Front cover: *Platoma heteromorphum* (Gigartinales, Rhodophyta); a gelatinous red alga of the Arabian Sea (see Schils & Coppejans, p. 254).
Gelatinous red algae of the Arabian Sea, including Platoma heteromorphum sp. nov. (Gigartinales, Rhodophyta)

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INTRODUCTION

The study of the benthic marine algal flora of the Arabian Sea started with Borgesen (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 & Banaioon 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). Predreae fedmannii Borgesen 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 microscopic 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).


Plants are bright red 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 second 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 carposporangia reach a diameter of 9.5–17 μm.

REMARKS: Of the 17 currently recognized *Dudresnaya* P. Crouan & H. Crouan species (Robins & Kraft 1985; Searles & Ballantine 1986; Kajimura 1993, 1994; Tabares et al. 1997; Afonso-Carrillo et al. 2002), *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* because of 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.
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"E), 1 May 2000, subtidal: ~19.4 m, leg. T. Schils (SMM 496, SMM 497). Tanzania: Ruvula Beach (Mnazi Bay, Mtwarra 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, Mtwarra 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 study).

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 pseudiodotchomous 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 hydropogous cell, which initiates a carpogonium by an oblique division. The occurrence of two carpogonia on a single carpogynous cell, which initiates a carpogonium by an oblique division, is scarcely ever observed (Fig. 6). Auxiliary-cell filaments (6–12 cells long) with an enlarged subterminal hydropogous cell are flanked by two enlarged, deeply staining cells. The occurrence of two carpogonia on a single carpogynous cell, which initiates a carpogonium by an oblique division, is scarcely ever observed (Fig. 6). Auxiliary-cell filaments (6–12 cells long) with an enlarged subterminal hydropogous cell are flanked by two enlarged, deeply staining cells.

The supporting cell (sc) bears two subsidiary auxiliary cells (sac). Slide MAS 139x. Scale bar = 25 μm.

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.

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

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connecting filaments directly. Generative auxiliary cells are formed in an intercalary position in separate cortical filaments and are characterized by their obpyriform shape (6.5–9.5 μm × 6–10 μm). Two gonimoblasts are formed, which mature sequentially and produce angular carpogonial branches (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’a Zzarri (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, 6–8 m, leg. T. Schils (MAS 137) (holotype).

Remark: Platoma heteromorphum fits the generic definitions of female reproductive structures and post-fertilization events presented by Masuda & Guiry (1994). The presence of gland cells and subsidiary auxiliary cells, together with various morphological features (Kajimura 1997; Kraft & Abbott 1997; Norris & Bucher 1977) 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 Schouboe ex De Toni and P. tenue Howe & Taylor. Its morphology and especially the post-fertilization events (Table 1) differ from the well-documented (Itô 1984; Kajimura 1997) Japanese species, P. izunosimense. In that species, the fertilized carpogonium does not divide into 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 with 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 lateral 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 post-fertilization 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

