



Taxonomic review of the species of *Pterocladia* (Gelidiales, Rhodophyta)

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Abstract

Segregating *Pterocradiella* from *Pterocladia* stimulated new taxonomic studies of the species originally assigned to *Pterocladia*. A total of 28 species are ascribed to the genus, one of them with doubts. Thirteen of the 27 names are synonyms. Three of the remaining 14 species belong with *Gelidium*, including *G. americanum*, *G. mcNabbianum* (Dawson) comb. nov. and *G. musciformis*. Seven other species belong with *Pterocradiella*, including *P. bartlettii* (Taylor) comb. nov., *P. bulbosa*, *P. caerulea*, *P. caespitosa* (Kyllin) comb. nov., *P. caloglossoides* (Howe) comb. nov., *P. capillacea* and *P. melanoidea*. Two species are retained in *Pterocladia*, the type *P. lucida* and *P. rectangularis*. Two others, *P. heteroplatos* and *P. media* are placed in *incertae sedis* as additional studies of fertile materials are needed to determine their generic status. The genus *Pterocladia* now appears to include two large-sized species restricted to Australia-New Zealand. *Pterocradiella* has 8 small-sized species (including *P. minima*), mainly inhabiting tropical and subtropical waters. Future research documenting sexual reproduction in *Gelidiella* and solving the presently recognized heterogeneity in *Gelidium* will help to trace the relationships between *Pterocradiella* and these two genera.

Introduction

The genus *Pterocradiella* includes species with carpogonia directed to both surfaces of the thallus, nutritive filaments growing centripetally forming a virtually solid cylinder around the central axis and cystocarps usually attached to one side of the cystocarp floor, producing chains of carposporangia from the remaining three sides (Santelices & Hommersand, 1997; Santelices, 1997a).

The most distinctive morphological characters of this new genus is seen in transection of the mature cystocarp. The ovoid or triangular-shaped cavity exhibits chains of carposporangia radiating from a core of gonimoblast filaments surrounding the central axis. Despite interspecific differences in early and late stages of carpogonia and cystocarp development (Santelices, 1997a), this structure is present in all species to be included in *Pterocradiella*.

Segregating *Pterocradiella* from *Pterocladia* motivates re-examination of the species originally assigned to *Pterocladia*. Such an evaluation is made in this study. A list of all species originally assigned to *Pterocladia* is compiled and the taxonomic status of all taxa is evaluated either through new studies on cystocarpic structure or based on data in the literature. A morphological and geographic characterization of the two genera is presented.

The type materials of several species originally assigned to *Pterocladia* did not include fertile female plants. In the present study, care has been taken to use cystocarpic plants resembling closely the type materials, collected within the known geographic range of the species, and previously identified by a taxonomist with experience in the group.

Table 1. Specimens examined in this study

| Species | Locality and date | Determined by | Collection number |
|---|---|------------------|------------------------------|
| <i>Pterocladia bartlettii</i> Taylor | Calabash Bay Manchester Parish Jamaica 22 III 1956 Tetrasporic | W.R. Taylor | W.R. Taylor 56–199 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | On rocks, Bananier, Le Guadeloupe (Antilles) 1 April, 1944 | W.R. Taylor | W.R. Taylor 22345 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | On rocks, Bananier, Le Guadeloupe (Antilles) 31 April, 1944 Tetrasporic | W.R. Taylor | W.R. Taylor 22382 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | Port Morant St. Thomas Parish, Jamaica 15 II 1956 Cystocarpic | W.R. Taylor | W.R. Taylor 56–13 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | Calabash Bay Manchester Parish Jamaica 3 IV 1956 Tetrasporic | W.R. Taylor | W.R. Taylor 56–352 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | Playa Tallaboa, Guayanilla, southern coast of Puerto Rico 31 I 1959 Tetrasporic | M. Díaz-Piferrer | D.B. 418 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | Guánica, southern coast of Puerto Rico 17 I 1959 | M. Díaz-Piferrer | D.B. 288 (U.M.) |
| <i>Pterocladia bartlettii</i> Taylor | Bai Anglais Aquín, Haiti Jan. 1929 Tetrasporic | W.R. Taylor | W.R. Taylor 14107 (U.M.) |
| <i>Pterocladia caespitosa</i> (Kylin) Norris | Seychelles: northeast point of Mahé I. October 25, 1964 On crustose coralline Cystocarpic and Tetrasporic | M. Wynne | M. Wynne 3P-21 (U.M.) |

Table 1. (continued)

| Species | Locality and date | Determined by | Collection number |
|--|--|-----------------|-------------------------|
| <i>Pterocladia caloglossoides</i> (Howe) Dawson | Point Joe, California, USA June 22, 1963 Cystocarpic | G.J. Hollenberg | U.S. 085690 |
| <i>Pterocladia caloglossoides</i> (Howe) Dawson | Growing on rocks, low littoral, Fairview Point, Laguna Beach, Orange County, California, USA Dec. 1936 | G.J. Hollenberg | U.S. 077815 |
| <i>Pterocladia mcnabbiana</i> Dawson | Protected rocks, Bahia Culebra, Costa Rica Cystocarpic | E.Y. Dawson | U.S. 1777 (ex B.F.) |
| <i>Pterocladia mcnabbiana</i> Dawson | Protected bay near La Union, Golfo de Fonseca, El Salvador Sept. 6, 1960 | E.Y. Dawson | U.S. 21874 (ex B.F.) |

U.S. = USA National Herbarium, Smithsonian Institution.

U.M. = Herbarium of the University of Michigan.

Materials and methods

General procedures followed those described in previous morphological studies (e.g. Santelices, 1991a,b; 1997a; Santelices & Flores, 1995; Santelices & Hommersand, 1997). Herbarium specimens of *Pterocladia caloglossoides*, *P. caespitosa*, *P. bartlettii* and *P. mcnabbiana* were available for study (Table 1). Fertile female gametophytes were examined under a stereomicroscope for cystocarps. A sample of 3–5 cystocarps of different sizes and presumably different maturation stages was obtained from different blades. Cystocarps in herbarium specimens were gradually rehydrated, avoiding tissue damage, and fixed in a 10% formaldehyde solution in seawater. Fixed cystocarps were embedded in gelatin and sections cut 20–30 µm thick to avoid destruction of sporogenous tissue, using a Leitz freezing microtome. Sections were stained with 1% aniline blue and mounted in 50% Karo (registered Trade Mark) corn syrup. Photomicrographs were taken with a Nikon Biophot Microscope. Slides with transections are deposited in the algal collection of the Sala de Sistemática, Pontificia Universidad Católica de Chile (SS/UC).

