val_pac) - MAS EC - MAS WC - S&O NC

DASYCLADALES

DASYCLADACEAE

Neomeris van-bosseae Howe (Neo_van) - SOC NC - S&O SC

POLYPHYSACEAE

Acetabularia sp. (Ace_spe) - SOC NC - S&O NC - S&O SC

ULVALES

ULVACEAE

Enteromorpha sp. (Ent_spe) - MAS SG - SOC NC

Ulva sp. (Ulv_spe) - MAS WC - MAS SG - SOC NC - S&O NC - S&O SC

MAGNOLIOPHYTA

ALISMATALES

CYMODOCEACEAE

Halodule uninervis (Forsskål) Ascherson (Hal_uni) - MAS SG - SOC NC - SOC SG

Syringodium isoetifolium (Ascherson) Dandy (Syr_iso) - MAS SG

Thalassodendron ciliatum (Forsskål) den Hartog (Tha_cil) - MAS SG - SOC NC - S&O NC

HYDROCHARITACEAE

Halophila decipiens Ostenfeld (Hal_dec) - S&O SC

Halophila ovalis (R. Brown) Hooker (Hal_ova) - MAS SG - SOC SG

Thalassia hemprichii (Ehrenberg) Ascherson (Tha_hem) - SOC SG

CHAPTER 8

SYNTHESIS AND PERSPECTIVES

The present study investigates the marine plant communities of the Arabian Sea, largely composed of macroalgae. The Arabian Sea is situated in the northern Indian Ocean, bordering the Gulf of Aden and the African continent to the west, and the Gulf of Oman and the Indian sub-continent to the east. The ecology and oceanography of the Arabian Sea are governed by the seasonal monsoon winds, which initiate coastal upwelling in particular areas. The marine biocoenoses of these upwelling shores are relatively understudied and seem to represent a distinct entity within the Indian Ocean. The Socotra Archipelago (Yemen) and Masirah Island (Oman) are situated in two geographically differing upwelling areas within the Arabian Sea, and both contain a wide diversity of habitats in a restricted area. The uniqueness of the plant communities of these islands is expressed in their floristic, biogeographic and ecological aspects. The taxonomic issues are discussed first, followed by the community analyses.

Species inventories

The inventories of marine macroalgae and seagrasses from the study area, which are used in the ecological analyses, contain several new species records for the region. The number of new records from the investigated areas are as follows, where the first number represents the marine plants identified to species level and the second those only identified to generic level (the first records of these genera, or species differing from those previously reported): Masirah Island, 90 and 19 species; Oman, 48 and 12 species; Socotra Archipelago, 130 and 28 species; Yemen, 92 and 20 species. Further taxonomic studies on macroalgae from the Arabian Sea will result in more new records, especially as complex species groups (e.g. *Laurencia*), epiphytes and crustose algae have largely been omitted or lumped into groups in the pilot studies.

Taxonomy and biogeography at species level

The species records form the basic input data for the analyses, hence the taxonomic studies on Arabian Sea algae in the first chapters (*2-5*). Chapters 2 and 3 report on the gelatinous red algae belonging to the Dumontiaceae, Nemastomataceae, Schizymeniaceae and Naccariaceae. In addition to the morphological and anatomical observations, the study of reproductive structures and post-fertilization events in these algae show their importance for reliable species identifications. Based on these detailed examinations, *Platoma heteromorphum* and *Reticulocaulis obpyriformis* are newly described species from Masirah Island and the Socotra Archipelago, respectively. Many gametophytes of the gelatinous reds are seasonally present, reflecting cyclic changes in environmental conditions resulting from physical phenomena (e.g. upwelling) or other temporal variables (e.g. day length). The study of the Dumontiaceae, Nemastomataceae and Schizymeniaceae of the Arabian Sea (*chapter 2*) and their occurrence throughout the Indo-Pacific, shows that their distribution is at present insufficiently known. Unpublished data of Indian Ocean records (Ghent University Herbarium) indicate that these species are more wide-spread and cover a larger area than currently known, making them useless in traditional biogeographic analyses based on species distributions. In contrast, both *Reticulocaulis* species (*chapter 3*) show links with distant regions, where their absence in the intervening areas is unlikely to be a result from of undersampling. The Naccariaceae is a small family with a specific life cycle and particular reproductive traits. No representatives of this family have been recorded for the Indian Ocean, apart from an unpublished collection of *Naccaria naccarioides* from Western Australia (G.T. Kraft & G.W. Saunders pers. comm.). The studied gelatinous red algae thus show contrasting geographic distributions within the Indo-Pacific: disjunct (Naccariaceae) versus continuous (Dumontiaceae, Nemastomataceae and Schizymeniaceae). These algae can therefore be useful in investigating specific biogeographic questions using a combined molecular and anatomical approach. The degree of genetic divergence of ubiquitous species (e.g. *Predaea weldii*) could serve as a measure of biogeographic relatedness throughout the whole Indo-Pacific. The families Nemastomataceae and Schizymeniaceae have recently been separated based on distinct post-fertilization events. Additional molecular studies on other genera of these families could shed light on the phylogeny. Moreover, the validity of today's morphospecies could be verified by genetic analyses e.g. species diversity within the enigmatic genus *Titanophora*, as representatives of these families have been underrepresented in molecular studies. In order to establish the importance of vicariance events versus the long-distance dispersal of disjunctly distributed Arabian Sea taxa, molecular analyses of the two *Reticulocaulis* species from Arabia and *R. mucosissimus* from Hawaii could illustrate such phylogeographic relationships. Additional sequencing of the two other Naccariaceae genera, *Naccaria* and *Atractophora*, and the presumably related genus *Liagorothamnion* would clarify the ordinal classification of these genera and the suggested subdivision into different families (see *chapter 3*). In conclusion, a holistic approach of molecular, biogeographic and anatomic studies on these gelatinous red algae could lead to a sound species concept based on various biological aspects. Ideally, such a baseline study on Arabian Sea taxa could serve as a model within the above red algal families.

Chapter 4 discusses a new species, *Chamaebotrys erectus*, from the Socotra Archipelago belonging to the Rhodymeniales. *Chamaebotrys* has recently been erected by Huisman (1996) based on characters of reproductive structures, viz. terminal tetrasporangia in nemathecial sori. The remarkable features that readily discern *C. erectus* from both other *Chamaebotrys* species are its large, upright thallus and the *in situ* (remaining fixed on the tetrasporophyte) germination of the tetraspores into gametophytes. In addition to the compound thalli with tetrasporic and cystocarpic parts, free-living gametophytes also occur. The unusually large size, with respect to both other representatives of the genus, is most probably linked to the upwelling of cold and nutrient-rich water, as the species was only collected from Socotra's south coast. *Champia gigantea*, another Rhodymeniales species, is similarly endemic to the Arabian Sea and characterized by an exceptionally large thallus. The description of *C. erectus* includes the first observation of a carpogonial branch within the genus, supporting its affinity with *Coelarthrum* and its classification within the Rhodymeniaceae.

