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Grammephora peyssonnelioides gen. et sp. nov. (Rhodophyta, Rhodymeniaceae) from the Solomon Islands, South Pacific

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SUMMARY

A new genus and species of red alga in the Rhodymeniaceae, *Grammephora peyssonnelioides*, is described from both shallow and deepwater habitats in the Solomon Islands, South Pacific. The new genus and species is characterized by prostrate overlapping lobes with a strongly cartilaginous flexible texture, distinct surface linear markings perpendicular to the growing margins, and a compact three to four celled medulla of relatively small refractive cells. Tetrasporangia are elongate and decussately divided, and occur in large scattered dorsal surface sori. Cystocarps are prominent and conical, on the dorsal surface of the blade, with a network of nutritive filaments and basal nutritive tissue around the suspended, centrally located carposporophyte, with all gonimoblast initials becoming carposporangia. The columnar fusion cell is uniquely crowned by a ring of discoid cells of nonalgal origin.

Key words: *Grammephora peyssonnelioides* gen. et sp. nov., morphology, new genus, new species, reproduction, Rhodophyta, Rhodymeniaceae, Solomon Islands, taxonomy.

INTRODUCTION

The family Rhodymeniaceae (Harvey 1849) belongs to the red algal order Rhodymeniales and at present comprises some 30 temperate to tropical genera (Womersley 1996; Saunders *et al*. 2004; Gavio & Fredericq 2005). The Rhodymeniaceae includes taxa displaying a variety of features, making it difficult to assign a single defining character to circumscribe the family. Recent molecular investigations (Saunders & Kraft 1994; Strachan *et al*. 1995; Saunders *et al*. 1999) hinted at a polyphyletic origin to the Rhodymeniaceae, which suggests a need for further subdivision of the family.

The Solomon Islands (Fig. 1) occupy a total land area of 27 556 km^2 spread over 992 islands aligned over more than 1500 km in the southwestern Pacific Ocean, and comprise marine ecosystems among those with the highest biodiversity in the world (Lovell *et al*. 2004; Green *et al*. 2006). The first major survey of marine algae from that region was by Womersley and Bailey (1970), later supplemented by an extensive survey by Payri *et al*. (2005). In this paper we report a new genus and species of marine red algae from the Solomon Islands with morphological and reproductive characters that clearly place it in the Rhodymeniaceae, although its combination of characters differs from those of any other genus in the family.

MATERIALS AND METHODS

Material was collected by scuba at three different sites in the New Georgia Group located in the Western province of the Solomon Islands (Fig. 1). Part of the material was stored in 5% buffered formalin in seawater, and the rest was dried as herbarium specimens. Dried material was rehydrated in weak detergent solution prior to sectioning using a freezing microtome. Sections were stained using 1% acidified aniline blue and made permanent if necessary by mounting in 60% clear corn syrup. Drawings were made using a microscope with a camera-lucida attachment. Macrophotographs were taken with a Nikon E-995 digital camera (Nikon Corporation, Tokyo, Japan); photomicrographs were obtained using an Olympus BH2 compound microscope fitted with an Olympus C-5050 digital camera (Olympus Optical, Tokyo, Japan), and the resulting files processed into figures by computer software (Adobe Photoshop; Adobe Illustrator). Voucher specimens have been deposited in the herbaria of PC and NOU-IRD (Phycological Herbarium, Institut de Recherche pour le Développement, Nouméa, New Caledonia). Herbarium

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Fig. 1. Map of the Solomon Islands, showing the main island groups and the numbers of the collecting stations for this study.

abbreviations are in accordance with Holmgren *et al*. (1990). Accession numbers preceded by the letter 'S' refer to microscope slide collections.

RESULTS

Grammephora N'Yeurt *et* Payri, gen. nov.