Results

The species of Pterocladia

A total of 28 species have been assigned to the genus *Pterocladia*. All but one are included in Table 2.

The species excluded is *Pterocladia? tripolitana* De Toni & Levi (1888), collected in Tripoli, Libya, and assigned with doubts to the genus. Apart from the inclusion of this species in a floristic list of the algae from Libya (Nizamuddin et al., 1979) no additional report on this taxon has been found.

Thirteen of the 27 species (Table 2) are synonyms of species now included in *Gelidium* or *Pterocladia*. Six other species have been transferred either to *Gelidium* (*G. americanum*, *G. musciformis*) or to *Pterocladia* (*P. bulbosa*, *P. caerulea*, *P. capillacea* and *P. melanoidea*). One species, *Pterocladia lucida* is the type species of the genus; the generic status of the remaining seven species is critically assessed in the following pages.

Species re-examined

Pterocladia bartlettii Taylor, 1943, p. 156; pl. 4, Figure 2; 1960, p. 359, pl. 46, Figure 2; Díaz-Piferrer, 1970, p. 172; Edwards, 1970, p. 34, Figures 120, 122; Ganesan, 1989, p. 45.

This species has been reported from Texas and the Gulf of Mexico (Edwards, 1970), several Caribbean Islands, including Cuba, Jamaica, Haiti, Puerto Rico, Hispaniola and Guadalupe (Taylor, 1943, 1960) and various localities in Venezuela (Isle Coche; States of Aragua and Sucre; Díaz-Piferrer, 1970; Ganesan, 1989).

Table 2. Present status of the species originally assigned to the genus *Pterocladia*

| Taxon | Present Status | References |
|---|-------------------------------------|---|
| 1. <i>P. americana</i> Taylor | Transferred to <i>Gelidium</i> | Santelices 1976 |
| 2. <i>P. bartlettii</i> Taylor | Transferred to <i>Pterocladia</i> | This study |
| 3. <i>P. bulbosa</i> Loomis | Transferred to <i>Pterocladia</i> | Santelices 1997a |
| 4. <i>P. capillacea</i> (Gmelin) Bornet et Thuret | Transferred to <i>Pterocladia</i> | Santelices & Hommersand 1997 |
| 5. <i>P. caerulescens</i> (Kützting) Santelices | Transferred to <i>Pterocladia</i> | Santelices & Hommersand 1997 |
| 6. <i>P. caespitosa</i> (Kylin) Norris | Transferred to <i>Pterocladia</i> | This study |
| 7. <i>P. caloglossoides</i> (Howe) Dawson | Transferred to <i>Pterocladia</i> | This study |
| 8. <i>P. complanata</i> Loomis | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 9. <i>P. densa</i> Okamura | Synonym of <i>P. capillacea</i> | Santelices 1991a |
| 10. <i>P. heteroplatus</i> (Børg.) Rao & Kaliaperumal | In the genus <i>Pterocladia</i> | Børgesen 1934, Umamaheswara Rao & Kaliaperumal 1980 |
| 11. <i>P. lindaueri</i> Fan | Synonym of <i>P. capillacea</i> | Adams 1994 |
| 12. <i>P. lucida</i> (R. Brown) J. Agardh | Type species of <i>Pterocladia</i> | Adams 1994, Womersley 1994 |
| 13. <i>P. mcNabbiana</i> Dawson | Transferred to <i>Gelidium</i> | This study |
| 14. <i>P. media</i> Dawson | In the genus <i>Pterocladia</i> | Dawson 1958, Stewart 1974 |
| 15. <i>P. melanoidea</i> (Schousboe ex Bornet) Dawson | Transferred to <i>Pterocladia</i> | Santelices & Hommersand 1997 |
| 16. <i>P. mexicana</i> Taylor | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 17. <i>P. musciformis</i> Taylor | Transferred to <i>Gelidium</i> | Santelices 1991a |
| 18. <i>P. nana</i> Okamura | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 19. <i>P. okamurai</i> (Setchell & Gardner) Taylor | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 20. <i>P. parva</i> Dawson | Synonym of <i>P. caloglossoides</i> | Stewart & Norris 1981 |
| 21. <i>P. pinnata</i> (Hudson) Papenfuss | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 22. <i>P. pyramidale</i> (Gardner) Dawson | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 23. <i>P. rectangularis</i> (Lucas) Womersley & Guiry | In the genus <i>Pterocladia</i> | Lucas 1931, Womersley & Guiry 1994 |
| 24. <i>P. rigida</i> Loomis | Synonym of <i>P. caerulescens</i> | Santelices 1976 |
| 25. <i>P. robusta</i> Taylor | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 26. <i>P. tenuis</i> Okamura | Synonym of <i>P. capillacea</i> | Stewart 1968 |
| 27. <i>P. tropica</i> Dawson | Synonym of <i>P. caerulescens</i> | Santelices 1976 |

The materials available for study (Table 1) agree well with the descriptions of the species provided by Taylor (1943, 1960) and Felicini and Perrone (1994). The larger thalli are up to 5–6 cm tall, bushy, dull purplish, with many narrow, entangled erect axes. Attachment often is by cylindrical or slightly compressed rhizomatous branches which bear holdfasts at variable distances. Erect axes are compressed below, flattened above, up to 0.6 mm wide, up to 150 μm thick, divided into secondary axes similar to the primary erect axes but slightly more cylindrical. Primary and secondary branchlets are of variable shapes and disposition. Frequently the branchlets form bilateral series along the margins of axes but also they may occur on only one side of the axes or several (4–5) branches may originate from a somewhat expanded part of frond. Small branchlets are oblanceo-

late, older branchlets are elongated, linear and ligulate, often ending in a apiculate tip. Young tetrasporangial branchlets are often with sori in stichidium-like enlargements at the end of cylindrical or compressed branchlets and spores arranged in V-shaped rows. Older tetrasporangial branchlets are generally compressed, lacking the stichidium-like enlargement and the V-shaped arrangement of spores.