The last taxonomic chapter (*5*) focuses on *Izziella orientalis*. The species is widely distributed throughout the (sub)tropical Indo-Pacific. The reassessment of the genus *Izziella* is based on *Liagora orientalis*. Abbott (1990) treated *Izziella abbottiae*, a species dedicated to her, as a synonym of *L. orientalis*. While analyzing the Liagoraceae (Nemaliales), the combined observations of the carpogonial branch, the cystocarp and the large subtending stalk (fused cells) clearly discerned *L. orientalis* from other Liagoraceae genera, justifying the reinstatement of *Izziella*. Upon the resurrection of *Ganonema* (Huisman & Kraft 1994), the reinstatement of the genus *Izziella* forms a second step in subdividing *Liagora* into several genera as the genus currently accommodates numerous taxa with a wide variety in morphology and cystocarp types (Kraft 1989; Huisman & Kraft 1994).

These taxonomic studies on Rhodophyceae of the Arabian Sea support previous anecdotal observations (Børgesen 1934; Wynne 2000) on the biogeographic affinities with distant areas (Australia, Hawaii, Japan, South Africa). The study on the macroalgae of the Socotra Archipelago considerably broadens the area for which these disjunctly distributed species were reported. Personal observations (T. Schils) during the course of this study supplement these findings, e.g. the Delesseriaceae. The provisional count totals 15 Delesseriaceae species for Yemen and Oman, which form a sympatric flora composed of typical East African algae (*Duckerella ferlusii*); certain South-East Asian and Pacific algae (*Zellera tawallina*); and general Indo-Pacific algae, including some rarely recorded Indian Ocean species (*Chauviniella coriifolia* and *C. jadinii*). Similar to *Chamaebotrys erectus*, exeptionally large endemic Delesseriaceae, *Cryptopleura robusta* M.J. Wynne and *Pseudogrinnellia barrattiae* M.J. Wynne, have been described for Oman (Wynne 1999a, b). The diverse distribution patterns of the Delesseriaceae flora, and their generally striking, “pretty” appearance (easily observed in the field), make them good subjects for establishing complete species lists for this group and thus improving biogeographic analyses within the Indo-Pacific. *Sympodothamnion*, another remarkable genus of the Ceramiales, has been collected from the Socotra Archipelago. This monospecific genus has only been known from southern Japan. Besides the biogeographic aspects, the species identity and its familial classification are of particular research interest. The genus has been classified in the Dasyaceae (Itono 1977) but the present consensus is in the Ceramiaceae (Athanasiadis 1996; de Jong *et al.* 1997). Our observations, however, strongly indicate a classification in the Rhodomelaceae. Other Rhodomelaceae taxa that are nowadays of biogeographic interest are the Amansieae (Masuda & Abe 2002; N’Yeurt 2002). Our Arabian Sea collections contain four species belonging to this tribe. Cornilly (2002) studied these specimens plus an obscure endemic from Yemen, *Amansia arabica* J. Agardh ex Newton *nom. inval.* The observed phytogeographic separation of *Amansia* and *Melanamansia* (Norris 1995) in the Indo-Pacific (excluding South Africa) cannot be supported for the Arabian Sea. This is consistent with recent findings of co-occurring *Amansia* and *Melanamansia* species in other areas of the Indo-Pacific (South & Skelton 1999; Masuda *et al.* 2000). Again, this group contains both widely distributed species [*Amansia rhodantha* (Harvey) J. Agardh and *Osmundaria melvillii* (J. Agardh) R.E. Norris] and species with disjunct distribution patterns [*Neurymenia nigricans* T. Tanaka & Itono: Natal (South Africa), Socotra (Yemen) and southern Japan; *Melanamansia daemelii* (Sonder) R.E. Norris: Hawaii, Masirah (Oman), Queensland (Australia) and Socotra (Yemen)]. The endemic *Amansia arabica*, again characterized by a large thallus size, most probably needs to be transferred to the genus *Melanamansia*. The above mentioned representatives of the Ceramiales may prove to be useful in DNA marker and molecular clock analyses in the future, which could reveal an insight in the phylogeographic patterns (genetic history and gene flow) and important vicariant events (divergence rates) of Arabian Sea macroalgae. Recent cryptic introductions that could obscure these patterns are suspected to be minimal as (i) the number of harbours in the Arabian Sea is limited, (ii) the examined subtidal rhodophytes are unlikely candidates for anthropogenic dispersal and (iii) the latter are rather ineffective in subsequent settling. The first molecular clock (Zuccarello & West 2002) and phylogeographic studies (Zuccarello *et al.* 2002) on Ceramiales have already revealed interesting and unexpected results.

Ecology and biogeography at community level

The analysis of the subtidal relevé data from the Socotra Archipelago identified distinct plant communities corresponding to their geographic location within the archipelago (*chapter 6*). In contrast to the particular distribution pattern of a specific taxon (see *Biogeography at species level*), we here analyse the biogeographic affinity of all the species in a community. The two contrasting algal communities of the main island are those of the upwelling affected south coast and the upwelling protected north coast. Both communities comprise well-developed macroalgal stands (no significant difference in species richness, biomass and alpha diversity of the quadrats), but differ substantially in species composition (beta diversity indices). The biogeographic affinities, expressed by the Simpson coefficient, of both communities also vary (*chapter 6*). Socotra's south coast shows a lower general affinity with the Indian Ocean flora than the north coast. In general, the biogeographic affinities of the Socotran communities within the Indian Ocean increase from a minimum in southern Africa to a maximum along the tropical East African coast of Kenya and Tanzania. The affinities then decrease within the Arabian Sea towards a low in Iran and Pakistan (a result of undersampling). Thereafter the affinities within the eastern Indian Ocean remain rather constant and low. Besides the north and south coast, four additional plant communities were identified. The eastern tip of Socotra Island harbours a community with elements of both previous entities, however, with a markedly higher affinity for the south coast flora. The mixed community of this transition zone includes the most species-rich and most diverse quadrats of the archipelago, largely attributable to the particular red algal flora. The intense and complex current patterns, regulating temperature and supplying a constant nutrient flow, around the eastern tip are suspected to be beneficial for algal growth. The biogeographic affinities of the transition zone are intermediate between those of the north and the south coast. The algal assemblages of the outer islands are subject to large fluctuations in phosphate concentration and temperature, resulting from the limited coastal area and the drastic changes in the surrounding current patterns. The species composition of this community is most similar to that of Socotra's south coast and its biogeographic affinities run parallel to those of different communities for each of the three main Indian Ocean regions (East African coast, Arabian Sea and eastern Indian Ocean). The remaining two communities, the seagrass beds of Qalansiyah Lagoon and the coral dominated communities of the north coast, differ substantially in species richness, diversity and biomass from the previous communities. The species composition of these plant communities, however, demonstrates links with the north coast. Both communities are regarded as sub-entities of the north coast, being habitats that are governed by peculiar environmental conditions (e.g. high salinities, high temperature and substantial sand cover) and biotic competition (especially with corals). This results in an impoverished floristic species richness and a low floristic diversity. The biomass stands (fresh weight per vegetation quadrat) of these two sub-entities vary from the lowest (coral dominated communities) to the highest (seagrass beds) observed values of the archipelago. From a phycological point of view, Socotra's south coast, the transition zone and the outer islands are the areas with a unique subtidal flora within the Indian Ocean, which are characterized by high species-richnesses and high diversity values. The development of these communities is closely linked with the phenomenon of coastal upwelling, shaping the unique Arabian Sea biocoenoses. Zoning and development plans of the Socotra Archipelago should designate part of these exclusive marine communities as conservation and monitoring areas. Socotra's north coast, including the coral dominated communities and the seagrass beds, is composed of common Indian Ocean macroalgae, but conversely it comprises unique faunistic communities for the Indian Ocean and regionally important nursing grounds. The marine organisms that show a high degree of endemism and allopatry are essentially different for the contrasting coasts. The faunistic composition of the northern communities is unique for the region, while the southern communities are characterized by a particular flora. The phenomenon of upwelling in this northern part of the Indian Ocean is the dispersal barrier for the warm- (northern coasts) as well as the cold-water biota (southern coasts).

