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

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

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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.

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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

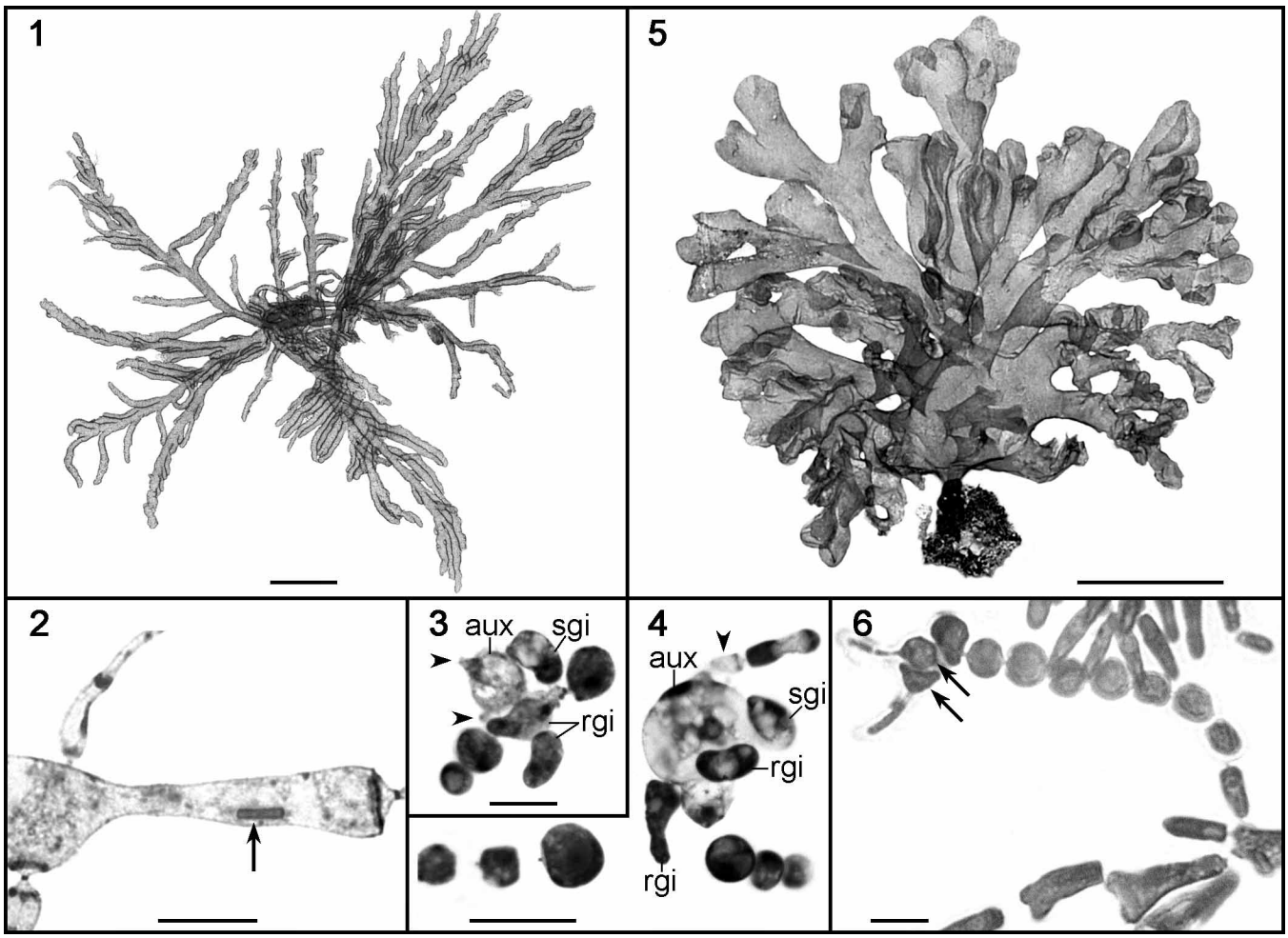
Dudresnaya capricornica Robins & Kraft 1985, p. 23 (Dumontiaceae)

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 study].

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 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.



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. 2 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.