Thallus prostratus, nullo modo calcifactus, e lobis superpositis constans. Textura valde cartilaginea, coriacea sed flexibilis. Signis distinctis linearibus et superficiaribus et perpendicularibus obtectus. Medulla densa et pigmentifer, e stratis 3–4 cellularum elongatarum usque ad ovoideas contentis refractivis atque stratis 3–4 cellularum ovoidearum corticaliumque gradiatim minorum, constans. Carposporophytum, super pavimentum cystocarpii per filamenta persistentia nutriciaque et per cellulas stellatas interconnexasque quae inter contextum basalem nutriciumque et pariem pericarpi et pavimentum cystocarpii sunt, suspensum. Cystocarpia prominentia, ostiolata et conica, in superficie laminae dispersa. Tetrasporangia intercalaria, elongata et decussate divisa in soris superficiaribus dispersis et elevatis.

Thallus prostrate, totally uncalcified, of overlapping lobes with a strongly cartilaginous, leathery but flexible texture, covered with distinct linear markings perpendicular to the thallus surface. Medulla dense and pigmented, of three to four layers of elongate to ovoid cells with refractive contents, and three to four layers of progressively smaller ovoid cortical cells. Carposporophyte suspended above the cystocarp floor by persistent nutritive filaments and interconnected stellate cells present between the basal nutritive tissue, pericarp wall and cystocarp floor. Fusion cell columnar, with a crown of small satellite cells of nonalgal origin. Cystocarps prominent, ostiolate and conical, on the dorsal surface of the blade. Tetrasporangia intercalary, elongate and decussately divided, in raised, scattered dorsal surface sori. Male plants unknown.

Etymology: *Grammephora* is derived from the Greek '*gramme'*, meaning 'line', and '*phora*', to bear, referring to the conspicuous parallel markings perpendicular to the thallus surface.

Type species: *Grammephora peyssonnelioides* N'Yeurt et Payri.

Grammephora peyssonnelioides N'Yeurt *et* Payri, sp. nov. (Fig. 2–21)

Thallus prostratus, (50)-70-(110) mm latus, atro-ruber, e lobis superpositis constans. Signis distinctis linearibus et superficiaribus et perpendicularibus ad margines crescentes, obtectus. Textura valde cartaliginea et coriacea. Medulla densa et pigmentifer, ex 3–4 stratis cellularum refractivarum 8–12 μm latarum et 20–25 μm longarum et elongatarum usque ad ovoideas, constans. Cortex 3–4-stratus, ex cellulis ovoideis progressive minoribus 2.5–10.0 μm diametro. Ramus carpogonialis-non-visus. Carposporophytum 300–400 μm altum, super pavimentum cystocarpii

suspensum per reticulum filamentorum persistentium nutriciorumque atque per cellulas stellatas interconnexasque inter magnam aream basalem 100–120 μm crassum cellularum nutriciarum interconnexarumque et paries pericarpii et pavimentum cycrocarpii. Cellula coalescens columnaris, coronam cellularum parvarum nonalgensium et ovalium praebens. Plurimae cellulae gonimoblasti carposporangia ovoidea 50–60 μm diametro, formantes. Cyctocarpia ostiolata, valde conica, usque ad 1500 × 950 μm, in superficie laminae dispersa, pericarpium densum 80–100 μm crassum praebentia. Tetrasporangia (90–120) × (30–50) μm, decussate divisa, intercalaria atque filamentis elongatis et sterilibus circumventa, in soris dispersis elevatisque 800–1000 μm longis, 500–800 μm latis et 300–320 μm altis. Plantae masculae-non-visae.