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<table>
<thead>
<tr>
<th>Feature</th>
<th><em>P. ardreanum</em></th>
<th><em>P. cyclocolpum</em></th>
<th><em>P. heteromorphum</em></th>
<th><em>P. izunosimense</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Branching pattern</td>
<td>broadly lobed, with deep incisions</td>
<td>irregular with rounded bifurcations at the apices, nonundulate</td>
<td>irregularly lobed</td>
<td>irregularly pinnate, often with forked branch apices, also palpate or irregular; surfaces undulate</td>
</tr>
<tr>
<td>Thallus shape</td>
<td>foliose with apparent calloses, blunt lobes and dentate to narrowly proliferous margins or ruffles</td>
<td>foliose to subcylindrical, with marginal proliferations</td>
<td>foliose to subcylindrical, with no calloses, no blade ruffling, but occasionally with proliferations</td>
<td>foliose, with or without proliferations</td>
</tr>
<tr>
<td>Thallus colour</td>
<td>deep reddish-brown</td>
<td>light pink to reddish-brown</td>
<td>deep red to bright red</td>
<td>reddish-brown to pinkish-red</td>
</tr>
<tr>
<td>Stipe</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Intercalary gland cells</td>
<td>present three (to four)–celled</td>
<td>present three-celled</td>
<td>occasionally present</td>
<td>probably absent</td>
</tr>
<tr>
<td>Carpogonial branch</td>
<td>present</td>
<td>possibly absent</td>
<td>occasionally present</td>
<td>no</td>
</tr>
<tr>
<td>Sterile cells on carpogonial branch</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Division of fertilized carpogonium</td>
<td>one of the two contacted subsidiary auxiliary cells</td>
<td>one or both diploidized subsidiary auxiliary cells and a cortical cell distal to one of them</td>
<td>one of the two contacted subsidiary auxiliary cells and the cortical cell distal to it</td>
<td>one or both diploidized subsidiary auxiliary cells and a cortical cell distal to one of them</td>
</tr>
<tr>
<td>Origin of connecting filament initiation</td>
<td>?; direct fusion without division is observed</td>
<td>secondary (Fig. 23) and tertiary gonimoblast</td>
<td>Oman (Arabian Sea)</td>
<td>no</td>
</tr>
<tr>
<td>Distribution</td>
<td>Hawaiian Islands</td>
<td>Caribbean, Mediterranean, north-eastern Atlantic, Western Australia</td>
<td>Arabian Sea</td>
<td>southern Japan</td>
</tr>
</tbody>
</table>

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 post-fertilization 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.

**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 study).

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 intercalar 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 these 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 four 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 gonimoblast initial (Fig. 21). The resulting gonimoblast cells divide profusely and initiate a large subspherical primary gonimoblast (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 gonimoblasts (Fig. 26) are initiated sequentially, lateral to the first gonimoblast. 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 gonimoblast (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). Because *P. laciniosa* would have priority over *P. tokidae* if the two species were combined, and because 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.

***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′30″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′37″E), 8 November 1999, subtidal, 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 el al., 1996; Ballantine & Aponte 1997; Huismans 1997; Phillips 1997; Abbott 1999; Coppejans & Millar 2000; Huismans 2000; De Clerck et al. 2002; this study).

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. The medullary filaments’ size varies in the range 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); the conical carpogonium has a blunt distal (4.5–7 μm), the hypogynous cell subspherical (5.5–9 μm), the hypocarpogonium has a slightly blunter distal (9.5–13 μm) and 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 [one to four tiers, each consisting of one to two (to three) 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 first divides 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.

**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 vs 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).

**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′39″E), 12 March 1999, subtidal: − 6 m,

**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.
Figs 32–35. Predaea weldii.
Fig. 32. A diploidized auxiliary cell (aux) with (laterally) an incoming connecting filament (icf). 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.

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
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.
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 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 three to five 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. Mature carposporangia are subspherical to ellipsoidal and measure 12–45 μm in diameter.

REMARKS: Differences in habit were the main characteristics described earlier in this article. Among these species, 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 Tit. 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 post-fertilization events in Titanophora species (Masuda & Guiry 1994). The Socotran plants fitted both species descriptions and the specimens were identified as Tit. pikeana, which is the earlier name. Additionally, the specimens agree with the description of Tit. 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’ (1992) point of view on the conspecificity of Tit. 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 characteristics described earlier in this article could be observed among the Titanophora plants of Socotra and South Africa. Because of 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 (vs separated filaments) and hence the difference in carpogonial branch organization compared with the observations of Mshigeni & Papenfuss (1980).

Our account of post-fertilization 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 earlier discussion on Platoma heteromorphum in this article), probably as a consequence of the fact that the carpogonial complex we observed was in an early post-fertilization stage. In addition, the diploidization events differed for both subsidiary auxiliary cells. The fertilized carpogonium in Tit. 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 post-fertilization 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, *Gibbsmitthia 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 (T. Schils, O. De Clerck & E. Coppejans, 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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