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Gelidiella minima sp. nov. (Rhodophyta) from Victoria, Australia: Implications for the Generic Classification of the Gelidiaceae

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Gelidiella minima sp. nov. (Gelidiaceae, Gelidiales) is described from the shallow subtidal of Point Lonsdale, Victoria, Australia, where it grows on shell fragments and both calcareous and non-calcareous encrusting algae. Plants form lax, entangled mats consisting of narrow, creeping axes attached at intervals by peg-like, penetrating holdfasts. Branches arise at the points of attachment, and either reflex and re-attach or become erect, 0·5–1·5 mm in length and reproductive. Medullary rhizines, characteristically found in the erect axes of all genera of the Gelidiaceae except for *Gelidiella*, are not formed in any part of the thallus of *G. minima*. Irregularly cruciately divided tetrasporangia occur in terminal stichidia or, occasionally, in lateral branches; stichidia are flattened, and sporangia are produced in acropetally developed rows of (4–)6(–7). Gametangial plants are monoecious and protandrous; spermatangia are formed subterminally on the erect branches and persist below the cystocarps. Mature cystocarps are uniporate and unilocular, with carposporangia in chains of 2–3 formed from gonimoblasts radiating from the region of the axial cell. *G. minima* differs from other species of the genus *Gelidiella* in its diminutive size, largely prostrate axes, and numbers of tetrasporangia per row. This is the first detailed report of the gametangia and cystocarps for a species of *Gelidiella*. It is suggested that a reorganization of the species of *Gelidiella* and *Pterocladia* based on features of the development of the cystocarp will likely lead to a more natural attribution of species within the two genera. This is not possible at present, as cystocarps are unknown in most species of *Gelidiella*, including the type species *G. acerosa* (Forsskål) Feldman et Hamel.

Twenty-two species of the largely tropical to warm-temperate marine algal genus *Gelidiella* have been described (Maggs & Guiry, 1987). Most of these species have been reported to form tetrasporangia, but there are no reports of gametangial or cystocarpic plants other than a preliminary description of an unnamed species from India (Sreenivasa Rao & Trivedi, 1986?, p. 257). Species of *Gelidiella* are usually relatively small (2–20 mm long), turf-forming or solitarily creeping algae generally characterized as members of the Gelidiales without internal rhizines, which are found in the medulla of the erect axes in all other genera of the order. *Gelidiella* was referred to the family Gelidiellaceae by Fan (1961, p. 317) on the basis of a lack of sexual reproduction and an absence of rhizines. The discovery, however, of rhizines in the medulla at the attachment points of *Gelidiella calcicola* Maggs et Guiry (1987) from the North Atlantic, led these authors to suggest that the Gelidiellaceae Fan should be included in the Gelidiaceae, although this is disputed by Santelices (1990). The virtual absence of cystocarpic plants in species of *Gelidiella* has nevertheless made it difficult to assess the relationships between this genus and other genera of the Gelidiaceae.

G. minima sp. nov., here described from the shallow subtidal of Point Lonsdale, Victoria, Australia, forms lax spreading mats produced by arching branches that frequently re-attach to the substratum. Reproductive structures are produced terminally on erect branches up to 1·5 mm in

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length. The total absence of rhizines suggests a close relationship with the species currently included in the genus *Gelidiella*, although this genus is probably polyphyletic but is presently circumscribed on the basis of an autapomorphy (virtual absence of rhizines). Comparison of the cystocarp structure of *G. minima* with some species presently referred to *Pterocladia* indicates a close relationship, although the type species of *Pterocladia, P. lucida* (Turner) J. Agardh, as illustrated by Fan (1961) seems to be significantly different in its cystocarp structure.

MATERIALS AND METHODS

Plants collected in the subtidal of Point Lonsdale, Victoria, Australia on 1 March 1989 were initially fixed in 4% Formalin/seawater and subsequently transferred to a solution of 85% ethanol and 15% methanol. Plants were mounted whole in 60% Karo® corn syrup after staining for 1–2 min. in 1% Phloxine in water. *G. minima* was difficult to section due to its small size, but the following procedure was found to give good results: plants preserved in alcohol were allowed to air-dry under a tungsten bulb for 5–10 min. and small pieces were sectioned by hand with a razor-blade using a stereo microscope for orientation. Sections were rehydrated in water, stained with aqueous solutions of 1% Phloxine or 2% Aniline Blue acidified with 1N HCl, and mounted in corn syrup.

Herbarium abbreviations are in accordance with those of Holmgren, Keuken & Schofield (1981).

OBSERVATIONS

G. minima sp. nov. (Figs 1–17)

Description. Thallus porphyreus tegetes tenues formans, 1–2 cm latus, stolonibus prostratis arcuatisque axes erectos 0·5–1·5 mm altos ferentibus; stolones et rami erecti teretes usque ad compressos, 50–150(−200) μm lati et 40–100 μm crassi; crassi; stolones hapteris paxilliformibus rhizoideorum confertorum, 80–160 μm longi, 40–80 μm diametro, oppositi ramo, epilithici in concharum fragmentis et in algis crustosis et calcareis et non calcareis. Structura uniaxialis cellulam apicalem parum protrudentem praebens. Cellulae corticales exteriores plus minusve isodiametrae, rotundae usque ad angulares, in seriebus longistrorsum plus minusve positae; protoplastus (5–)6–10 μm latus, pariete 1·5–2·5 μm crasso; pauci cloroplasti per cellulam, discoidei usque ad laminares; pili prope apices ramorum erectorum. Cortex 2–3 cellulas crassus, cellulis interioribus in lineis satis regularibus longistrorsum et parum elongatis; cellulae axiales in serie (5–)6–11 distincta transversaque, parietibus crassis, (2·5–)4–6 μm diametro et 30–40 μm longae; rhizinae absentes.