Thallus prostrate (50)-70-(110) mm broad, dark reddish, of overlapping lobes, strongly cartilaginous and leathery in texture, covered with distinct surface linear markings which are perpendicular to the growing margins. Medulla dense and pigmented, of three to four layers of elongate to ovoid refractive cells 8–12 μm wide and 20–25 μm long; cortex three- to four-layered, of progressively smaller ovoid cells 2.5–10.0 μm in diameter. Carpogonial branch not seen. Carposporophyte 300–400 μm high, suspended above the cystocarp floor by a network of persistent nutritive filaments and interconnected stellate cells present between a large basal patch of interconnected nutritive cells 100–120 μm thick and the pericarp walls and cystocarp floor. Fusion cell columnar, with a crown of small nonalgal oval cells. Most gonimoblast cells forming ovoid carposporangia 50–60 μm in diameter. Cystocarps ostiolate, prominently conical, to 1500 × 950 μm, scattered on the blade surface, with a dense pericarp 80–100 μm thick. Tetrasporangia (90–120) × (30–50) μm, decussately divided, intercalary and surrounded by elongate sterile filaments, in scattered, at times marginal, raised sori 800–1000 μm long, 500–800 μm wide and 300–320 μm high. Male plants not seen.

Etymology: the specific epithet refers to the new alga's superficial resemblance to the calcified red algal genus *Peyssonnelia*, with which it could be confused.

Holotype and type locality: PC 0062766, Hele Pass, Vangunu Island, Solomon Islands (sampling station S826: 08°40.324′S, 157°50.249′E), 4 July 2004, –6 m, *leg. C. E. Payri*, cystocarpic (Fig. 2).

Paratype collection: PC 0062767, Vatana Point, Vangunu Island, Solomon Islands (sampling station S824), 3 July 2004, –55 m, *leg. C. E. Payri* (one cystocarpic and two tetrasporic thalli).

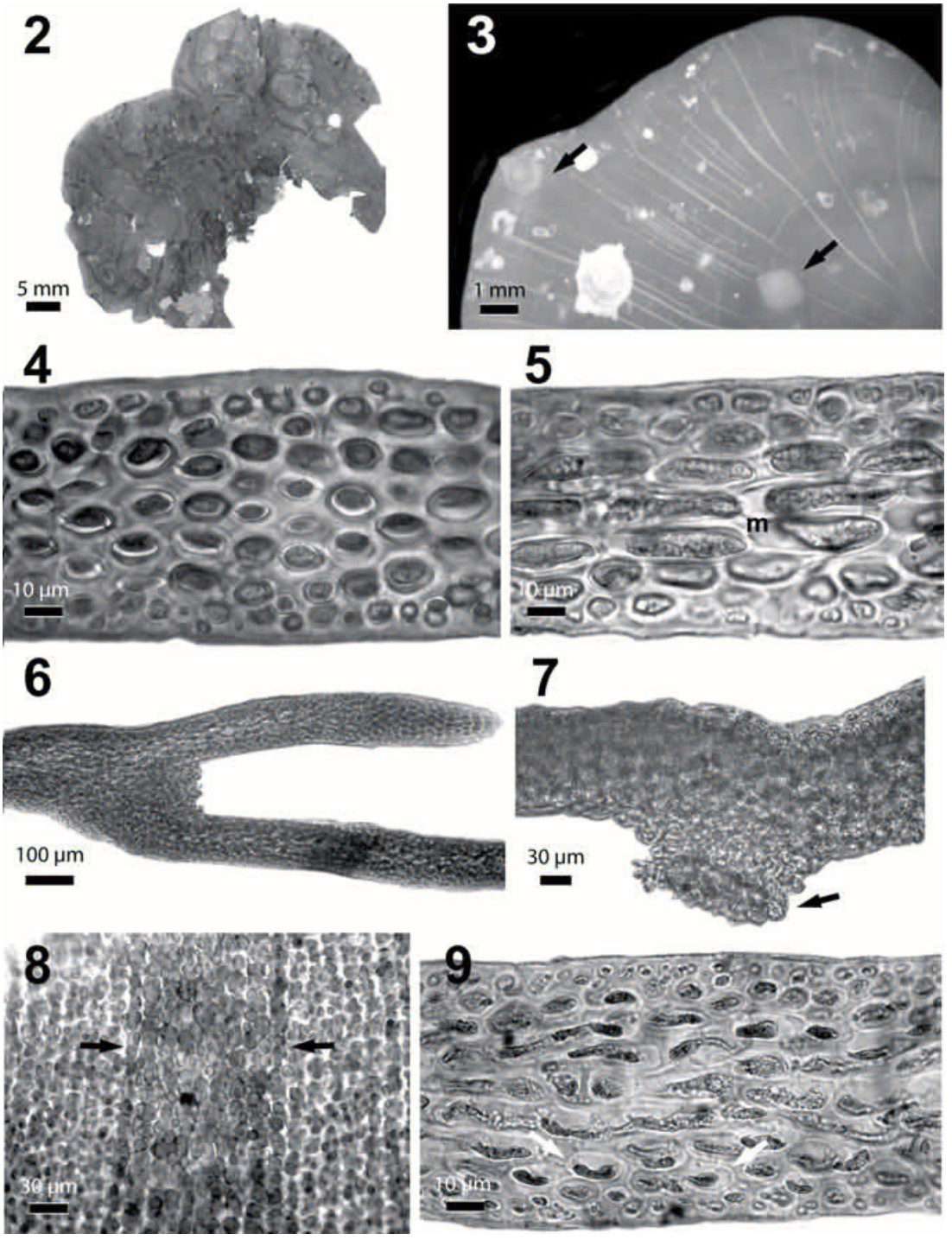
Other material examined: NOU-IRD 469, Kohingo, New Georgia Island, Solomon Islands (sampling station S829), 6 July 2004, –70 m, *leg. J. L. Menou* (cystocarpic).