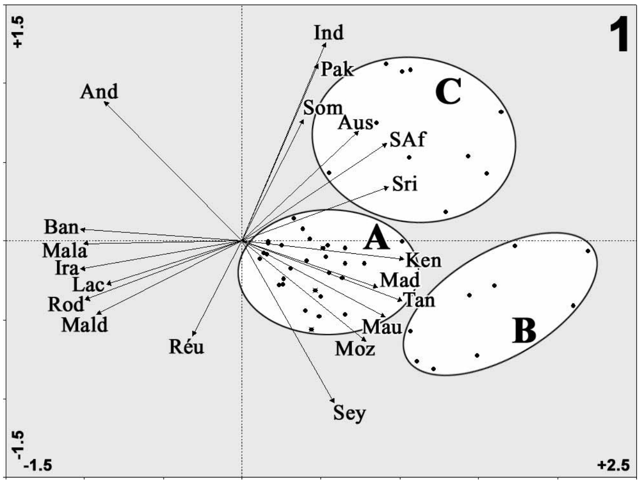

Fig. 1. Principal Component Analysis of the Indian Ocean distribution of the macroalgal species in the site inventories. The Indian Ocean distribution for each species of a particular site is documented, after which the species records per country are counted for each site. The species lists of the different sites are then treated as the sample input and the Indian Ocean nations are used as the species input. The included nations are: South Africa (SAf), Mozambique (Moz), Madagascar (Mad), Réunion (Réu), Mauritius (Mau), Rodrigues (Rod), Tanzania (Tan), Seychelles (Sey), Kenya (Ken), Somalia (Som), Iran (Ira), Pakistan (Pak), Laccadive islands (Lac), Maldives (Mald), Sri Lanka (Sri), Bangladesh (Ban), Andaman islands (And), Malaysia (Mala), Indonesia (Ind), Western Australia (Aus). Three site groupings have been discerned: the clusters A, B and C. The eigenvalues of the first two axes are 0.827 and 0.042, respectively.

In a second ecological approach (*chapter 7*), the subtidal plant assemblages of the Socotra Archipelago and Masirah Island are analyzed by means of complete species inventories for the different sample sites. The resulting ordinations from species lists have a somewhat lower resolution than those from quadrat data for Socotra, i.e. certain communities (transition zone and outer islands) are grouped into larger ones (Socotra's north and south coast). The ordination reveals six communities. Similar communities of Socotra and Masirah are grouped into larger entities (four biotopes) based on the ordination results, the tripartite similarity index and the congruous biogeographic affinities within the Indian Ocean (founded on specific as well as generic records). The environmental conditions and the indicator species that characterize these communities and biotopes are discussed. The combined interpretation of the ordination including environmental parameters (especially chlorophyll a) and the biogeographic analyses show a stronger effect of upwelling for Masirah, resulting in macroalgal communities that are more divergent from the East African flora in comparison to those of Socotra. All investigated communities, however, have a strong phytogeographic affinity with the East African coast. A synopsis is represented in the Principal Component Analysis (hereafter PCA) of the macroalgal distributions (Indian Ocean nations) from the species inventories of the Socotra and Masirah sites (Fig. 1). The very high eigenvalue of the first axis (0.827) shows that the separation of countries according to this axis is by far the most important component of the analysis. The species inventories of Masirah and Socotra (dots in Fig. 1) have high affinities with the (sub)tropical countries of

East Africa, Western Australia, Sri Lanka and the east coast of South Africa. The biogeographic affinities with other countries and islands of the eastern and central part of the Indian Ocean are markedly lower. The PCA shows three distinct site groupings (Fig. 1). Cluster A includes sites with a high biogeographic affinity for East Africa, which belong to the following communities (for abbreviations see *chapter 7*): MAS WC, S&O NC, SOC NC and SOC SG. Cluster B groups sheltered sites, also harbouring communities (part of MAS SG and S&O SC) with high affinities for the East African flora. Cluster C (MAS EC and S&O SC) is separated from clusters A and B by the second axis. The low eigenvalue of this axis, adding only 4.2 % of the variation in species composition, indicates that, besides the high East African affinity, a limited number of its species have marked affinities with local (e.g. Pakistan and Somalia) and distant (e.g. South Africa and Western Australia) cold-temperate floras.