Organa reproductionis subterminalia in ramis erectis (300–)800–1500 μm longis. Thalli sexuales monoecii et proterandri. Rami carpogoniorum ignoti. Cystocarpia matura 200–250 μm distantia ab apice, 240–320 μm lata, singularia in ramis erectis, unilocularia; systema basale ramosum e cellulis parvis factum catenas 2–3 carposporangiorum maturescentium terminaliter formans; carposporangia ovoidea usque ad parum angulata, 20–35 μm diametro, chloroplasto stellato centrali; cellulae tenues arachnoideaeque e base carposporophyti ad pericarpium traseuntes. Spermatangia in soris subterminalibus formantia, ex cellulis exterioribus corticalibus excisa, bina quaternaque aggregata, elongata, 1–2 μm diametro, saepe persistentia ad bases cystocarpiorum maturorum.

Tetrasporangia in soris subterminalibus (160–)200–250(–300) μm lata et 300–500(–1000) μm longa, in seribus sporangiorum (4–)6(–7) similium aetate regulatim et acropete evolutis, excisa e ambobus lateribus cellularum axialium et sic in seriebus 2, subsphaerica usque ad parum ovoidea, (23–)30–45 μm diametro, cruciatim usque ad irregulatim divisa; chloroplastus stellatus.

Holotypes: Plantae tetrasporangiferae et gametangiferae (Figs 1–14), Point Lonsdale, Victoria, Australia, 2·5–4 m profunditate *Kraft* et *van Amerongen*, 1.iii.1989; holotypus in AD, A60496; isotypus in GALW, 8059.

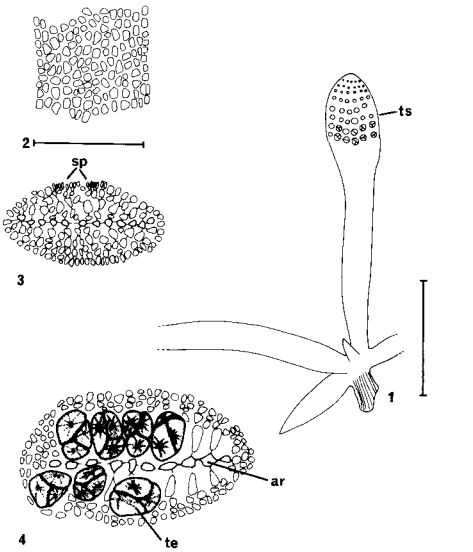
Thallus red-brown, forming thin entangled mats, 1–2 cm across, with prostate, arching branched stolons bearing erect branches 0·5–1·5 mm high; stolons and erect branches terete to compressed, 50–150(–200) μm

broad and 40–100 μm thick, stolons with peg-like holdfasts of massed rhizoids, 80–160 μm long and 40–80 μm in diameter, situated opposite a branch; epilithic on shell fragments, crustose calcareous and non-calcareous algae. Structure uniaxial with a slightly protruding apical cell. Outer cortical cells more or less isodiametric, rounded to angular, more or less in lengthwise rows, protoplast (5–)6–10 μm across, with the wall 1·5–2·5 μm thick, chloroplasts few per cell, discoid to laminate; hairs present near apices of erect branches. Cortex 2–3 cells thick, with inner cells in fairly regular lines lengthwise and slightly elongate; axial cells, periaxial cells and their second-order derivatives forming a distinct transverse row of (5–)6–11, thick walled, (2·5–)4–6 μm in diameter and 30–40 μm long; rhizines absent.

Reproductive organs subterminal on erect branches (300–)800–1500 μm long. Sexual thalli monoecious and protandrous. Carpogonial branches unknown. Cystocarps mature at 200–250 μm from apices, 240–320 μm across, single on erect branches, unilocular, with a branched basal system of small cells forming chains of 2–3 carposporangia maturing terminally, carposporangia ovoid to slightly angular, 20–35 μm in diameter with a central stellate chloroplast, slender arachnoid cells traversing from the base of the carposporophyte to the pericarp. Spermatangia formed in subterminal sori, cut off from outer cortical cells in groups of 2 or 4, elongate, 1–2 μm in diameter, frequently persisting at the base of mature cystocarps.

Tetrasporangia in subterminal sori (160–)200–250(–300) μm broad and 300–500(–1000) μm long, in regular acropetally developed rows of (4–)6(–7) sporangia of similar age, cut off from both sides of the axial cells and thus in two rows, subspherical to slightly ovoid, (23–)30–45 μm in diameter, cruciately to irregularly divided, chloroplast stellate.

Holotype. A pressed, interwoven clump of tetrasporangial and gametangial plants (Figs 1–17), Point Lonsdale, Victoria, Australia, 2·5–4 m depth, *Kraft* and *van Amerongen*, 1 March 1989; holotype in AD, A60496; isotype in GALW, 8059.