Transections through immature cystocarps (Figure 1a) show rounded, nearly isodiametric nutritive cells, forming a ring of tissue around the axial cells. Cystocarps in more advanced stages of development (Figures 1b, 1c) exhibit carposporangia in chains at the tip of carposporangial filaments. The gonimoblast cells on the lower side of the cystocarp link to inner cortical cells and do not form carposporangia. Carpospores appear as if radiating from a core of

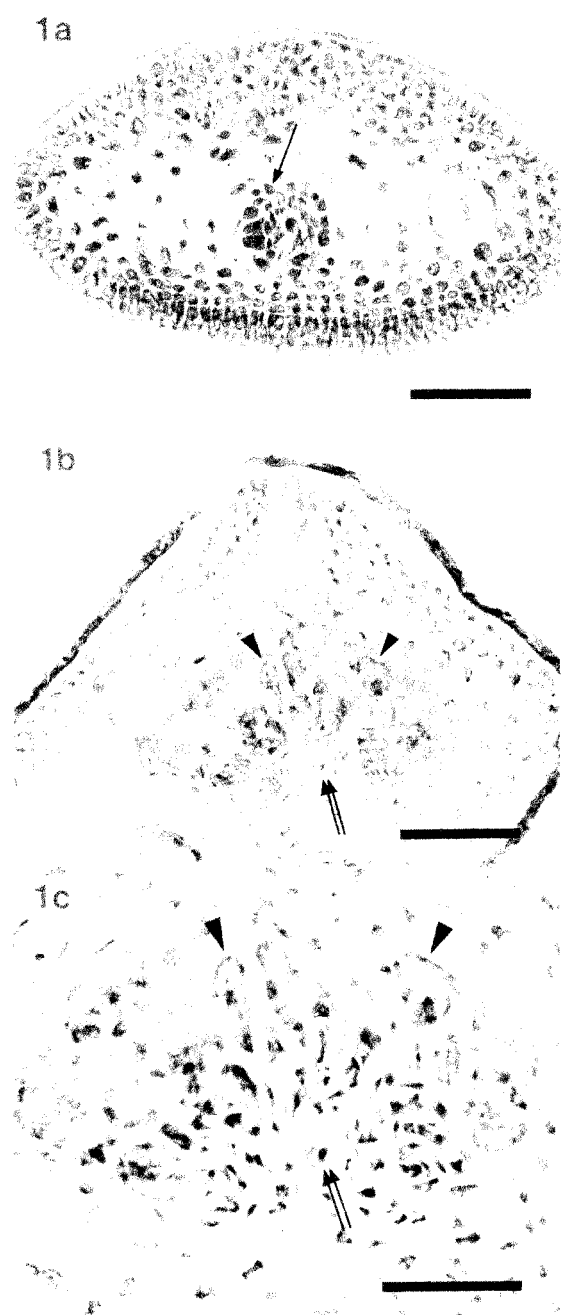


Figure 1. Cross sections of cystocarps of *Pterocladia bartlettii* at different maturation stages. a) Cross-section of young cystocarp. Nutritive cells (black arrow) form a ring around the central axis (white arrow). The upper cystocarpic wall is slightly pushed on the upper side while the gonimoblast attaches to the cortical cells in the cystocarpic floor. Bar = 50 μ m. b) Mature cystocarp. Chains of spores appear as if radiating from the central axis (double arrow). Note the triangular shape of the cystocarpic cavity. Bar = 30 μ m. c) Enlargement of spores (arrow head) radiating from the axial cell (double arrow). Bar = 30 μ m.

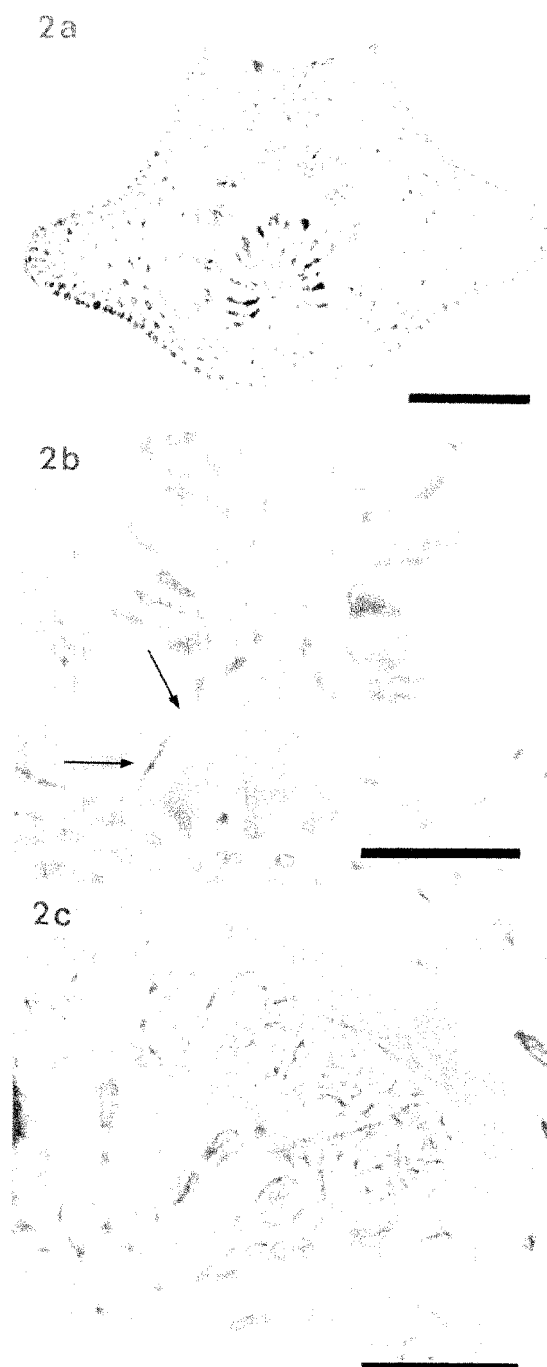


Figure 2. Cross section of a mature cystocarp of *Pterocladia caespitosa*. a) General view of the gonimoblast attached to the cystocarpic floor by elongated cortical cells and chains of carpospores radiating from the placental tissue. Bar = 100 μ m. b) Details of the cortical cells (arrows) attaching the gonimoblast to the cystocarpic floor. Bar = 30 μ m. c) Closer view of chains of carpospores maturing basipetally. Bar = 30 μ m.

gonimoblast filaments surrounding the central axis. The cystocarp wall is elevated on one side, forming a single cavity. This cystocarpic structure is typical of the genus *Pterocladia*. Therefore the new combination *Pterocladia bartlettii* (Taylor) Santelices is proposed, based on *Pterocladia bartlettii* Taylor, 1943: p. 156, pl. 4, Figure 2.