Distribution: So far only known from New Georgia Island and Vangunu Island, Northern Solomon Islands.

Habitat: Growing on the outer reef slope, from –6 m down to –70 m in the vicinity of reef channel, together with other macroalgae such as *Cryptonemia* spp., *Peyssonnelia* spp. and *Galaxaura* spp.

Habitat and vegetative morphology: Plants (Fig. 2) are prostrate (50)-70-(110) mm broad, uncalcified, strongly cartilaginous and leathery in texture, translucent dark reddish in color, with a reflective sheen, and do not adhere well to paper when dry. The surface of the thallus is covered with distinct whitish linear markings, perpendicular to the growing margins (Fig. 3). These characteristic lines, about 200–300 μm wide, are the result of locally larger, more pigmented and refractive inner cortical cells 15–25 μm in diameter, as opposed to 7–8 μm in diameter in other parts of the thallus (Figs 8,9). Growth is by means of overlapping lobes, initiated by the unequal dichotomous division of marginal regions of the thallus (Fig. 6). Blades are (90)-100–110-(140) μm thick, with a dense pigmented medulla consisting of three to four layers of elongate to ovoid refractive cells 8–12 μm wide and 20–25 μm long, surrounded on either side by a three to four layered cortex of progressively smaller ovoid cells 2.5–10.0 μm in diameter (Figs 4,5). Inner cortical cells are ovoid and deeply refractive, 5–10 μm in diameter; outer cortical cells are subglobose, deeply pigmented, 2–5 μm in diameter. Attachment to the substratum is strong, via discrete, short, pad-like holdfasts on the inferior surface (Fig. 7).

Reproductive morphology: Carpogonial branches were not seen in our female material despite repeated searches (presumably because the plants were already fertilized), but are assumed to be three- to four-celled and issued from inner cortical cells, as per the family (Womersley 1996). Early postfertilization stages of the gonimoblast were not found in the limited material available for our study, despite repeated sectioning. The developing and mature carposporophyte (Figs 11–16), centrally suspended in the cystocarp cavity by a robust network of nutritive filaments and stellate cells, is about 300–400 μm high, outwardly developing, and has a basal columnar fusion cell 20–23 μm in diameter and 45–50 μm high, with a characteristic 'crown' of 10–12 small, clear oval satellite cells about 5 × 15 μm (Figs 16,17). Below the fusion cell lies an extensive patch of basal nutritive tissue 100–120 μm thick consisting of a network of darkly staining oval to elongate cells 15–30 μm in diameter. The suspended patch of nutritive cells is centrally linked to the cystocarp floor via a pillar-like 'umbilical' nutritive filament about 250 μm long and 20–30 μm in diameter, issued from a modified outer medullary cell (Fig. 13). In addition, a prominent network of persistent, elongate, laterally connected nutritive filaments and