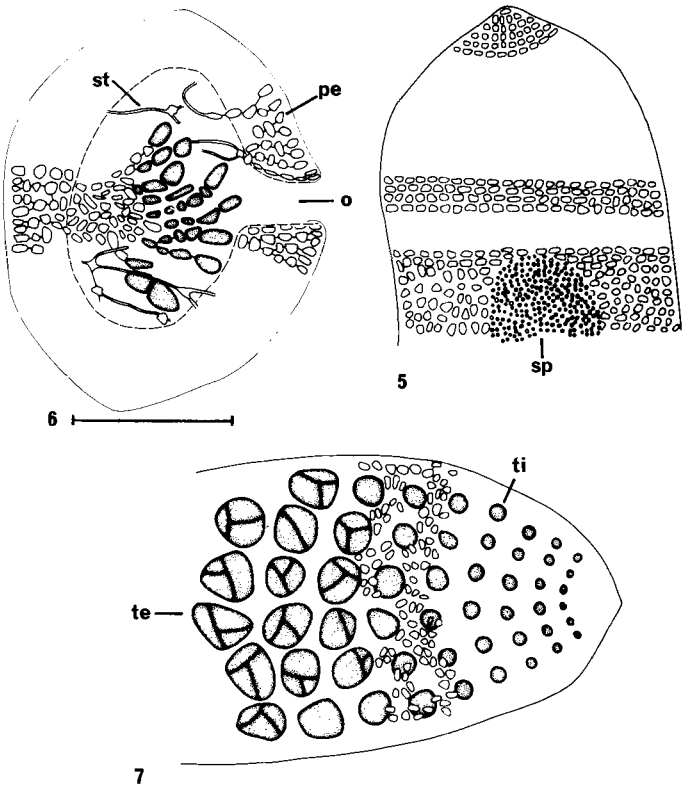


FIGS 1–4. Morphology of *Gelidiella minima* sp. nov. Holotype (Scale bars: Fig. 1 = 200 μm; Figs 2–4, as Fig. 2, = 50 μm). Fig. 1. Habit of portion of plant showing apical tetrasporangial stichidium (ts). Fig. 2. Outer cortical cells in surface view. Fig. 3. Transverse section of gametophytic plant with young spermatangial sorus (sp). Fig. 4. Transverse section of mature tetrasporangial sorus showing tetrasporangia (te) and the axial row (ar) of medullary cells.

Distribution. Known only from the type locality.

External appearance and vegetative morphology

Plants are red-brown in colour, forming lax entangled mats, 1–1·5 mm thick and 1–2 cm in extent. The thallus is composed of prostrate, arching stolons bearing reflexed, repent branches or fertile erect axes. Stolons and erect branches (Figs 1, 12, 16) are terete to compressed, 40–100 μm thick and 50–150(–200) μm broad, with holdfasts of massed rhizoids forming a penetrating (particularly in calcareous substrata), peg-like holdfast 80–160 μm long and 40–80 μm in diameter (Fig. 1), situated opposite a branch or branches.

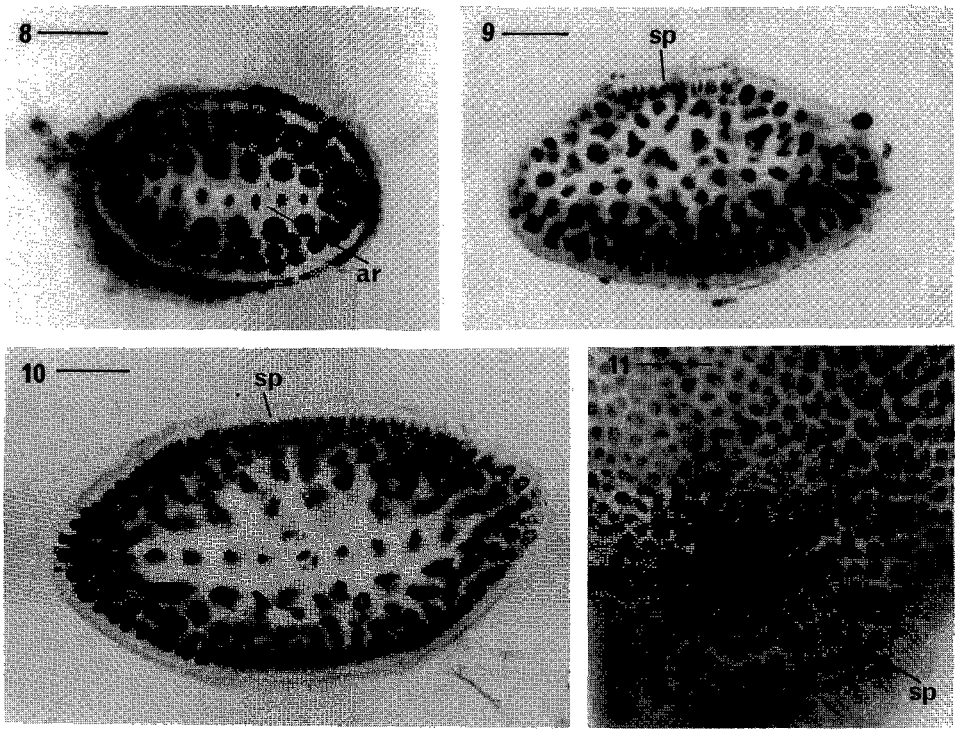


FIGS 5–7. Morphology of *Gelidiella minima* sp. nov. Holotype. (Scale bars: Figs 5–7, as on Fig. 6, = 50 μm). Fig. 5. Apex of gametophytic plant showing developing spermatangial sorus (sp). Fig. 6. Transverse section of mature cystocarp showing short chains of carposporangia, ostiole (o), and network of stretched cells (st) transversing from the base of cystocarp to the pericarp (pe), and ostiole (o). Fig. 7. Apex of tetrasporangial plants showing development of tetrasporangial initials (ti) and tetrasporangia (te) in rows.