Pterocladia caespitosa (Kylin) R.E. Norris, 1987, p. 42

Basionym: *Gelidium caespitosum* Kylin, 1938, p. 8, Figures 2E–2H; R.E. Norris, 1992, p. 11–12, Figures 3–4.

The plants collected and identified by M. Wynne in Seychelles Isles agree well with previous descriptions of this species, which up to now has been known from Kenya, Natal and Mozambique (Felicini & Perrone, 1994). The thalli are up to 10 mm high and 1 mm broad, formed by cylindrical, stoloniferous creeping axes and erect, mostly unbranched slightly flattened branches. Branches with obtuse ends. Infrequently with small branchlets close to the distal end. Cortex formed by 3 layers of cells, increasing in size inwardly. Medulla of 4–5 layers of larger medullary cells with scattered rhizoidal filaments. Tetrasporangia in single, extensive sori in the somewhat expanded tips of erect branches. Tetraspores initially arranged in V-shaped rows. Arrangements tend to be lost in older sori.

A transection through a mature cystocarp shows the gonimoblast disposed in the central part of the single cavity (Figure 2a), attached to the cystocarpic floor by elongated cortical cells (arrows in Figure 2b) that extend from the inner cortex to the fertile placental tissue around the axial cell. Orderly arranged chains of carposporangia radiate from the gonimoblast tissue (Figures 2a and 2c). Mature carpospores (Figure 2c) are much larger than those immediately below along each chain. They form a ring around the sporogenous tissue, suggesting simultaneous maturation of many of them.

A longitudinal section of the cystocarps of the plants from the Seychelles fully agrees with the longitudinal section of the cystocarps of this species illustrated by Norris (1987, Figure 8; 1992, Figure 2b) using fertile female thalli from Natal. This cystocarpic structure, however, corresponds to the genus *Pterocladia*. Therefore, the new combination *Pterocladia caespitosa* (Kylin) Santelices is proposed, based on *Gelidium caespitosum* Kylin, 1938, p. 7, Figures 2E–2H.

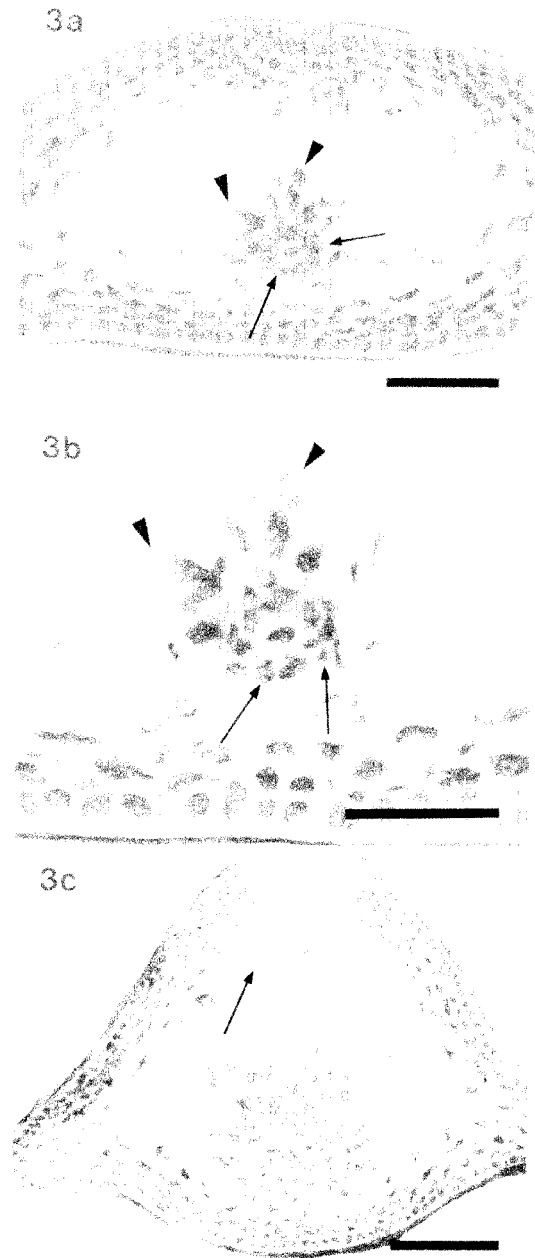


Figure 3. Cross section of cystocarps of *Pterocladia caloglossoides* at different maturation stages. a) Cross section of a young cystocarp showing the cystocarpic wall elevated on one side, the gonimoblast attached to the cystocarpic floor, nutritive cells (arrows) forming a ring around the central axis and a few carpospores differentiating (arrow heads). Bar = 50 μ m. b) Enlargement of Figure 3a showing the central axis, the ring of nutritive cells (arrows) and chains of carposporangia (arrow head) differentiating at the tip of carpogonial filaments. Bar = 30 μ m. c) Cross section through a triangular-shaped, mature cystocarp. Chains of carpospores appear as if they were radiating from the central filament. Elongated, cortical cells extend from the inner cortex to the placenta of fertile tissue (arrow). Bar = 100 μ m.