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. 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″), 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 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 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 re-collected 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 four to eight 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

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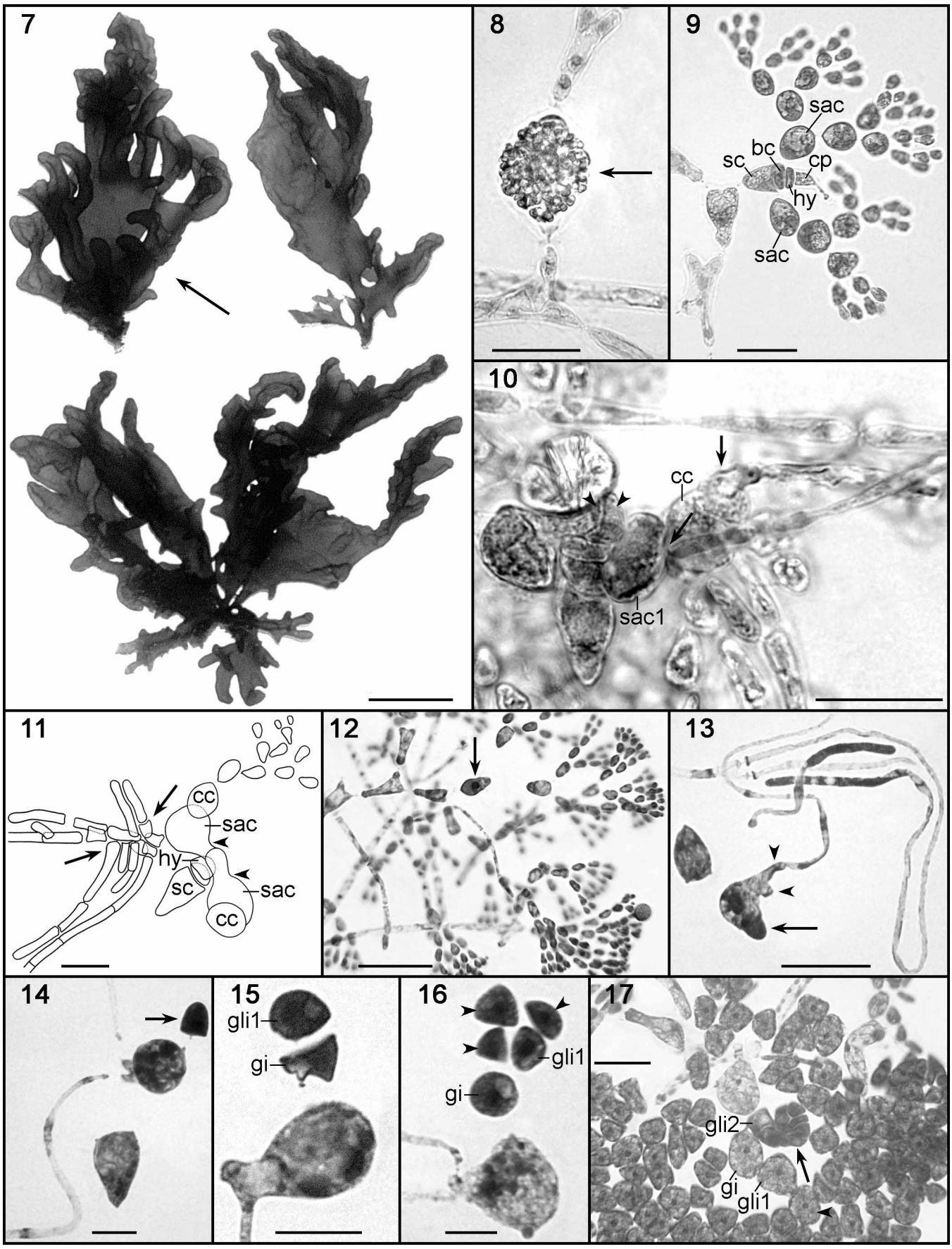
Figs 7–17. *Platoma heteromorphum.*
Fig. 7. Habit of female gametophytes, including the holotype (arrow), MAS 139. Scale bar = 2 cm.
Fig. 8. Large intercalary gland cell (arrow) in the inner cortex. Slide MAS 139x. Scale bar = 25 μm.
Fig. 9. A three-celled carpogonial branch consisting of an oval basal 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.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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 (16–21 μm × 11–13 μm) and deep staining with Aniline Blue. 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.