Outer cortical cells are rounded to angular in surface view (Fig. 2), widely spaced, with a protoplast (5–)6–10 μm in diameter and a wall 1·5–2·5 μm in thickness. The cuticle is 4·0–6·5 μm in thickness (Fig. 8). Discoid to laminate chloroplasts (5–8) are in a parietal position in the cortical cells. Hair cells 75–100 μm long are formed as extensions of cortical cells near the apices, have an apical blob of cytoplasm 7·5–10 μm long, and are most frequently formed terminally on the reproductive branches. Cortical cells are arranged in 2–3 layers (Figs 8–9), and in fairly regular lines in surface view (Figs 2, 13, 16); the innermost cells are (5–)6·5–7·5 μm in diameter and (5–)7·5–10 μm long. Axial and periaxial cells, together with their second-order derivatives, are produced in a distinct transverse row of (5–)6–11 thick-walled cells, and are (2·5–)4–6 μm broad and 30–40 μm long. This row of cells remains obvious throughout the plant (Figs 3, 8–10). Rhizines are absent in all parts of the thallus.

Reproduction

Gametangial plants are monoecious. Outer cortical cells divide periclinally to form one or two elongate spermatangial initial cells giving rise to a further initial laterally (Figs 3, 9–10). Two spermatangia are formed at the apices of each of these initials; each cortical cell thus gives rise to two or four spermatangia, 1–2 μm in diameter and 3–4 μm long. Spermatangia are generally mature at about 120 μm from the apices of the erect gametangial branches. The spermatangial sori tend to be localized