Sheppard *et al.* (1992) suspected that most of the biotic distributions in the Arabian Seas (comprising the Red Sea, Gulf of Aden, Arabian Sea, Gulf of Oman and Persian Gulf) are no more than chance distributions and that the area as a whole constitutes a single biogeographic sub-region. Besides the odd exception (e.g. high local endemism of butterflyfish), Sheppard *et al.* (1992) believe that biogeographic patterns result from insufficient time for complete dispersal after the start of the Holocene and inadequate "mixing" of fauna throughout the various suitable habitats in the Indian Ocean. These authors remarked that a designation on a smaller biogeographic scale might be possible for some fish, yet for other groups, notably the plants, there is no justification for any sub-provincial division. Various analysis techniques (*chapters 6, 7*), however, detect distinct subtidal plant communities and biotopes according to differences in the governing environmental parameters. Of these, the upwelling affected plant communities typify a peculiar Arabian Sea flora. Certain species of these communities show disjunct distribution patterns throughout the Indo-Pacific and are also suspected to be of biogeographic importance within the larger Arabian region. Combined with the discovery of an increasing number of endemic algae, this leaves us to conclude that the Arabian Sea constitutes a phytogeographic (sub)province within the Indo-Pacific and the larger Arabian region. Prospective fieldwork in the northern Arabian Sea (Al Qad, Oman) would extend the investigated area considerably, being excellent to test biogeographic (dis)continuities towards the border of the Arabian Sea and the Gulf of Oman. Questions of interest include: (i) the degree of divergence from the East African flora, (ii) the impact of upwelling on these communities, (iii) the use of this location in a geographic gradient, from the Arabian Sea over the Gulf of Oman towards the Persian Gulf, in order to test the macroalgal turnover according to the decrease in substratum availability (sedimentary coasts as a biogeographic barrier). Recently, the first temperature loggers have been installed at Masirah Island (Wilson 1999) in an attempt to achieve accurate coastal data on a detailed temporal and spatial scale. These precise coastal data are needed for understanding the relationship between the environmental conditions and the biotic interactions (e.g. competition between algae and corals).

Seasonality

Nizamuddinia zanardinii is a large, endemic fucoid of the upwelling regions within the Arabian Sea. In reporting *N. zanardinii* for the Socotra Archipelago, Kemp (1998) noticed differences in seasonal growth between the Socotran populations and those of the southern

Arabian shores. Two explanatory hypotheses were proposed: (i) a temporal shift of up to six months in the growth cycle of *N. zanardinii* for Socotra in comparison to the mainland populations, or (ii) two (re)productive peaks of this alga at Socotra, whereas one for the southern Arabian plants. Although initially planned, due to practical complications (see *chapter 1*), extended observations on macroalgal seasonality were not feasible during the course of this study. The observations during the three field trips, however, can shed some light on the seasonal growth of this keystone species. The temporal co-occurrence (November 1999) of mature, fertile *N. zanardinii* specimens in intertidal rock pools at Masirah and the undeveloped small rosettes at Barr al-Hikman, seem to indicate that periods of reproductivity and growth can fluctuate within a specific geographic area dependent on its habitat and/or zonation of occurrence. Similar differences were observed for the Socotra Archipelago: whereas Kemp (1998) reports on reproductive spikes in February-March 1996 and Leliaert (2000) collected fertile axes in January-February 1999, only small plants were noticed during the field trip in March-May 2000. This suggests the existence of two reproductive periods (cf. Hadramout coast of Yemen, Ormond & Banaimoon 1994) related to both upwelling periods, with temporal (annual) and local fluctuations. In addition, it is suspected that the (re)productive response of the *Nizamuddinia* populations from Yemen and Oman is greater during the southwest monsoon as opposed to the northeast monsoon.

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HOOFDSTUK 9

SYNTHESE EN PERSPECTIEVEN

In deze studie worden de mariene plantengemeenschappen, voornamelijk bestaande uit macrowieren, van de Arabische Zee onderzocht. De Arabische Zee is gelegen in het noordelijk deel van de Indische Oceaan en grenst in het westen aan de Golf van Aden en het Afrikaans continent, en in het oosten aan de Golf van Oman en het Indisch subcontinent. De ecologie en de oceanografie van de Arabische Zee worden bepaald door de seizoenale moessonwinden, die in bepaalde gebieden kustgebonden opwelling induceren. De mariene levensgemeenschappen van deze opwellingskusten zijn relatief weinig bestudeerd en blijken binnen de Indische Oceaan een aparte eenheid te vormen. De Socotra Archipel (Jemen) en het eiland Masirah (Oman) bevinden zich in twee geografisch gescheiden opwellingsgebieden van de Arabische zee en bevatten beide een grote diversiteit aan habitats op een beperkte oppervlakte. De uniciteit van de plantengemeenschappen van deze eilanden komt tot uiting in hun floristische, biogeogeografische en ecologische aspecten. In deze studie worden de taxonomische onderwerpen eerst behandeld, gevolgd door de gemeenschapsanalysen.

Soortenlijsten

De soortenlijsten van de Arabische Zee die in de ecologische analysen gebruikt werden bevatten verschillende nieuwe soortswaarnemingen voor de regio. Het aantal nieuwe waarnemingen voor de onderzochte gebieden worden hier achtereenvolgens vernoemd, het eerste cijfer vertegenwoordigt het aantal mariene planten die tot op de soort gedetermineerd zijn en het tweede cijfer deze tot op genusniveau (de eerste waarnemingen van deze genera, of soorten verschillend van de tot op heden vermelde taxa): het eiland Masirah, 90 en 19 soorten; Oman, 48 en 12 soorten; de Socotra Archipel, 130 en 28 soorten; Jemen, 92 en 20 soorten. Toekomstige taxonomische studies naar macrowieren van de Arabische Zee zullen ongetwijfeld in nieuwe soortswaarnemingen resulteren, zeker wanneer deze zich toeleggen op complexe soortengroepen (b.v. *Laurencia*), epifyten en korstvormende wieren, die grotendeels verzuimd werden in deze eerste studies.

Taxonomie en biogeografie op soortsniveau

De soortswaarnemingen vormen steeds de basisgegevens van de uitgevoerde analysen, bijgevolg werden de taxonomische studies naar de wieren van de Arabische Zee in de eerste hoofdstukken besproken (*2-5*). De hoofdstukken 2 en 3 rapporteren over de gelatineuze roodwieren van de families Dumontiaceae, Nemastomataceae, Schizymeniaceae en Naccariaceae. Naast de morfologische en anatomische waarnemingen, is de studie van de reproductieve kenmerken en de post-fertilisatiegebeurtenissen van belang met betrekking tot betrouwbare soortsidentificaties van deze wieren. Op grond van dit gedetailleerd onderzoek, werden de soorten *Platoma heteromorphum* en *Reticulocaulis obpyriformis* nieuw beschreven van respectievelijk het eiland Masirah en de Socotra Archipel. Veel gametofyten van de gelatineuze roodwieren zijn slechts seizoenaal aanwezig, wat de cyclische veranderingen in de milieuomstandigheden ten gevolge van fysische fenomenen (b.v. opwelling) en andere temporele variabelen (b.v. daglengte) weergeeft. De studie van de