The moniliform outer cortex consists of discrete, dichotomous branch systems that are four to eight cells long with blunt apices. The inner cortical cells are elongate and include X- [cf. *Platoma 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 the inner gonimoblast cells are discernible as large globose cells (17–22 μm in diameter; Fig. 17) in the mature non-ostiolate 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 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* Schousboe *ex* De Toni and *P. tenue* Howe & Taylor. Its morphology and especially the post-fertilization 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 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 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 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

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, nonundulate	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	three (to four)–celled	three-celled	three-celled	three-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

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

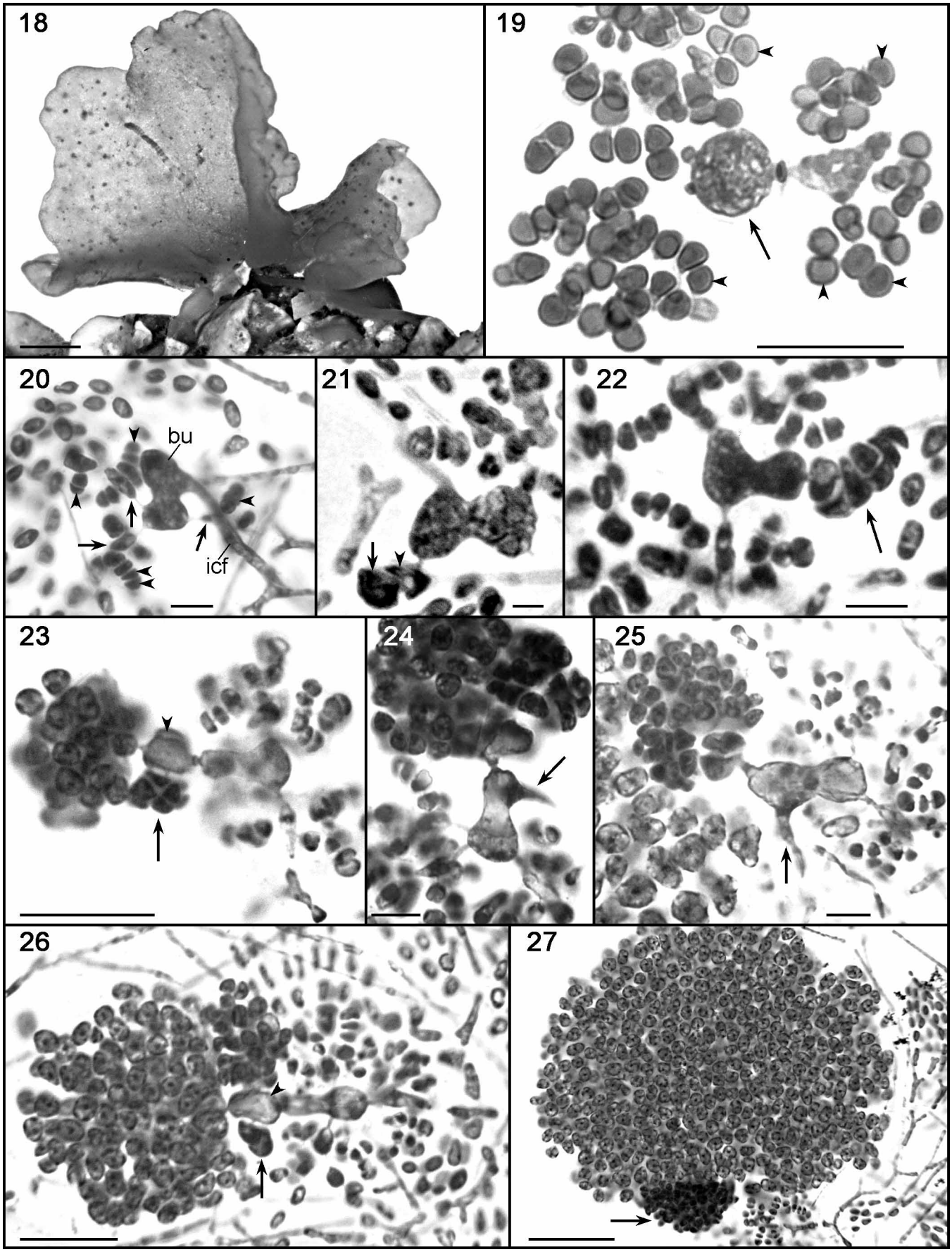
SPECIMENS EXAMINED: **Oman**: Masirah Island, in between Ra's Abu Rasas and Ra's Zarri (site 25), 22 November 1999, subtidal: − 11 m, leg. T. Schils (MAS 530). **Yemen**: Darsa Island, south coast (ALG-21: 12°06′36″N, 53°17′48″E), 8 April 2000, subtidal: − 21 m, leg. T. Schils (SMM 209). Rocky platform 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 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 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 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). 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),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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′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.* 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 × 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 [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′59″E), 12 March 1999, subtidal: − 6 m,