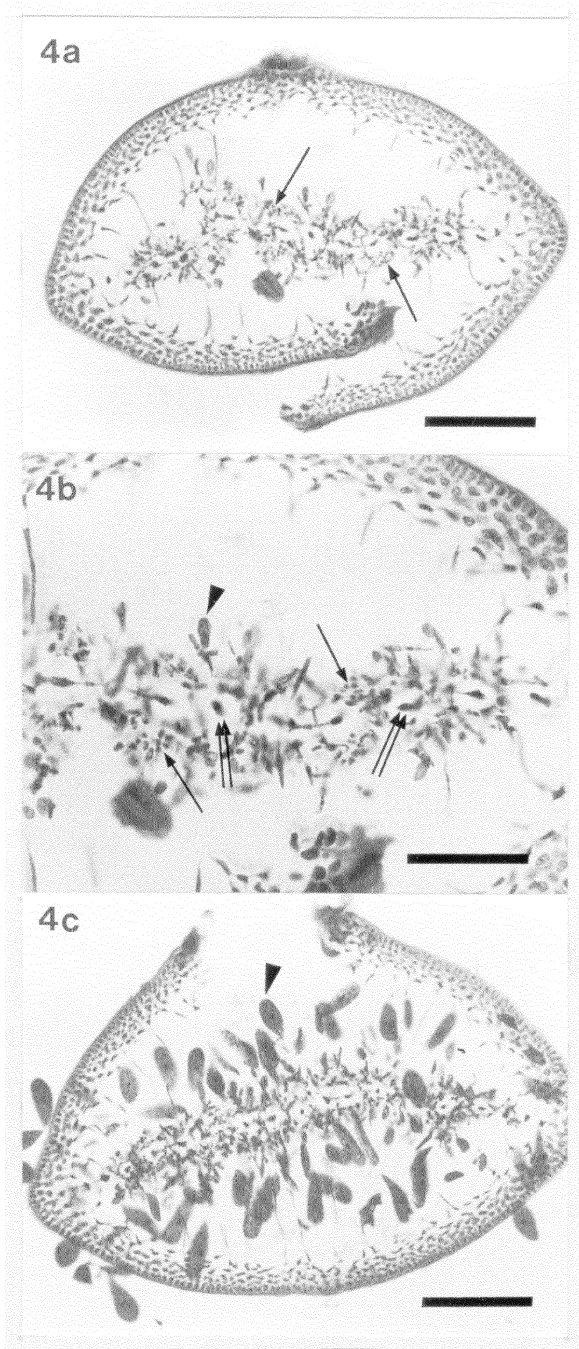


Figure 4. Typical *Gelidium*-type cystocarp in fertile female gametophytes of *Pterocladia mcnabbiana*. a) and b) Cross section through a young cystocarp. The two locules develop at approximately the same rate; nutritive filaments (arrows) form a core around each second order cell (double arrow). Gonimoblast filaments and differentiating carpospore (arrow head) can also be seen. Bar in Figure 4a = 100 μm , in Figure 4b = 50 μm . c) Transection through a cystocarp with mature carpospore (arrow head) and two ostioles. Bar = 100 μm .

Pterocladia caloglossoides (Howe) Dawson, 1953, p. 76–77, pl. 6, Figure 1; Norris & Hollenberg, 1969, p. 116; Hollenberg & Abbott, 1969, p. 49; Acleto, 1973, p. 31; Abbott & Hollenberg, 1976, p. 349; Santelices, 1977, p. 78, Figures 6d, 6e; Santelices & Abbott, 1978, p. 218; Stewart & J.N. Norris, 1981, p. 281; Cribb, 1983, p. 34, pl. 7, Figures 2–5; R.E. Norris, 1987, p. 39; Renfrew et al., 1989, Figures 39–41; Hatta & Prud'Homme van Reine, 1991, p. 373, Figure 13

Basionym: *Gelidium caloglossoides* Howe, 1914, p. 96, pl. 34, Figure 7, pl. 35; Weber van Bosse, 1921, p. 226; Norris, 1992: p. 13–14, Figure 5.

Synonym: *Pterocladia parva* Dawson, 1953, p. 77, pl. 6, Figure 2; 1954, p. 42, Figures 33a–c; Jaasund, 1977.

Repeated findings of this species document a widespread distribution in temperate and warmer waters, specially in the Pacific. It has been found along Pacific South America from central Chile to northern Peru, along Pacific North America, from Mexico to Washington, U.S.A., and in British Columbia, Canada. Also it has been reported from the Hawaiian Islands, Indonesia and the Great Barrier Reef in Australia. Outside the Pacific, it has been found in Guadeloupe Is., Natal and Tanzania.

Despite this extended geographic distribution, several morphological characters remain fairly constant in all collections so far reported. They include divaricate branches, produced radially and often opposite the attachment points, the occurrence of one row of medullary cells, the large size of the cortical cells and the V-shaped arrangement of young sporangia.

The specimens studied (Table 1) agree well with previous descriptions of this species. They are up to 1.2 cm high and have both creeping and erect axes. Creeping axes are mostly cylindrical, sometimes flattened, 150–200 μm wide, attached to the substratum by small peg-like holdfasts. Erect axes are formed at many points of attachment, arising in numbers of 1–5, flattened except at the base, up to 600 μm broad, generally unbranched or with irregularly arranged branchlets of irregular lengths. Erect axes also may become repent, exhibiting attachment discs and erect branchlets. Cortex with three to four layers of rounded, pigmented cells and medulla with a simple row of thick-walled axial cells surrounded by rhizoidal filaments. Tetrasporangia not found in the specimens studied.

A transection through immature cystocarps show nearly isodiametric nutritive cells (arrows in Fig-

ures 3a and 3b) forming a ring around the axial cell. Carposporangia in short chains (Figures 3a and 3b) differentiate at the tip of gonimoblast filaments. The cystocarpic wall is elevated on one side, forming a single cystocarpic cavity, while the gonimoblast cells on the lower side of the cystocarp link to inner cortical cells.

Cystocarps in more advanced stages of development (Figure 3c) appear triangular-shaped in cross section, with the gonimoblast attached to the cystocarp floor and chains of carposporangia that appear radiating from a core of gonimoblast filaments surrounding the central axis. Carpospores form chains at the tip of carposporangial filaments and mature basipetally. The gonimoblast cells on the lower side of the cystocarp link to inner cortical cells and do not form carposporangia. Elongated, internal cortical filaments extend from the inner cortex to the placenta of fertile tissue around the axial cell. This internal cystocarpic structure is typical of the genus *Pterocladia*. Therefore, the new combination *Pterocladia caloglossoides* (Howe) Santelices is proposed, based on *Gelidium caloglossoides* Howe, 1914, p. 96, pl. 34, Figure 7, pl. 35.