Dumontiaceae, Nemastomataceae en Schizymeniaceae van de Arabische Zee (*hoofdstuk 2*) en hun voorkomen over het Indo-Pacifisch gebied, toont dat de verspreiding momenteel onvoldoende gekend is. Ongepubliceerde gegevens van Indische Oceaanwaarnemingen (Herbarium Universiteit Gent) geven aan dat deze gelatineuze roodwieren meer algemeen verspreid voorkomen en een groter gebied beslaan dan tot op heden werd aangenomen. Bijgevolg zijn deze soorten onbruikbaar voor traditionele biogeografische analysen gebaseerd op soortsverspreidingen. Het omgekeerde geldt voor beide *Reticulocaulis*-soorten (*hoofdstuk 3*) die een verband vertonen met ver verwijderde gebieden en waarvan de afwezigheid in de tussenliggende gebieden waarschijnlijk niet toe te schrijven is aan een gebrek aan bemonsteringen. De Naccariaceae is immers een kleine familie die gekarakteriseerd wordt door een specifieke levenscyclus en typerende reproductieve kenmerken. Buiten de ongepubliceerde waarneming van *Naccaria naccarioides* voor West-Australië (G.T. Kraft & G.W. Saunders pers. med.), is er voordien geen enkele Naccariaceae vermeld voor de Indische Oceaan. De bestudeerde gelatineuze roodwieren hebben dus contrasterende geografische verspreidingen in de Indo-Pacific: hetzij dispers (Naccariaceae), hetzij ononderbroken (Dumontiaceae, Nemastomataceae en Schizymeniaceae). Daarom kunnen zij een uitgelezen groep zijn om biogeografische vragen te beantwoorden vanuit een gecombineerde moleculair-anatomische invalshoek. De graad van genetische divergentie tussen specimens van wijdverspreide soorten (b.v. *Predaea weldii*) uit verschillende gebieden van de Indo-Pacific kan gebruikt worden om de biogeografische verbanden te kwantificeren. De families Nemastomataceae en Schizymeniaceae werden recent gescheiden op basis van verschillen in post-fertilisatiegebeurtenissen. Bijkomende moleculaire studies naar andere genera van deze families kunnen een inzicht bieden in hun fylogenie. Aanvullend hierbij kan de status van de huidige morfologisch gedefinieerde soorten geëvalueerd worden aan de hand van hun genetische informatie (b.v. de opheldering van de soortendiversiteit binnen enigmatische genera zoals *Titanophora*), aangezien vertegenwoordigers van deze families tot op heden ontoereikend geïncludeerd werden in moleculaire studies. Om het belang van vicariantiegebeurtenissen ten opzichte van de mogelijkheden tot lange-afstandsverbreiding voor disjuncte Arabische Zee taxa vast te stellen, kan de moleculaire analyse van de twee *Reticulocaulis* soorten uit Arabië en *R. mucosissimus* uit Hawaï zulke onderliggende fylogeografieën ophelderen. Aanvullende sequenties van de twee andere Naccariaceae genera, *Naccaria* en *Atractophora*, en het waarschijnlijk verwante genus *Liagorothamnion* kunnen nieuwe argumenten bieden voor hun plaatsing op ordeniveau en hun onderverdeling in de verschillende families (zie *hoofdstuk 3*). Besluitend kunnen we stellen dat een holistische benadering van moleculaire, biogeografische en anatomische studies naar deze gelatineuze roodwieren een eenduidig soortsconcept kan opleveren. Idealiter zullen de onderzochte Arabische Zee taxa dan als een model voor deze roodwierfamilies kunnen fungeren.

In hoofdstuk 4 wordt een nieuwe Rhodymeniales soort, *Chamaebotrys erectus*, afkomstig van de Socotra Archipel beschreven. *Chamaebotrys* werd recent beschreven door Huisman (1996) op basis van reproductieve kenmerken, namelijk de terminale tetrasporocysten in nemathecium sori. De opmerkelijke eigenschappen die *C. erectus* onderscheiden van beide andere *Chamaebotrys*-soorten zijn de grote, rechtopstaande thallus en de *in situ* (vastgehecht aan de tetrasporofyt) kieming van de tetrasporen tot gametofyten. Naast de samengestelde tetrasporofyt- en carposporofytthallus, zijn er ook vrijlevende gametofyten aangetroffen. De uitzonderlijke grootte, in vergelijking met de andere vertegenwoordigers van het genus, staat waarschijnlijk in verband met de opwelling van koud, nutriëntenrijk water aangezien de soort enkel ter hoogte van de zuidkust van Socotra ingezameld werd. *Champia gigantea* is een gelijkaardige Rhodymenialessoort: een endeem van de Arabische Zee, gekenmerkt door een opmerkelijk grote thallus. In de bespreking van *C. erectus* wordt de eerst geobserveerde carpogoniumtak van het genus beschreven. Deze ondersteunt de nauwe verwantschap met *Coelarthrum* en de plaatsing van het genus in de Rhodymeniaceae.

Het laatste taxonomisch deel (*hoofdstuk 5*) behandelt het wier *Izziella orientalis*, een wijdverspreide soort in de (sub)tropische Indo-Pacific. De revalorisatie van het genus *Izziella* is gebaseerd op *Liagora orientalis*. Abbott (1990) beschouwde de aan haar opgedragen soort, *Izziella abbottiae*, als synoniem van *L. orientalis*. Tijdens het screenen van de Liagoraceae (Nemaliales) van de Arabische Zee kon *L. orientalis* duidelijk onderscheiden worden van andere Liagoraceae genera. Dit gebeurde op basis van de gecombineerde kenmerken van de carpogoniumtak, het cystocarp en het grote ondersteunend complex van versmolten cellen, wat de heroprichting van het genus *Izziella* verantwoordde. In navolging van de beschrijving van *Ganonema* (Huisman & Kraft 1994), vormt de heroprichting van het genus *Izziella* een tweede stap in het opsplitsen van het genus *Liagora* in meerdere genera. Dit lijkt ook logisch omdat het genus momenteel vele taxa omvat met een grote verscheidenheid in morfologie en cystocarptypes (Kraft 1989; Huisman & Kraft 1994).