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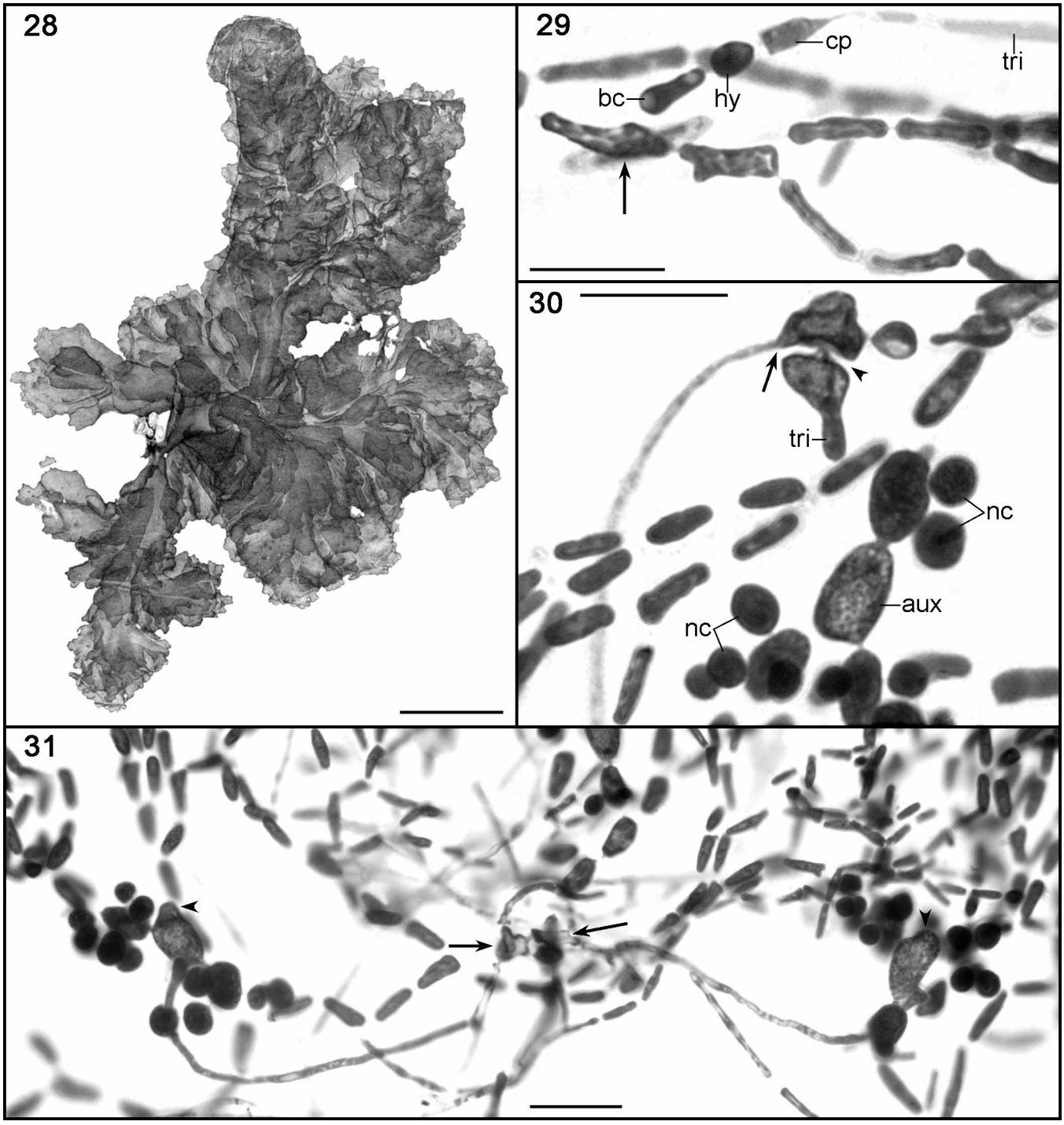
Figs 18–27. *Predaea laciniosa.*
Fig. 18. Habit of a female gametophyte, MAS 530. Scale bar = 1 mm.
Fig. 19. Nutritive cells (arrowheads) and an undiploidized generative auxiliary cell (arrow) in an intercalary position in a cortical filament. Slide SMM 209b. Scale bar = 25 μm.
Fig. 20. Diploidized auxiliary 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.
Figs 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.