Figs 2–9. *Grammephora peyssonnelioides*: habit and vegetative morphology. 2. Habit of pressed Holotype (PC 0062766). 3. Detail of thallus surface of liquid-preserved portion of Paratype (PC 0062767), showing characteristic linear markings and two bent, conical cystocarps (arrows). 4. Transverse section of thallus showing ill-defined medullary region progressively grading into cortex (PC 0062767). 5. Transverse section in older portion of thallus, showing more elongate medullary cells (m) (PC 0062767). 6. Transverse section of overlapping lobes, initiated by the unequal dichotomous division of marginal regions of the thallus (PC 0062767). 7. Detail of hapteroid holdfast (arrow) (PC 0062767). 8. Detail in region of linear marking (delimited by arrows), showing locally larger, more refractive inner cortical cells (PC 0062767). 9. Transverse section in region of linear markings, showing enlarged inner cortical cells (white arrows) (PC 0062767).

Table 1. Comparison of selected characters between *Grammephora* and selected other genera of the Rhodymeniaceae†

Genus	Habit	Texture	Surface markings	Medulla	Refractive cells	Carposporophyte location	Nutritive filaments	Tetrasporangia
Grammephora (this study)	Prostrate lobes prominent, with stellate cells in surface sori	Cartilaginous intercalary, decussate,	Abundant	Pigmented, not clearly demarcated from cortex	Abundant throughout	Centrally suspended, connected to cystocarp floor by nutritive filaments	Prominent, with stellate cells	Intercalary, decussate, in surface sori
Asteromenia Huisman and Millar (1996); 138	Stipitate, peltate to stellate blades	Cartilaginous	Absent	Unpigmented, clearly demarcated from smaller-celled cortex	Sparse, in cortex	Directly on cystocarp floor	Present or absent, filamentous	Cruciate, scattered in cortex
Cordylecladia J. Agardh (1852); 702	Erect, terete to compressed thallus	Cartilaginous	Absent	Unpigmented, clearly demarcated from smaller-celled cortex	Rare	Directly on cystocarp floor	Weakly developed or absent, filamentous	Terminal or intercalary, decussate or cruciate, in sori
Erythrymenia Schmitz ex Mazza (1921); 107	Erect, ovate to foliose blades	Solid, thick	Mottled surface	Unpigmented, clearly demarcated from smaller-celled cortex	Rare	Directly on cystocarp floor	Ephemeral, filamentous	Intercalary in cortex, cruciate
Hymenocladia J. Agardh (1852); 772	Erect, complanately branched flattened to terete thallus	Solid	Absent	Unpigmented, clearly demarcated, intermixed with small cells	Rare	Directly on cystocarp floor	Absent	Intercalary in cortex, very large, tetrahedral
Microphyllum Weber-van Bosse (1928); 464	Prostrate, lobed, laterally attached blade	Foliose	Absent	Unpigmented, clearly demarcated from smaller-celled cortex	Sparse, in cortex	Directly on cystocarp floor	Absent	Unknown
Rhodymenia Greville (1830); 84	Usually erect, occasionally prostrate	Cartilaginous or foliose	Absent	Unpigmented, clearly demarcated from smaller-celled cortex	Sparse, in cortex	Directly on cystocarp floor	Absent	Terminal or intercalary, decussate or cruciate, in sori or nemathecia