Deze taxonomische studies naar de Rhodophyceae van de Arabische Zee onderschrijven vroegere anecdotische waarnemingen (Børgesen 1934; Wynne 2000) van de biogeografische affiniteit met ver afgelegen gebieden (Australië, Hawaï, Japan, Zuid-Afrika). De studie naar de macrowieren van de Socotra Archipel vergroot het verspreidingsgebied van deze disjunct verspreide soorten aanzienlijk. Persoonlijke waarnemingen (T. Schils) in de loop van deze studie bevestigen deze bevindingen. De Delesseriaceae van het bestudeerde gebied vormen hier een goed voorbeeld van. Het voorlopige aantal soorten Delesseriaceae voor Jemen en Oman bedraagt 15. Deze vormen een sympatrische flora bestaande uit typisch Oost-Afrikaanse wieren (*Duckerella ferlusii*); bepaalde Zuidoost-Aziatische en Pacifische wieren (*Zellera tawallina*); en algemene Indo-Pacifische wieren, inclusief enkele zeldzame Indische Oceaansoorten (*Chauviniella coriifolia* en *C. jadinii*). Gelijkaardig aan *Chamaebotrys erectus* zijn er uitzonderlijk grote Delesseriaceae endemen, *Cryptopleura robusta* M.J. Wynne en *Pseudogrinnellia barrattiae* M.J. Wynne, beschreven voor Oman (Wynne 1999a, b). De gemengde verspreidingspatronen van de Delesseriaceae flora en hun opvallend fraai uitzicht (gemakkelijk waar te nemen op het terrein) maken deze wieren uitgelezen studieobjecten om volledige soortenlijsten van deze groep op te stellen en aan de hand hiervan nauwkeurige biogeografische analysen uit te voeren. *Sympodothamnion* is een ander opmerkelijk genus van de Ceramiales dat ingezameld werd rond de Socotra Archipel. Dit monospecifieke genus was enkel gekend voor zuidelijk Japan. Naast de biogeografische aspecten, zijn de soortsidentiteit en de plaatsing op familieniveau boeiend. Het genus werd oorspronkelijk ondergebracht in de Dasyaceae (Itono 1977) maar de huidige consensus is dat het tot de Ceramiaceae behoort (Athanasiadis 1996; de Jong *et al.* 1997). De observaties van de Socotra specimens duiden evenwel op een plaatsing in de Rhodomelaceae. Andere Rhodomelaceae taxa die actueel van biogeografisch belang zijn behoren tot de Amansieae (Masuda & Abe 2002; N'Yeurt 2002). Onze inzamelingen includeren vier soorten van deze tribus. Cornilly (2002) bestudeerde deze specimens, aangevuld met een obscure endeem van Jemen, *Amansia arabica* J. Agardh ex Newton *nom. inval.* De veronderstelde fytogeografische scheiding van *Amansia*- en *Melanamansia*-soorten (Norris 1995) in de Indo-Pacific (uitgezonderd Zuid-Afrika) is niet van toepassing in de Arabische Zee. Dit stemt overeen met recente waarnemingen van hun gemeenschappelijk voorkomen in andere gebieden van de Indo-Pacific (South & Skelton 1999; Masuda *et al.* 2000). Ook deze wiergroep omvat zowel algemene soorten [*Amansia rhodantha* en *Osmundaria melvillii* (J. Agardh) R.E. Norris] als disjunct verspreide soorten [*Neurymenia nigricans* T. Tanaka & Itono: Natal (Zuid-Afrika), Socotra (Jemen) en zuidelijk Japan; *Melanamansia daemelii* (Sonder) R.E. Norris: Hawaï, Masirah (Oman), Queensland (Australië) en Socotra (Jemen)]. De endeem *Amansia arabica*, eveneens gekenmerkt door grote afmetingen, zal hoogstwaarschijnlijk in het genus *Melanamansia* geplaatst moeten worden. In de toekomst kunnen de hierboven besproken vertegenwoordigers van de Ceramiales belangrijk blijken in studies met DNA merkers en moleculaire kloktoepassingen. Die zouden een inzicht kunnen bieden in de fylogeografische patronen (genetische voorgeschiedenis en genenuitwisseling) en de belangrijke vicariantiegebeurtenissen (divergentiesnelheden) van de macrowieren in de Arabische Zee. Recente cryptische introducties, die deze patronen kunnen vervagen, worden verondersteld van minimaal belang te zijn aangezien (i) het aantal havens in de Arabische Zee beperkt is, (ii) de onderzochte subtidale roodwieren minder geschikt zijn voor antropogene verspreiding en (iii) ze minder succesvol zijn in de daaropvolgende vestiging. De eerste moleculaire klok (Zuccarello & West 2002) en fylogeografische studies (Zuccarello *et al.* 2002) naar de Ceramiales leverden reeds interessante en onverwachte resultaten op.

Ecologie en biogeografie op gemeenschapsniveau

De analyse van de infralitorale opnamegegevens van de Socotra Archipel resulteerde in duidelijk verschillende plantengemeenschappen, overeenstemmend met hun geografische positie in de archipel (*hoofdstuk 6*). In tegenstelling tot het focussen op bepaalde taxa met een bijzonder verspreidingspatroon (zie *Biogeografie op soortsniveau*), wordt hier de biogeografische affiniteit van alle samenstellende soorten van een gemeenschap nagegaan. De twee contrasterende wiergemeenschappen van het hoofdeiland zijn deze van de noord- en de zuidkust. Het zijn beide goed ontwikkelde wiergemeenschappen (geen significant verschil in soortenrijkdom, biomassa en alfa-diversiteit van de kwadraten) die evenwel verschillen in hun soortensamenstelling (beta-diversiteitsindices). De biogeografische affiniteiten, weergegeven door de Simpson coëfficiënt, van beide gemeenschappen zijn ook anders (*hoofdstuk 6*). De zuidkust van Socotra vertoont een lagere algemene affiniteit met de Indische Oceaanflora in vergelijking met deze van de noordkust. Algemeen kan gesteld worden dat de biogeografische affiniteit van de wiergemeenschappen rond Socotra met de Indische Oceaanflora stijgt van een minimum in zuidelijk Afrika tot een maximum ter hoogte van de tropische kusten van Kenia en Tanzania. Die affiniteit daalt dan weer ter hoogte van de Arabische Zee naar een minimum voor Iran en Pakistan (wellicht een artefact door de schaarse bemonstering). Daarna blijft de affiniteit in de oostelijke Indische Oceaan tamelijk constant en laag. Naast de noord- en zuidkust, werden vier bijkomende plantengemeenschappen geïdentificeerd. Het oostelijke uiteinde van het eiland Socotra herbergt gemeenschappen met elementen van beide voornoemde entiteiten, evenwel met een merkelijk hogere affiniteit voor de flora van de zuidkust. De gemengde gemeenschap van deze overgangszone bevat de meest soortenrijke en diverse kwadraten van de archipel, voornamelijk wegens de bijzondere roodwierflora. De intense en complexe stromingspatronen rond dit oostelijk uiteinde reguleren de temperatuur en zorgen voor een constante nutriëntenaanvoer, twee gunstige factoren die wiergroei bevorderen. De biogeografische affiniteit van de overgangszone is intermediair tussen deze van de noord- en de zuidkust. De wiervegetaties van de omringende eilandjes zijn onderhevig aan grote fluctuaties in fosfaatconcentratie en temperatuur, een gevolg van het beperkte kustgebied en de drastische veranderingen in de omgevende stromingspatronen. De soortensamenstelling van deze gemeenschap is het meest gelijkaardig aan dat van Socotra's zuidkust en de biogeografische affiniteiten zijn gelijkaardig aan die van andere gemeenschappen, maar verschillend voor elk van de drie hoofdregio's binnen de Indische Oceaan (Oost-Afrikaanse kust, Arabische Zee en de oostelijke Indische Oceaan). De laatste twee gemeenschappen, de zeegrasvelden van de Qalansiyah lagune en de koraal-gedomineerde gemeenschap van de noordkust, zijn essentieel verschillend in soortenrijkdom, diversiteit en biomassa van de vorige vier gemeenschappen. De soortensamenstelling van deze plantengemeenschappen vertoont echter wel verbanden met de noordkust. Beide gemeenschappen kunnen beschouwd worden als sub-entiteiten van de noordkust. Deze habitats worden door uitzonderlijke milieuomstandigheden beïnvloed (zoals hoog zoutgehalte, hoge temperatuur en zandbedekking) alsook door biotische competitie (voornamelijk met koralen). Deze veroorzaken een verarmde floristische soortenrijkdom en een lage floristische diversiteit. De biomassa's (versgewicht per vegetatieopname) van deze twee sub-entiteiten variëren van de laagste (koraal-gedomineerde gemeenschap) tot de hoogste waarden (zeegrasvelden) voor de Socotra Archipel. Vanuit algologisch standpunt zijn Socotra's zuidkust, de overgangszone en de omringende eilanden, gebieden met een unieke infralitorale flora in de Indische Oceaan. Zij worden gekenmerkt door een hoge soortenrijkdom en een hoge diversiteit. Het ontstaan van deze unieke gemeenschappen is nauw verbonden met de invloed van de kustgebonden opwelling in de Arabische Zee. Het is van cruciaal belang dat toekomstige bestemmings- en ontwikkelingsplannen voor de Socotra Archipel delen van deze exclusieve mariene gemeenschappen aanduiden als beschermde gebieden en ze opvolgen in een monitoringsprogramma. De noordkust van Socotra, inclusief de koraal-gedomineerde gemeenschappen en de zeegrasvelden, huisvest enerzijds algemene Indische Oceaanwieren, maar anderzijds ook unieke faunagemeenschappen en gebieden die belangrijk zijn als kraamkamers van mariene fauna. De groepen van mariene organismen die een hoge graad van endemisme en allopatrie vertonen zijn essentieel verschillend voor de contrasterende kustgebieden. De faunistische samenstelling van de noordelijke gemeenschappen is uniek voor de regio, terwijl de zuidelijke gemeenschappen gekenmerkt worden door een bijzondere wierflora. Het fenomeen van opwelling is zowel voor de warm- (noordkusten) als koudwaterbiota (zuidkusten) de verbreidingsbarrière in dit noordelijk deel van de Indische Oceaan.