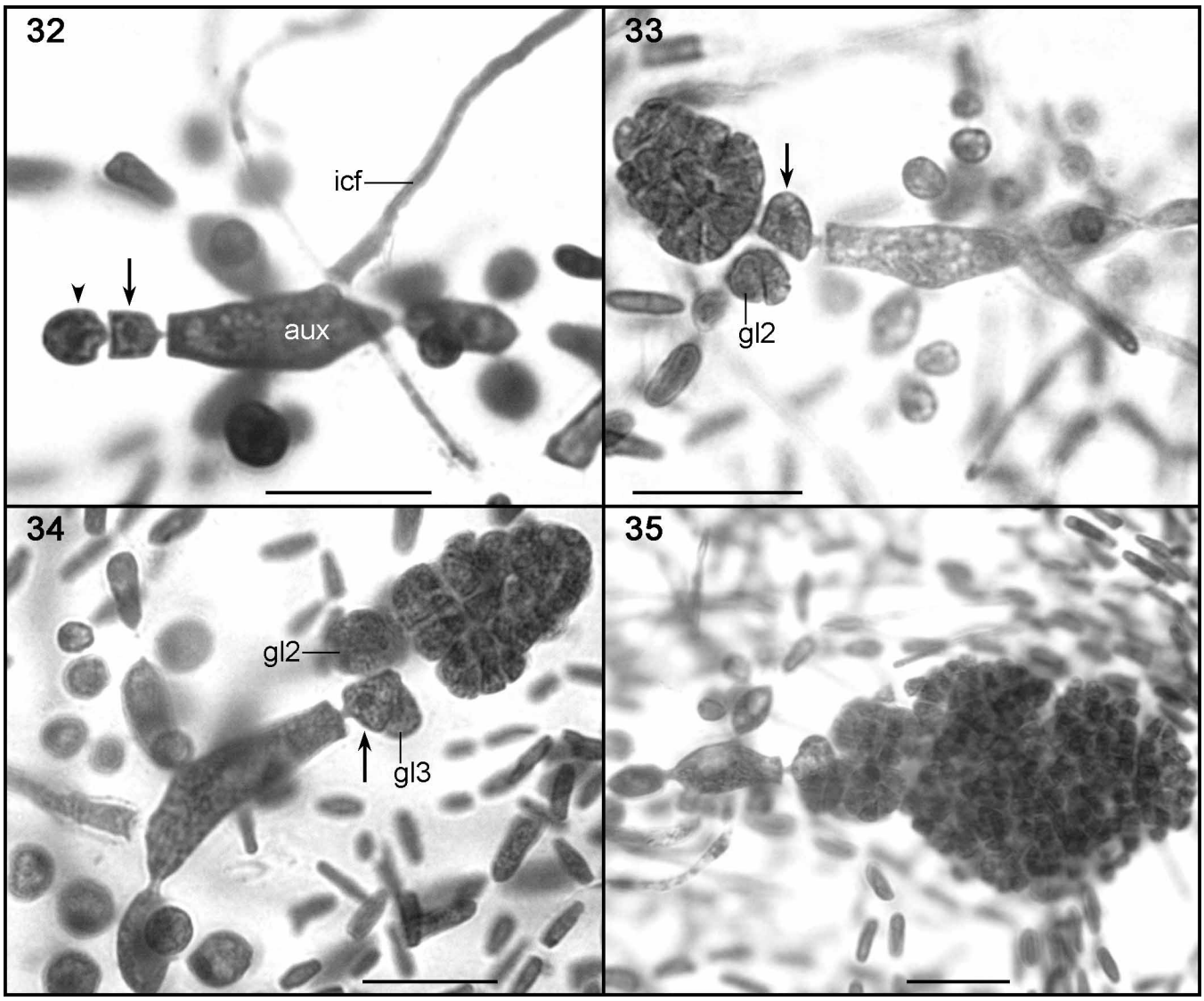
Figs 28–31. *Predaea weldii.*

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.