†Sources: present paper; Abbott (1999); Norris (1991); Weber-van Bosse (1928); Womersley (1996).

distinctly stellate interconnected cells 10–20 μm in diameter is present between the basal nutritive tissue and the inner upper and lateral pericarp wall and corners of the cystocarp floor. Gonimoblast filaments are branched, with most cells becoming ovoid carposporangia 50–60 μm in diameter, organized in sequentially maturing lobes. Cystocarps (Figs 10,11) are narrowly ostiolate, prominently conical and almost invariably bent to an angle of about 45°, to 1500 μm high and 950 μm wide, scattered on the superior blade surface. The cystocarp chamber is about 500–600 μm in diameter, with a dense, pseudoparenchymatous pericarp 80–100 μm thick. The bent nature of the cystocarp renders the carposporophyte nonaligned with the narrow ostiole, making transverse anatomical sections showing both the complete, mature gonimoblast and the ostiole virtually impossible. Tetrasporangia (Figs 17–21) are elongate (90–120) × (30–50) μm, decussately divided, of various ages and intercalary in fertile filaments in scattered, ovoid, raised surface sori 1400–1600 μm long, 500–800 μm wide and 300–320 μm high. They are surrounded by elongate sterile filaments 2.5–5.0 μm in diameter. The sori are disproportionately large, more than twice as thick as the supporting thallus. Male plants were not seen.