In een tweede ecologisch luik (*hoofdstuk 7*) worden de infralitorale vegetaties van de Socotra Archipel en het eiland Masirah geanalyseerd aan de hand van volledige soortenlijsten voor de verschillende bemonsteringsplaatsen. De ordinatieresultaten van de soortenlijsten hebben een lagere resolutie in vergelijking met deze van de vegetatieopnames van Socotra. Bepaalde gemeenschappen (overgangszone en omringende eilanden) worden namelijk niet afzonderlijk geïdentificeerd en zitten vervat in andere gemeenschappen (noord- en zuidkust van Socotra). De ordinatieverwerking toont zes plantengemeenschappen aan. Vergelijkbare gemeenschappen van Socotra en Masirah worden gegroepeerd in grotere eenheden (vier biotopen), gebaseerd op ordinatieresultaten, de driedelige similariteitsindex en overeenstemmende biogeografische affiniteiten (gebruikmakend van zowel soorts- als genuswaarnemingen). De milieuomstandigheden en de indicatorsoorten die deze gemeenschappen en biotopen kenmerken worden besproken. De gecombineerde interpretatie van de ordinatie met milieuparameters (voornamelijk chlorofyl a) en de biogeografische analysen wijst er op dat het effect van opwelling groter is voor Masirah. Dit wordt weerpiegeld in wiergemeenschappen die meer gedivergeerd zijn van de Oost-Afrikaanse flora. Alle bestudeerde gemeenschappen vertonen nochtans een uitgesproken fytogeografische affiniteit met de Oost-Afrikaanse kust. Een overzicht hiervan wordt gegeven in de Principale Componenten Analyse (hierna PCA) van de wierverspreidingspatronen (landen van de Indische Oceaan) voor de soortenlijsten van Socotra en Masirah (Fig. 1). De bijzonder hoge eigenwaarde van de eerste as (0,827) wijst er op dat de scheiding van landen volgens deze as veruit de belangrijkste component in de analyse is. De soortenlijsten van Masirah en Socotra (punten in Fig. 1) vertonen een hoge affiniteit met de (sub)tropische landen van Oost-Afrika, West-Australië, Sri Lanka en de oostkust van Zuid-Afrika. De biogeografische affiniteit met andere landen en eilanden van het oostelijk en centrale deel van de Indische Oceaan is merkelijk lager. De PCA geeft drie aparte groepen van staalnameplaatsen weer (Fig. 1). Cluster A omvat de bemonsteringsplaatsen met een hoge biogeografische affiniteit voor de Oost-Afrikaanse kust, die behoren tot de volgende gemeenschappen (afkortingen: zie *hoofdstuk 7*): MAS WC, S&O NC, SOC NC en SOC SG. Cluster B groepeert beschutte sites, ook samengesteld uit gemeenschappen (delen van MAS SG en S&O SC) met een hoge affiniteit voor de Oost-Afrikaanse flora. Cluster C (MAS EC en S&O SC) wordt gescheiden van de clusters A en B volgens de tweede as. De lage eigenwaarde van deze as, een bijdrage van slechts 4,2 % aan de totale variatie in de soortensamenstelling, laat zien dat behalve de sterke gelijkenissen met Oost-Afrika, een beperkt aantal soorten een speciale affiniteit vertonen met lokale (b.v. Pakistan en Somalië) en verafgelegen (b.v. West-Australië en Zuid-Afrika) koud-gematigde flora's.