Pterocladia heteroplatos (Børgeesen) Umamaheswara Rao & Kaliaperumal, 1980, p. 109–111, Figure 1.

Basionym: *Gelidium heteroplatos* Børgeesen, 1934, p. 3, Figure 3; Durairatnam, 1961, p. 50, pl. 12, Figures 5–7; Umamaheswara Rao & Sreeramulu, 1970, p. 36.

This species was described from materials collected by Børgeesen in Malabar Hill, Bombay, on littoral rocks facing the Arabian Sea (Børgeesen, 1934). The specimens are up to 6 cm tall, forming dense tufts or low mats on rocky substrate, attached by discoid holdfasts arising from prostrate axes. Erect axes are alternately terete and compressed, the flattened parts reaching a breadth of up to about 600–800 μm . Axes are simple to distichously and irregularly branched; branches alternate, opposite, rarely secund, narrow, terete, subterete or compressed at the base, broadened above, sometimes tapering at the summits. The thallus has a cortex of 2–3 layers of pigmented cells and a medulla of subcylindrical cells, surrounded by thick walled rhizoids. Tetrasporangial sori with sterile margins; sori scattered on the compressed branches and branchlets.

Cystocarps are described (Umamaheswara Rao & Kaliaperumal, 1980, Figure 1c) as unilocular, with marked swelling and one ostiole, rarely two, on one side of the frond. Since the illustration of the cystocarp did not include a transection of the cystocarp, no conclusion is possible at this time on the species belonging to *Pterocladia* or *Pteroclatiella*. The illustration of the tetrasporangia (Umamaheswara Rao & Kaliaperumal, 1980, Figure 1b) suggests tetrasporangia arising acropetally but not forming V-shaped rows.

Several authors (e.g.: Børgeesen, 1934; Santelices, 1977; Umamaheswara Rao & Kaliaperumal, 1980) have called attention to the morphological similarity between *Pterocladia heteroplatos* and *Gelidium crinale* f. *luxurians* Collins. Umamaheswara Rao & Kaliaperumal (1980) in fact indicated that in other studies Børgeesen (1939, 1943) treated *G. heteroplatos* as *G. crinale*. When cystocarps were found, Umamaheswara Rao & Kaliaperumal (1980) indicated that since bilocular cystocarps had been described for *Gelidium crinale*, the Indian species with unilocular cystocarp corresponded to *Pterocladia*. The authors apparently were unaware of the finding (Stewart, 1974) of unilocular cystocarps in materials of *Gelidium crinale* f. *luxurians* and the inclusion of this last species in the concept of *Pterocladia media* (see below). It appears, therefore, that comparative studies using fertile, representative specimens of *P. heteroplatos*, *P. media* and *G. crinale* f. *luxurians*, are needed to determine the generic and the specific status of this taxon.

Pterocladia mcnabbiana Dawson, 1957, p. 14, Figures 4c–d; Dawson, 1961, p. 409, pl. 2, Figures 5–6; Dawson et al., 1964, p. 41, pl. 62, Figure c; Stewart & J.N. Norris, 1981, p. 274

As Felicini & Perrone (1994) indicated, there are few records of this species, which has only been collected in the tropical Pacific coast of America. *Pterocladia mcnabbiana* was first described from small, mat forming gelidioids living in extremely warm, sheltered areas in inner Golfo Dulce, Golfo Dulce, Costa Rica (Dawson, 1957). The type materials were collected from the iron hull of a sunken ship. Later, Dawson (1961) reported the same species forming small mats in protected shores, in Bahia Culebra, El Salvador. In both places the plants were short (up to 2 cm high), consisting of prostrate and erect axes. The prostrate system is conformed by ramified, subcylindrical, stoloniferous axes, about 100 μm diam., attached at frequent intervals to the substratum. They

give rise to erect or decumbent, simple or sparingly pinnate branches. These branches can be subcylindrical, stoloniferous or flattened, ligulate, up to 0.7 mm wide. Upper branchlets end in elongated, attenuated, subcylindrical, flagelliform extensions.

A cross section through the frond shows an outer cortex of 1 layer of small cells, 3–6 μm diam., an inner cortex of 1–2 layers of larger (8–12 μm diam.) cells and a narrow medulla, 22–25 μm wide, with rhizines scattered through it. Tetrasporangia borne in terminally expanded, flat, often digitiform, stichidial branches.

The species was later found in Puerto Peñasco, Gulf of Mexico (Stewart & Norris, 1981) and in northern Peru (Talara; Dawson et al., 1964). However, these last materials were assigned with doubts because the thalli were larger (up to 7 cm high) and more luxuriant than those from Costa Rica and El Salvador. In addition, the tetrasporangial branchlets were compound rather than simple. Later treatments of the Peruvian flora (Acleto, 1973) have not included this species.

New studies on some of the materials from Costa Rica and El Salvador examined by Dawson (Table 1) yield cystocarpic branchlets among the thalli collected in Bahía Culebra, Costa Rica. A transection through an immature cystocarp (Figures 4a and 4b) shows nutritive filaments forming a network of short chains around second- and third-order cells. A section through a more mature cystocarp shows a *Gelidium*-type cystocarp (Figure 4c) with two cavities separated by a placenta of fertile tissue, producing carpospores towards both sides of the fronds. The mature cystocarp is biconvex and has numerous, elongated, parallel inner-cortical filaments extending from the cortex to the placenta. The two cystocarpic locules are approximately symmetrical.

Given the above cystocarpic structure, this species should be removed from the genus *Pterocladia* and transferred to *Gelidium*. Therefore, the new combination *Gelidium mcnabbianum* (Dawson) Santelices is proposed, based on *Pterocladia mcnabbiana* Dawson, 1957, p. 14, Figures 4c–d.