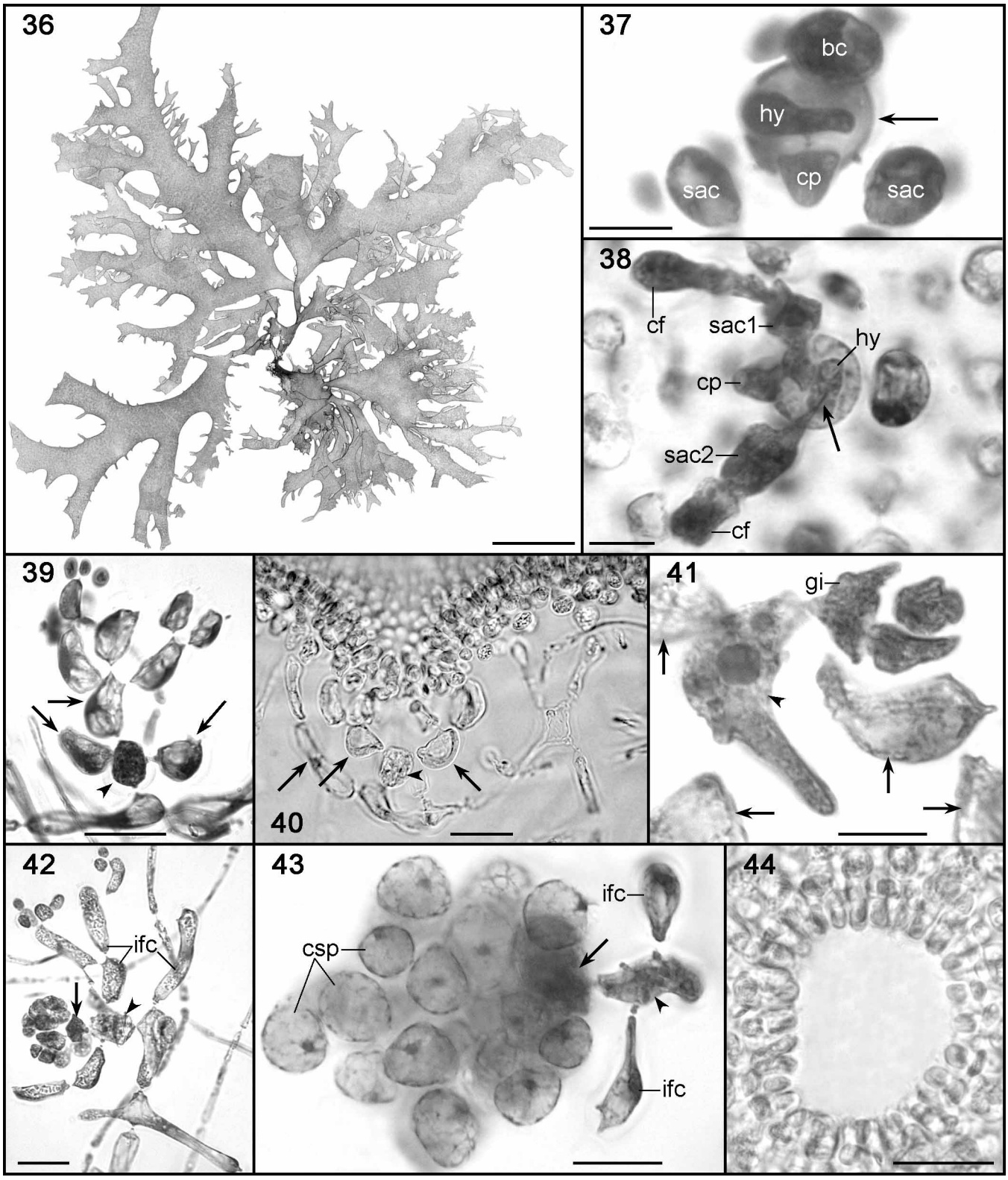
Figs 32–35. *Predaea weldii.*
Fig. 32. A diploidized auxiliary cell (aux) with (laterally) an incoming connecting filament (icf). Two subsequent transverse divisions of the diploidized auxiliary cell originate in a gonimoblast initial (arrow) and the first gonimolobe initial (arrowhead). Slide MAS 002b. 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.

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 study).

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, 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



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

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 post-fertilization 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' (1992) point of view 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 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 *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 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

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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.

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 (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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