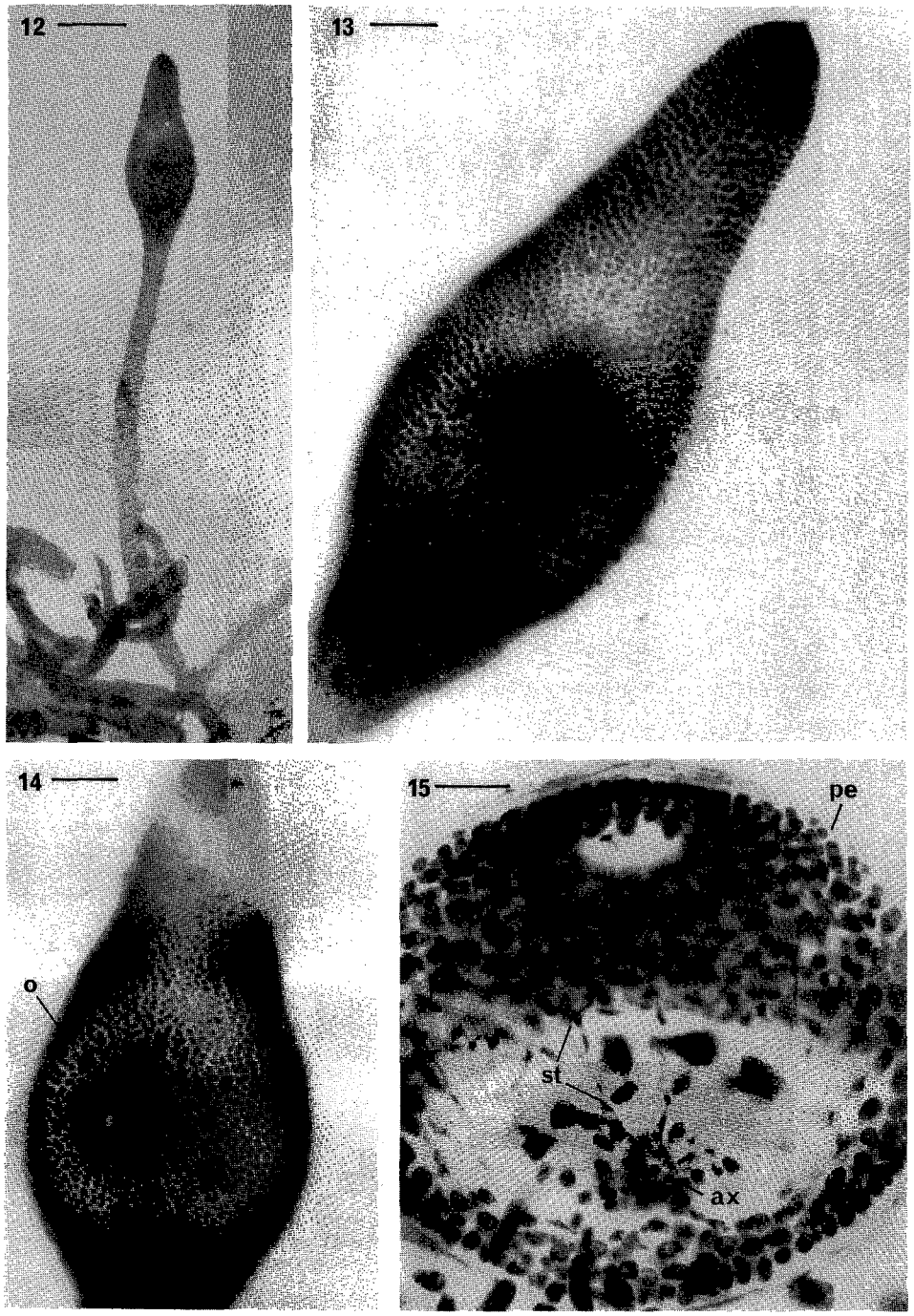


FIGS 8–11. Vegetative morphology and spermatangia of *Gelidiella minima* sp. nov. Holotype. Scale bars: Fig. 8 = 20 μm; Figs 9–11 = 15 μm). Fig. 8. Transverse section of a young erect axis. Note axial row (ar) comprising the axial cell and its second-order derivatives. Fig. 9. Transverse section of gametangial axis with young spermatangial sorus (sp). Fig. 10. Transverse section through mature spermatangial sorus (sp). Fig. 11. Surface view showing persistent spermatangia (sp) at the base of a young cystocarp.

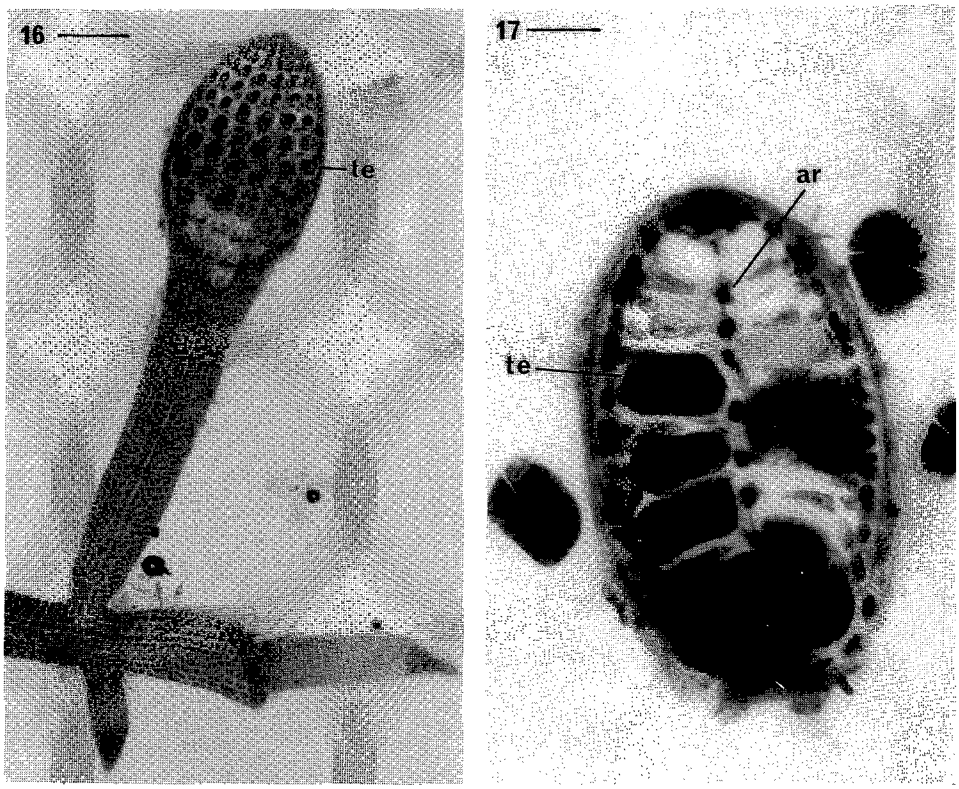
(Fig. 5): on a tip 180 μm broad, spermatangia occupied a band about 75 μm in width in the centre of the frond. Spermatangial sori tend to persist, even at the bases of mature cystocarps (Fig. 11).

Cystocarps are swollen 240–320 μm broad, about 200 μm in thickness, and mature at 200–250 μm from apices (Figs 12–14). Surface cortical cells in the area of cystocarp formation are smaller (5–7·5 μm in diameter), more regular in size, and more rounded (Fig. 13) than they are in non-reproductive parts of the fronds. The carposporophyte is 200–300 μm in length axially and 100–170 μm in width at its widest point. Cystocarps are unilocular, the carposporophyte developing to one side of the axial row of cells and radiating from the vicinity of the central axial cell (Figs 6, 15). Carpogonia and nutritive filaments were not observed. Clusters of small cells around the central axial cell grow outwards and form chains of carposporangial initials. At the same time, a cavity starts to form between the axial row of cells and the layer of cortical cells above it, the cells of the latter becoming stretched in the process. These stretched cells persist in the mature cystocarp in the form of slender stellate cells extending from the base of the carposporophyte to the pericarp, and ramifying between the carposporangia (Figs 6, 15). At maturity, carposporangia are arranged in branched or unbranched chains of 2–3(–5), with the more mature carposporangia terminating the chains (Fig. 6). Carposporangia are spherical, ovoid or angular, 25–35 × 20–25 μm. A single ostiole about 50 μm in diameter is formed centrally in the pericarp (Figs 6, 14–15). The pericarp in the immediate vicinity of the ostiole may be slightly raised.