Pterocladia media Dawson, 1958, p. 60, pl. 2, Figures 3–4; pl. 24, Figure 1; Stewart, 1974, p. 105–108, Figure 1; 1976, Figure 294; 1991, p. 73

Synonym: *Gelidium crinale* forma *luxurians* Collins, in Collins, Holden & Setchell, 1903 (PBA 1138); Collins, 1906, p. 111; Gardner, 1927, p. 277, pl. 46, Figure 1, pl. 47, Figure 3.

This species was described from a single collection of vegetative specimens gathered in intertidal habitats in La Jolla, California, U.S.A. Lacking fertile materials, Dawson (1958) probably included this species in the genus because axes were flat, ligulate, simple or sparingly branched and rhizines extremely scant and absent from some sections. When present they were sparsely scattered in the innermost medullary line. Dawson (1958) also suggested the species was intermediate in size between the very small *P. musciformis*, *P. mcnabbiana*, *P. caloglossoides*, and *P. parva* and the larger *P. pyramidale* and *P. complanata*.

As stated earlier (Table 2), *Pterocladia musciformis* and *P. mcnabbiana* belong with *Gelidium* while *P. caloglossoides*—including *P. parva*—and *P. capillacea*—including *P. pyramidale* and *P. complanata*—are now included in *Pterocladia*. Given the significant changes in species concept and generic limits that have occurred since its original description, and in the absence of fertile thalli among the type materials, *Pterocladia media* may in fact belong with *Gelidium*, *Pterocladia*, or *Pterocladia*.

No other reference to this species was made until Stewart (1974) studied collections of *Gelidium crinale* f. *luxurians*. Originally described by Collins, 1906 from materials collected in San Diego, its status was raised by Gardner (1927) to that of a variety; he also described vegetative and tetrasporic plants. Reviewing the Californian species of *Pterocladia*, Stewart (1974) found that numerous collections of small, narrow, sparsely branched gelidiaceous algae had been identified as belonging to this variety. However, these specimens could also be included in the morphological concept of *Pterocladia* accepted at that time. Three of these specimens have unilocular cystocarps. Therefore, Stewart (1974) concluded *G. crinale* var. *luxurians* should be transferred to the genus *Pterocladia* and the species with which the material could most appropriately be placed was *Pterocladia media*. To accommodate *G. crinale* var. *luxurians*, Stewart (1974) expanded significantly the description of *P. media*.

However, a comparison of the original description of *Pterocladia media* (Dawson, 1958) with the description and illustrations of *Gelidium crinale* f. *luxurians* provided by Gardner (1927) suggest important intraspecific differences. *P. media* reaches up to 3 cm tall while *G. crinale* f. *luxurians* is 6–7 cm tall; *P. media* has stoloniferous, creeping axes attached at short intervals by short, peg-like holdfasts, while *G. crinale* f. *luxurians* attaches itself by short rhizoids; erect axes in *P. media* are described as simple or sparingly inde-

terminately branched, usually by proliferations from broken ends. In upper parts the axes may develop one or more groups of many closely set, distichous, determinate, compressed branchlets mostly only 1.0–1.5 mm long. By contrast, in *G. crinale* var. *luxurians*, the main branches are mostly of three orders, each order reduced slightly in size, and chiefly distichous. While the medullary cells in *G. crinale* var. *luxurians* are described as uniform in size and appearance, the medulla of *P. media* is described as formed by two types of cells, an outer medulla of 3–4 cell layers of heavily pigmented isodiametric to elongate ellipsoidal cells and a narrow inner medulla of slender, much elongated pale cells.

Even though the species in the genera *Gelidium* and *Pterocladia* are morphologically variable, the above range and magnitude of variability suggests interspecific differences. Unfortunately Stewart's (1974) analysis did not document individuals that could be intermediate between *P. media* and *G. crinale* var. *luxurians* with respect to the above characters. Moreover there was no attempt to critically confront the specimens distributed by Collins as *G. crinale* f. *luxurians* in the Phycotheca Boreali-Americana (N° 1138) with materials later identified by others as belonging to this same species. None of the PBA N° 1138 materials examined by Stewart (1974) were fertile. All three cystocarpic specimens had been assigned to the species by later workers.

The above data suggest that the inclusion of *Gelidium crinale* f. *luxurians* as part of *Pterocladia media* is suspect. The materials described may represent one or two species, any one of which, or both, may belong to the genus *Pterocladia*. A new study of the materials available, including critical comparisons of original and later collections, seems advisable before further actions are taken on the taxonomy of these species.

Pterocladia rectangularis (Lucas) Womersley & Guiry, 1994, p. 141–142, pl. 40 D–F; pl. 41 K

Basionym: *Gelidium rectangulare* Lucas, 1931, p. 407, pl. 23, Figure 1.

This species was described (Lucas, 1931) from materials collected in Flinders Bay, Western Australia. Thalli can reach up to 30 cm high, formed by one to several pinnate to bipinnate axes, with pinnae and pinnules arising in close, regular series almost at right angles to the parent branch, becoming denuded below and attached by a fibrous holdfast. Axes are compressed, 1.5–2.5 mm broad throughout their length, thickened near the thallus base and above 600–

800 μ m thick. Pinnae are up to 15 mm long, up to 1.5 mm broad, slightly constricted at the base. Cortex 2–3 cells thick and medulla of elongate cells. Rhizines profuse, mainly in outer medulla. Tetrasporangia in short-stalked stichidia, terete to slightly compressed, becoming swollen terminally or centrally, up to 1.5 mm long and 150 μ m broad.

In 1994, Womersley and Guiry (in Womersley, 1994) reported the first cystocarpic plant known of this species. They found a distinctive unilocular, single ostiole characteristic of *Pterocladia* and transferred the species to this genus.

In their treatment of the species of *Pterocladia*, Womersley and Guiry distinguished between the broad-based carposporophyte typical of *Pterocladia lucida* from the carposporophyte 'tufted around the axial cell' typical of *Pterocladia capillacea*. As explained in the introduction, such a distinction is the basis for segregating *Pterocladia* from *Pterocladia*. With respect to *P. rectangularis*, Womersley & Guiry (in Womersley, 1994) described the carposporophyte as broad-based, with carposporangia in short chains maturing apically. This morphology indicates this species should remain in the genus *Pterocladia*.