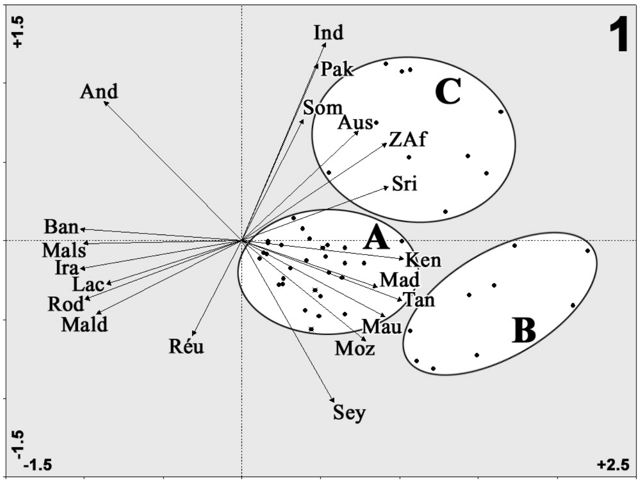

Fig. 1. Principale Componenten Analyse van de wierverspreiding in de Indische Oceaan gebaseerd op de soortenlijsten van de verschillende staalnameplaatsen. De Indische Oceaanverspreiding van elke soort van een bepaalde bemonsteringsplaats werd geregistreerd, waarna de soortswaarnemingen per land opgeteld werden voor elke site. De bemonsteringsplaatsen vormden de "sample input" en de Indische Oceaanlanden werden gebruikt als de "species input". De geïncludeerde landen zijn: Zuid-Afrika (ZAf), Mozambique (Moz), Madagaskar (Mad), Réunion (Réu), Mauritius (Mau), Rodrigues (Rod), Tanzania (Tan), Seychellen (Sey), Kenia (Ken), Somalië (Som), Iran (Ira), Pakistan (Pak), Laccadive eilanden (Lac), Malediven (Mald), Sri Lanka (Sri), Bangladesh (Ban), Andaman eilanden (And), Maleisië (Mals), Indonesië (Ind), West-Australië (Aus). Er worden drie groepen van staalnameplaatsen onderscheiden, namelijk de clusters A, B en C. De eigenwaarden van de eerste twee assen zijn respectievelijk 0,827 en 0,042.

Sheppard *et al.* (1992) verwachten dat de verspreidingspatronen van de meeste soorten in de Arabische Zeeën (bestaande uit de Rode Zee, Golf van Aden, Arabische Zee, Golf van Oman en de Perzische Golf) niets meer dan kansverdelingen zijn en dat het gehele gebied één biogeografische subregio vormt. Behoudens enkele uitzonderingen (b.v. de hoge graad van endemisme onder de vlindervissen), veronderstellen Sheppard *et al.* (1992) dat de biogeografische patronen een gevolg zijn van de geringe verbreidingstijd sinds het begin van het Holoceen en het onvolledig mengen van fauna doorheen de geschikte habitats van de Indische Oceaan. Deze auteurs merken ook op dat de onderverdeling van de Arabische Zeeën in kleinere biogeografische eenheden mogelijk is voor bepaalde visgroepen, maar voor andere organismen, en in het bijzonder de planten, is er volgens hen geen aanleiding tot een indeling onder het niveau van een biogeografische provincie. Diverse analysetechnieken (*hoofdstukken 6, 7*) duiden nochtans op afzonderlijke plantengemeenschappen en plantenbiotopen in overeenstemming met de verschillen in milieuparameters. De door opwelling beïnvloede gemeenschappen zijn hiervan het meest typerend voor de unieke Arabische Zeeflora. Bepaalde soorten van deze gemeenschappen vertonen disjuncte verspreidingspatronen doorheen de Indo-Pacific en zijn waarschijnlijk ook van biogeografisch belang binnen de Arabische regio. Dit, in combinatie met het toenemend aantal beschreven wier-endemen, doet ons besluiten dat de Arabische Zee een fytogeografische (sub)provincie vertegenwoordigt in de Indo-Pacific en de Arabische regio. Toekomstig terreinwerk in de noordelijke Arabische Zee (Al Qad, Oman) kan het onderzoeksgebied aanzienlijk verruimen om biogeografische (dis)continuïteiten aan de grens van de Arabische Zee met de Golf van Oman vast te stellen. De belangrijke vraagstellingen zijn: (i) de graad van divergentie met betrekking tot de Oost-Afrikaanse flora, (ii) de impact van opwelling op deze gemeenschappen, (iii) het gebruik van deze lokatie in een geografische gradiënt, van de Arabische Zee over de Golf van Oman naar de Perzische Golf, om het verloop in wiersoorten te toetsen aan de afname in substraatbeschikbaarheid (sedimentkusten als biogeografische barrière). Recent werden de eerste temperatuurrecorders geplaatst rond Masirah (Wilson 1999) om accurate kustwatergegevens te bekomen op een gedetailleerde temporele en ruimtelijke schaal. Deze nauwkeurige gegevens zijn noodzakelijk om de relatie tussen milieuparameters en biotische interacties (b.v. de competitie tussen wieren en koralen) te kunnen begrijpen.

Seizoenaliteit

Nizamuddinia zanardinii is een groot bruinwier (Fucales) endemisch voor de opwellingsgebieden van de Arabische Zee. In de eerste vermelding van het wier voor de Socotra Archipel, merkt Kemp (1998) op dat er verschillen in seizoenale groei bestaan tussen de populaties van Socotra en deze van zuidelijk Arabië. Twee hypothesen werden geopperd: (i) een temporele verschuiving in de groeicyclus (tot zes maanden) van *N. zanardinii* rond Socotra in vergelijking met de populaties van het vasteland, of (ii) twee (re)productieve pieken voor dit wier ter hoogte van Socotra, in tegenstelling tot één voor deze van zuidelijk Arabië. Hoewel initieel vooropgesteld, waren langere periodes van terreinwerk in functie van een seizoenaliteitsonderzoek niet mogelijk ten gevolge van praktische problemen (zie *hoofdstuk 1*). Toch leverden de waarnemingen van de eerste drie veldwerkperiodes enig inzicht in de seizoenale groeipatronen van deze sleutelsoort. Het gelijktijdig voorkomen van zowel volgroeide, fertiele *N. zanardinii* specimens in de intertidale rotspoeltjes van Masirah als onontwikkelde, kleine rozetten ter hoogte van Barr al-Hikman, blijkt er op te wijzen dat de (re)productieve periodes kunnen fluctueren binnen een specifiek geografisch gebied, afhankelijk van het habitat en/of de zonatie van voorkomen. Gelijkaardige verschillen werden waargenomen voor de Socotra Archipel: terwijl Kemp (1998) de reproductieve assen opmerkte in februari-maart 1996 en Leliaert (2000) in januari-februari 1999, werden er enkel kleine thalli geobserveerd tijdens het terreinwerk in maart-mei 2000. Dit doet vermoeden dat er twee reproductieve periodes bestaan (cf. Hadramoutkust in Jemen, Ormond & Banaimoon 1994), gerelateerd aan de twee opwellingsperiodes, met temporele (jaarlijkse) en lokale fluctuaties. Hierbij wordt er van uitgegaan dat de (re)productieve respons van de *Nizamuddinia*-populaties van Jemen en Oman groter is gedurende de zuidwest- dan tijdens de noordoostmoesson.

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