In the holotype collection, tetrasporangial



FIGS 12–15. Cystocarp morphology of *G. minima* sp. nov. Holotype. Scale bars: Fig. 12 = 300 μm; Figs 13, 14 = 80 μm; Fig. 15 = 50 μm). Figs 12, 13. Surface of mature cystocarps. Cystocarps occur singly a short distance from the apices. Fig. 14. Surface view of mature cystocarp showing ostiole (o). Fig. 15. Transverse section of cystocarp showing origin of gonimoblast (g) and stretched cells (st) from axial cell (ax); most carposporangia have become dislodged. Stretched cells extend from gonimoblast to the pericarp (pe).



FIGS 16–17. Morphology of tetrasporangial plants of *G.* minima sp. nov. Holotype. Scale bars: Fig. 16 = 150 μm; Fig. 17 = 30 μm). Fig. 16. Portion of tetrasporangial plant showing tetrasporangia sorus with tetrasporangia forming in regularly arranged rows consisting of six tetrasporangia (te). Fig. 17. Transverse section of tetrasporangial sorus showing the development of tetrasporangia (te). Some sporangia have become dislodged and the axial row (ar) is clearly seen.

plants were much more common than gametangial plants. Tetrasporangia are most frequently found at the apices of erect branches (Figs 1, 7, 16), but occasionally occur in small, lateral branches, generally produced in oposite pairs on stolons. Erect stichidial branches are (300–)800–1100 μm long, the fertile areas being (150–)200–250(–300) μm broad and 300–500(–1000) μm long. Tetrasporangia are arranged in distinct rows of (4–)6(–7) on both sides (Figs 4, 17) of the compressed stichidia. Tetrasporocytes are formed from the cortical cells and always arise acropetally in a sequential manner (Fig. 16). In most stichidia, 3–6 rows of undivided tetrasporocytes are present near the apices, followed by 2–4 rows of mature tetrasporangia and 2–20 or more rows of regularly arranged tetrasporangial cavities (Fig. 16). Occasionally, what appeared to be secondary tetrasporocytes and tetrasporangia were observed in these latter cavities, but most tetrasporangial cavities remain empty. Mature tetrasporangia are (23–)20–45 μm in diameter, and the spores are irregularly decussately or cruciately arranged (Figs 4, 17). Tetrasporangia are separated by elongate, almost colourless cells derived from subcortical cells; these bear two smaller cells, which in turn bear two surface cortical cells.

DISCUSSION

G. minima is an inconspicuous, spreading alga in which erect branches are usually terminated by reproductive structures. As six tetrasporangia are formed in a row in *G. minima*, species of *Gelidiella* with up to six

TABLE I. Species of *Gelidiella* with up to six or, rarely, seven tetrasporangia visible in lateral rows

Species of *Gelidiella*	Number of tetrasporangia in rows in side view	Size of tetrasporangia (μm)	Length of erect branches (mm)	Width of erect branches (μm)	Distribution
adnata Dawson	4	25	1–2	35–60	Vietnam
antipai Celan	2	(20–)30–60	1·0–1·5	(30–)40–60(–70)	Black Sea, Mediterranean, Pacific Mexico, Australia
lubrica (Kützing) J. Feldmann et Hamel	4–6	25–30	10–20	100–120	Mediterranean, Solomon Islands
minima sp. nov.	(4–)6(–7)	(23–)30–45	1·0–1·5	50–150(–200)	Australia
myrioclada (Børgesen) J. Feldmann et Hamel	3–6	27–38	10–20	60–160	India, Tanzania, Vietnam
pannosa (Feldmann) J. Feldmann et Hamel (= *tenuissima* J. Feldmann et Hamel)	1–6	12–40	2–3	50–135	Atlantic, Mediterranean, Thailand, Vietnam, Puerto Rico, Indonesia, Marshal islands
ramellosa (Kützing) J. Feldmann et Hamel	4–6	20–38	8–12	250–300	Australia, Japan, ?Mediterranean
sanctarum J. Feldmann et Hamel	4–6	30–40	to 20	60–100(–200)	Morocco, Guadeloupe

(or rarely seven) sporangia in clearly defined rows when viewed laterally are compared in Table I (see Maggs & Guiry, 1987 table II, for a list of species of *Gelidiella* and sources). The species listed in Table I fall into two distinct groups: those with erect branches up to 2 mm in length and those with erect branches 8 mm or more in length. The former group includes those species most closely related to *G. minima*: *G. adnata* Dawson (1954), *G. antipai* Celan (1938), and *G. pannosa*[1] (J. Feldmann) J. Feldmann et Hamel (1936). These three species, however, all form erect vegetative axes, as distinct from the largely prostrate growth of *G. minima*. In addition, *G. adnata* was described by Dawson (1954) as having adnate basal branching and pedicellate tetrasporangial stichidia. *Gelidiella antipai* forms only two sporangia per row (but four in a whorl), the erect branches are reported to be casepitose, and the thallus does not exceed 70 μm in width (Celan, 1938; Boudouresque, 1972). Plants of *Gelidiella pannosa* from the Mediterranean were described by Feldmann & Hamel (1936, p. 228) and Boudouresque (1969, 1970) as forming very fine (50–135 μm in diameter), cylindrical or rarely flattened erect axes.

In its repent, reflexed habit *G. minima* most closely resembles *G. calcicola* from the north-eastern Atlantic (Maggs & Guiry, 1987), but it is easily distinguished from this species by the nuber of sporangia in a row, which is generally 6 in the Australian species and 8–10 in the North Atlantic species, and the absence of rhizines in the attachment structures.