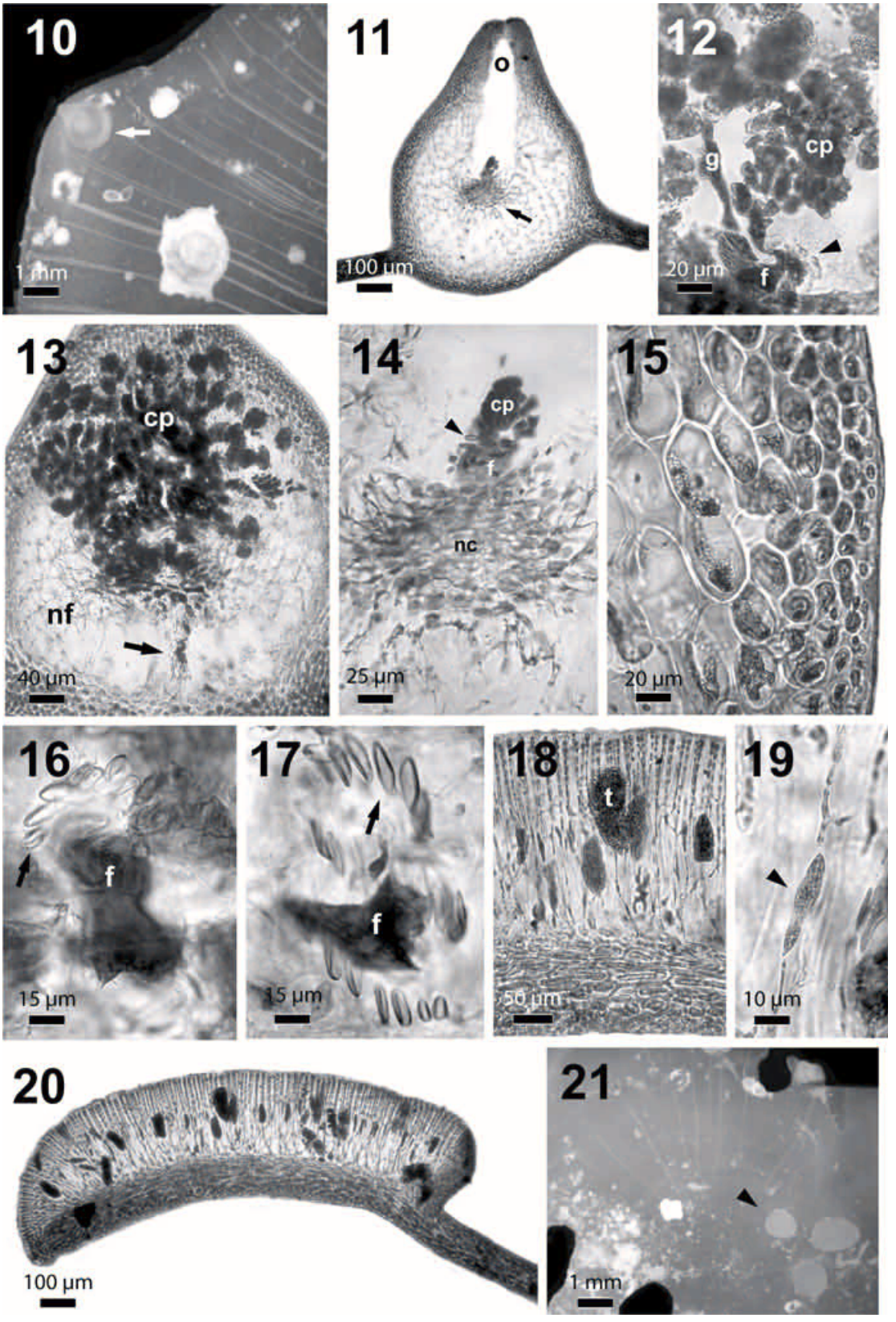
DISCUSSION

Grammephora belongs in the family Rhodymeniaceae because of the following diagnostic characters: (i) large conical cystocarps and carposporophytes with a columnar fusion cell; (ii) most gonimoblast initials branched and becoming sequentially maturing carposporangia; (iii) clusters of darkly staining nutritive cells below the carposporophyte; (iv) the presence of a network of nutritive filaments between the carposporophyte, pericarp walls and cystocarp floor; and (v) decussate, intercalary tetrasporangia in raised sori. Comparing *Grammephora* with some other related genera in the family (Table 1), the unique features of the new genus become apparent. None of the members of the family exhibit the largely prostrate, leathery habit with evident perpendicular markings distinctive of *Grammephora*, the poorly demarcated compact medulla, usually bent cystocarps or the uniquely suspended carposporophyte with a robust network of nutritive filaments and stellate cells that surround it. The overlapping mode of growth by unequal marginal divisions of the thallus and the peculiar discoid cells consistently surrounding the fusion cell also seem to be unique in the family. The exact origin and function of these satellite cells is unknown, but they were consistently found surrounding the fusion cell in all mature cystocarps sectioned, and are considered diagnostic of the genus.

The closest genus in the habit is *Rhodymenia* Greville, which can sometimes form lobed prostrate thalli. However, in *Rhodymenia* the medulla always consists of clear cells much larger than those in the pigmented cortex, which is abruptly and clearly demarcated. In addition, the carposporophyte sits on the cystocarp floor, there are no 'satellite' cells around the fusion cell, and nutritive filaments are not persistent and largely absent.

Another genus, *Microphyllum* Weber-van Bosse (1928; 464, figs 197–198), also forms prostrate, laterally attached thalli with prominently conical cystocarps. This rarely reported genus, consisting of the single species *M. borneensis* Weber-van Bosse, differs from *Grammephora* principally by its large-celled medulla, usually straight, not bent cystocarps, carposporophyte directly arising from the cystocarp floor, and lack of a network of nutritive filaments. Other reproductive stages are unknown in *Microphyllum*. Norris (1991; 593, figs 24,25) reports a *Microphyllum* cf. *borneense* from South Africa with a large-celled clear medulla, but his illustrated cross section of a cystocarp does not show the stellate cells lining the inner pericarp wall, which is shown in Weber-van Bosse's protologue of the type species from Indonesia. The pericarp wall in *Grammephora* is dense and pseudoparenchymatous, with stellate cells only present in the nutritive network surrounding the carposporophyte.