Two types of cystocarp are said to occur in the Gelidiales: one is unilocular with one potential ostiole, and carposporangia formed singly or in chains on a basal placenta; the other is bilocular with a central partition and two or more potential ostioles, and carposporangia formed singly or in terminal clusters from paired placentae on either side of the central partition (Bornet & Thuret, 1876, p. 59–61; Fan, 1961, p. 348; Santelices 1990).

[1] Erroneously referred to as "*Gelidiella tenuissima* Feldmann et Hamel" in South & Tittley (1986, p. 39), and several recent publications, referring to the comments in Feldmann & Hamel, (1936, p. 226). The correct name is *Gelidiella pannosa* (J. Feldmann) J. Feldmann et Hamel, as this name has nomenclatural priority (see Fan, 1961, p. 340, adnot.).

In terms of its vegetative and reproductive structures, *G. minima* clearly belongs to the Gelidiales. It probably possesses a *Polysiphonia*-type life history, the observed dominance of tetrasporphytes is likely to be little more than a feature of its population biology. Such dominance of tetrasporangial plants in the wild has been reported frequently in the Gelidiales (see Hommersand & Fredericq, 1988), which may be due to tetrasporangial plants being better suited to survival in certain habitats than gametangial plants. In some species of *Gelidium*, such as *G. pusillum* (Stackhouse) Le Jolis and *G. latifolium* (Greville) Bornet et Thuret (Dixon, 1985; Dixon & Irvine, 1977), gametangial plants are exceedingly rare, yet these species have a normal *Polysiphonia*-type life history sequence in culture (Rueness & Fredriksen, 1989; Guiry, unpubl. data).

The apical cell of *Gelidiella minima* and its derivative cells are typical of the Gelidiales, and although the persistence of the axial cell, perixial cells and their second-order derivatives in an identifiable row throughout the length of the thallus is not found in all species of the order, it does seem to be a feature of many of the smaller species, such as *G. calcicola* (Maggs & Guiry, 1987). The development of spermatangia, which have not been previously reported in the genus *Gelidiella*, is typical of the order (Fan, 1961; Akatsuka 1970, 1973, 1979; Hommersand & Fredericq, 1988). Young female reproductive structures and nutritive filaments were not found in *G. minima*, and no comment can be made on post-fertilization events and the initial development of the carposporophyte. The mature cystocarp is of the first type mentioned above: unilocular with a single ostiole, and carposporangia are formed from the base of the cystocarp. Of the genera with this type of vegetative morphology included in the Gelidiales, only *Pterocladia* has been reported to have this cystocarp structure (J. Agardh, 1851 p. xi, 1852, p.482; Bornet & Thuret, 1876, p. 60; Fan, 1961, p. 348, p. 335; Fredriksen & Rueness, 1990, p. 188). Although cystocarps have not been reported for any of the 22 described species of *Gelidiella* (Maggs & Guiry, 1987), Sreenivasa Rao & Trivedi (1986?) gave a preliminary account of the cystocarp of a "*Gelidiella* sp." from Diu I., off the Saurashtra coast of India. Full details were not given, but it would appear that the structure of the cystocarp is of the basal placenta-type described above.

If the cystocarp structure of *G. minima* is typical of the genus *Gelidiella* as a whole, then this genus is closely related to a number of putative species of *Pterocladia*. Fan (1961, p. 336 *et seq.*, pl. 41) described the development of the cystocarp in the type species of *Pterocladia*, *P. lucida* from New Zealand, and found that an unilocular cystocarp with one ostiole is formed. Unlike most other species attributed to *Pterocladia*, the cystocarp arises from a placental tissue which does not become separated from the wall of the cystocarp. The placenta is extensive and carposporangia do not arise centrally from the region of the axial cell, but rather from its whole surface. This may prove to be a valid generic character in the separation of true *Pterocladia* species from true *Gelidiella* species.

In *Pterocladia capillacea* (S. G. Gmelin) Bornet et Thuret, plants are only rarely found fertile in the North Atlantic and not at all in the British Isles (Dixon & Irvine, 1977, p. 135). Bornet & Thuret (1876, pp. 59–61, pl. 22, figs 1–3) carried out a detailed study of cystocarpic material from Biarritz, Atlantic France, describing and illustrating the cystocarp as being unilocular with the carposporangia arising in chains from a basal placenta. However, Bornet & Thuret (1876, p. 60) also noted that cystocarps with two ostioles occasionally occur (in which case the carposporophyte forms on both faces of an eccentric septum) although they considered these occurrences to be exceptional. Although *P. capillacea* is said to be widely distributed world-wide, there are some difficulties with reliable identification of the species, which are compounded by a general paucity of fertile plants. A further problem is that the lectotype of *Fucus capil-*

laceus S. G. Gmelin, the basionym, is an illustration of a plant in Gmelin (1768, pl. 15, fig. 1), said to have been collected somewhere in the Mediterranean. In the absence of a more precise type locality, it is difficult, given that several entities conforming to the general habit range associated with *P. capillacea* occur in the Mediterranean, to be certain what represents true *P. capillacea*. A much more satisfactory solution might be to suppress the use of Gmelin's illustration as a lectotype and to select instead a neotype, preferably of cystocarpic material. Nevertheless, it would appear that the types of cystocarp development in *P. capillacea* and *G. minima* are similar. Gonimoblasts in both are generally formed initially on a basal placenta in the cystocarp, arise mainly in the region of the axial cell, are borne in short, branched or unbranched chains, and are generally enclosed in a unilaterally bulging pericarp pierced by a single ositole. In *P. lucida*, although the carposporophyte is formed on a basal placenta, it is not restricted to the region of the axial cell. According to Fan (1961, p. 337), branched filaments develop from the fertilized carpogonium; these develop gonimoblast initials which divide repeatedly to produce septate filaments that form a tangled mass around the "central cells" (including the basal cells of the second and third orders), which results in an extensive placental area.

The cystocarp development of *Pterocladia melanoidea* (Schousboe ex Bornet) Fredriksen et Rueness as described by Fredriksen & Rueness (1990) is very similar to that of *G. minima* and *P. capillacea*. *P. melanoidea* had, for many years, been referred to the genus *Gelidium*, but cystocarps were unknown. Using cultured material, these authors were able to describe the cystocarp morphology and referred the species to the genus *Pterocladia* on the basis of the single ostiole and locule of the cystocarp. However, in a manner similar to *P. capillacea* and *G. minima*, the carposporangia arise in chains in the vicinity of the axial cell on the floor of the cystocarp. *P. melanoidea* is of further interest in that rhizines are very scarce in the medulla, and entirely absent in the younger parts of the fronds (Fredriksen & Rueness, 1990).

If *P. capillacea*, *P. melanoidea* and *G. minima* are closely related in terms of cystocarp morphology, they may indicate, collectively, that there is a relationship between overall front length and the presence of rhizines: in the largest of these species (*P. capillacea*; 100–150 mm high), rhizines are common in the medulla; in the intermediate species (*P. melanoidea*; 10–15 mm high), they are rare and only found in any quantity in the older parts of the thallus; in the smallest species (*G. minima*; 1·0–1·5 mm high), they are entirely absent. Although cystocarpic plants are unknown in *G. calcicola* (Maggs & Guiry, 1987), the structure of the thallus is very similar to that of *G. minima*, and the occurrence of rhizines only in the attachment structures of this species, which does not exceed 30 mm in length, could be regarded as further evidence of a relationship between absolute size and the occurrence of rhizines. Similarly, there could be a relationship between vegetative size and the extent of the cystocarpic placenta.

At present, a generic reallocation of species of *Gelidiella* and *Pterocladia* would be premature or not possible, as cystocarps are unknown for all described species of *Gelidiella* and undescribed or poorly known in many species of *Pterocladia*. Thus, if the presence/absence of rhizines is abandoned as a generic character in favour of cystocarp structure, generic placement of these species would not be possible. Nevertheless, the genus *Gelidiella* appears to be polyphyletic as presently circumscribed in that species with tetrasporangia in recognizable rows and species with scattered tetrasporangia (similar to those found in species of *Gelidium*) are included (Feldmann & Hamel, 1936; Maggs & Guiry, 1987). It is probably generically significant that *P. melanoidea*, *G. calcicola*, *G. minima*, and a number of other species of *Gelidiella* and *Pterocladia* all possess well-ordered rows of tetrasporangia, but they are

scattered in the type of species of *Gelidiella*, *G. acerosa* (Forsskål) J. Feldmann et Hamel (Maggs & Guiry, 1987). In *P. lucida* and *P. capillacea*, tetrasporangia appear to be scattered in the mature sori, but further studies of the arrangement of sporangia in the young sori are necessary.

Several different arrangements of genera are therefore possible. Characters such as the presence vs the absence of rhizines, scattered vs. ordered tetrasporangia, extensive vs. confined placenta, and one ositole vs. two or more may be considered clinal and the species of *Gelidiella*, *Pterocladia*, *Gelidium* included in a study genus. Alternatively, four genera can be recognized, based on shared, derived characters: *Pterocladia sensu stricto* with a single ostiole, broad basal placentation, and unordered tetrasporangia; *Gelidium* with two osioles, central placentation, and unordered tetrasporangia; *Gelidiella* with an unknown arrangement of ostioles and placenta (as cystocarps are unknown in the type species), and unordered tetrasporangia; and a fourth genus (for which no name is available) with a single ostiole, narrow basal placentation, and tetrasporangia in ordered rows. The latter genus would include *G. minima* and probably, several species currently referred to *Gelidiella*, *Pterocladia* and *Gelidium*.

However, until more detailed information becomes available on the structure and reproduction of genuine material of the type species of *Gelidiella* and *Pterocladia*, it seems best to maintain the *status quo* and to base *Gelidiella* on the absence of rhizines in the erect fronds and to include *G. minima* in this genus.

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Note added in proof. Recent collections of *Gelidiella minima* sp. nov. in South Australia conform in detail with the type material, but do show a few rhizines in the lower erect axes and in the stolons, and re-examination of the holotype shows 2–5 rhizines in some transverse sections but not in others. The taxonomic position of *G. minima* thus requires further investigation, but it is probably most closely related to *Pterocladia melanoidea* (Schousboe ex Bornet) Fredriksen et Rueness (1990, p. 182) from which it differs in its much smaller size and in shorter rows of tetrasporangia. However, many of the species currently included in *Pterocladia* and *Gelidiella* do not conform well with the type species of these genera and further detailed anatomical studies are necessary before a truly representative generic scheme can be elucidated. The diminutive size and largely creeping axes of *G. minima* are characters more in conformity with a number of species currently placed in *Gelidiella.*