Some of the characters of *Grammephora* are remarkable within the Rhodymeniaceae. The distinctly striated habit, apparently the result of controlled local variations in subcortical cell size and pigmentation, seems a feature not found in any other Rhodymeniales, but reminiscent of some members of the Peyssonneliaceae such as *Ethelia* (Weber-van Bosse) Weber-van Bosse. Externally, only the totally uncalcified, plastified-like nature of *Grammephora* precludes the casual observer from assuming it might not belong in the Peyssonneliaceae. One could speculate that 'camouflaging' as a theoretically inedible calcified plant might help deter herbivory. The very compact, pigmented medulla imparting a cartilaginous texture to the plant further reinforces the analogy between it and the Peyssonneliaceae. The suspended carposporophyte of *Grammephora* is another striking feature, perhaps not found in many other red alga. All current members of the Rhodymeniales have the carposporophyte issued directly from the cystocarp floor, whereas in *Grammephora* it is literally suspended from the pericarp walls by robust nutritive filaments and a network of stellate sterile cells, issued from the basal nutritive tissue. A further, relatively thick filamentous connection exists between the cystocarp floor and the carposporophyte. Coppejans and Millar (2000; 339, fig. 27) report an undescribed species from Papua New Guinea (PNG) forming spreading, prostrate, flat-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Figs 10–21. *Grammephora peyssonnelioides*: reproductive morphology (PC 0062767). 10. Detail of cystocarpic thallus, showing a mature cystocarp (arrow) which is bent towards the thallus margin. The white cone-like structure on the lower right is an encrusting diatom. 11. Transverse section of a developing cystocarp, showing the suspended carposporophyte surrounded by a network of nutritive filaments (arrow) and the long narrow ostiole (o). 12. Detail of developing carposporophyte, showing columnar fusion cell (f) with crown of small oval satellite cells (arrowhead), branched gonimoblast filament (gb) and carposporangia (cp). 13. General view of a mature cystocarp cavity, showing network of nutritive filaments (nf) surrounding the carposporophyte and carposporangial mass (cp), and pillar-like filaments (arrow) linking the carposporophyte to the cystocarp floor. 14. Detail of basal patch of nutritive cells (nc), fusion cell (f), satellite cells (arrowhead) and carposporangia (cp). 15. Transverse section of pericarp, showing compact, pseudoparenchymatous nature. 16. Detail of columnar fusion cell (f) and apical crown of clear, ovoid satellite cells (arrow). 17. Another view of the ovoid satellite cells (arrow) surrounding a fusion cell (f). 18. Transverse section of tetrasporangial sorus, showing decussate intercalary tetrasporangia (t) surrounded by elongate sterile filaments. 19. Detail of young undivided tetrasporangia (arrowhead), showing intercalary position in erect filament of sorus. 20. General cross-sectional view of mature tetrasporangial sorus. 21. General habit of tetrasporangial thallus, showing cluster of fertile sori (arrowhead).

tened blades that bear some resemblance to *Grammephora*. However, the PNG plants are highly dissected, firm and leathery and very strongly attached to the substratum by secondary holdfasts, unlike the flexible, smooth lightly attached and essentially non-dissected blades of *Grammephora*. Additionally, cystocarps in the PNG plants are reported to be in distinct nemathecia as in the Peyssonneliaceae, which is not the case for *Grammephora*, although enigmatic satellite cells around the fusion cell are reported for both entities.

It is hoped that future surveys of the Solomon Islands algal flora will yield more fertile collections of *Grammephora*, to gain a better understanding of the reproductive features of this remarkable plant, especially pre- and postfertilization stages. As work continues on the marine flora of the Solomon Islands and Melanesia, it is expected that more new species and genera will be found from this unique region of the world, whose marine algal biodiversity in all accounts is comparable to the richness found in other groups such as fish and corals (Green *et al*. 2006).

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