Discussion

Pterocladia and *Pterocladia*

In the present analysis, internal cystocarpic structure has proved to be a useful criterion in segregating species of *Pterocladia* from species of *Pterocladia*. All eight species presently assigned to *Pterocladia* (Table 3) exhibit a basically similar cystocarp structure, with chains of carposporangia radiating from a core of gonimoblast filaments surrounding the central axis. On the other hand, the two species now recognized in *Pterocladia* (Table 3) exhibit carposporophytes developing on one side of the basal placenta, gonimoblast linked through fusions to vegetative cells in the floor of the cystocarps and short chains of carposporangia produced on the other side. No intermediate situation has been found between these two structurally different patterns of cystocarp architecture, for which reason this basic character can be adopted as a diagnostic feature segregating the two genera. Reexamination of fertile female gametophytes should similarly allow generic identification of *Pterocladia media* and *P. heteroplatos*.

Table 3. Size, sporophyll shape, arrangement of spores and geographic distribution of species of *Pterocladia* and *Pteroclatiella*

| Taxon | Maximum height | Placement of Tetrasporangial sori | Arrangement of Tetrasporangia | Geographic Distribution | References |
|----------------------------------|----------------|--|---|--|--|
| <i>Pterocladia lucida</i> | 60 cm | In small pinnules or on ovate to elongate compressed ramuli | In regular arrangement near apex of sori, becoming mixed | New Zealand, S. Australia, Tasmania | Adams 1994 Womersley & Guiry 1994 |
| <i>rectangularis</i> | 30 cm | In stichidia, short-stalked, terete to slightly compressed, becoming swollen terminally or centrally | Arising acropetally | W. and S. Australia | Womersley & Guiry 1994 |
| <i>Pteroclatiella bartlettii</i> | 6–8 cm | Young tetrasporangial branchlets often with sori in stichidium-like enlargements. Older branchlets generally compressed, lacking stichidium-like enlargement | Forming V-shaped rows in young sori; lacking the V-shaped arrangement in older sori | Texas, Gulf of Mexico, Cuba, Jamaica, Haiti, Puerto Rico, Guadaloupe, Venezuela | Taylor 1960 Edwards 1970 |
| <i>bulbosa</i> | 3–4 cm | In stichidium-like enlargements | Arising acropetally | Hawaiian Isls. | Loomis 1960 Santelices 1977, 1997a |
| <i>caerulescens</i> | 6–8 cm | At the somewhat flattened apex of axes and branches | Irregular arrangement | Vietnam, Guam, Indonesia, Hawaiian Isles, New Caledonia | Santelices 1976, 1977, 1978 Hatta & Prud'Homme van Reine 1991 |
| <i>caespitosa</i> | 1–1.5 cm | In single extensive sori at the tip of erect branches | Initially in V-shaped rows. Arrangement tends to be lost in older sori | Kenya coast, Natal, Inhaca Isl. and Peninsula (Kenya) | Norris 1987 |
| <i>caloglossoides</i> | 1–3 cm | On somewhat expanded or rounded tips of erect branches | Arranged in V-shaped rows | Central Chile, northern Perú, Mexico, Washington (USA) and British Columbia (Canada) Hawaiian Isls., Indonesia Isls., Barrier Reef (Australia) Guadaloupe, Natal, Tanzania | Santelices 1977 Norris 1987 |

Table 1. (continued)

| | | | | | |
|------------------------|--------------------------|---|---|--|---|
| <i>capillacea</i> | 15–20 cm | Sori various in appearance. Elongated and extensive on terminal parts of the frond on limited to short branchlets | Sometimes arranged in V-shaped rows in young sori. Arrangement lost in older sori | Widespread in warm-temperate and tropical waters | Stewart 1968, Santelices & Stewart 1985 |
| <i>melanoidea</i> | 2–5 cm | Sori in stichidia-like flattened branch apices | Arranged in V-shaped rows | Mediterranean, Atlantic, Morocco, Senegal | Fredericksen & Rueness 1990 |
| <i>minima</i> | 1–2 cm | In terminal stichidia or, occasionally, in lateral branches | Sporangia produced in acropetally developed rows | Victoria, Australia | Guiry & Womersley 1992 |
| <i>Incertae sedis</i> | | Sori apically on branches in some plants. | Sporangia arranged in V-shaped rows in some plants. No arrangement in others | Between San Francisco and San Diego, California, USA | Stewart 1974, 1991 |
| <i>P. media</i> | 1–2 cm (1) 6–7 cm (2) | In others, sori without arrangements | | | |
| <i>P. heteroplatos</i> | 4–6 cm | Sori scattered on the compressed branches and branchlets | Illustration lacks arrangement in V-shaped rows | India, Ceylon | Umamaheswara Rao & Kaliaperumal 1980 |

(1) *P. media* Dawson(2) *G. crinale* f. *luxurians* Collins

Conspicuous size and geographic differences between *Pterocladia* and *Pteroclatiella* emerge from the reevaluation of the species originally assigned to *Pterocladia* (Table 3). This last genus now appears restricted to Australia-New Zealand and characterized by large-sized species. *Pteroclatiella*, on the other hand appears as a more diverse genus, with smaller-sized species, most of which inhabit tropical and sub-tropical waters although a few extend into temperate latitudes.

Pteroclatiella and *Gelidiella*

Working with small gelidiacean algae from the British Isles, Maggs and Guiry (1987) ascribed to *Gelidiella* a small, creeping alga found on calcareous substrata. The basis for such a decision was the presence of stichidia with tetrasporangia arranged in V-shaped rows and the lack of rhizines (hyphae) except at attachment points. *Gelidiella*, and the family Gelidiellaceae, had been previously characterized (Feldman & Hamel, 1936; Fan, 1961) on the basis of two negative features: (1) absence of internal rhizoids and (2) lack

of sexual generation. Noticing that Sreenivasa Rao & Trivedi (1986) had reported cystocarps in an undescribed species of *Gelidiella* from India, Maggs and Guiry (1987) concluded that Fan's distinction between the two families could not be sustained and that they should be merged. They suggested that *Gelidium* and *Gelidiella* should be reassessed on the presence or absence of tetrasporangia formed acropetally in chevron-like series.

Frederiksen & Rueness (1990), Santelices (1990) and Freshwater et al. (1995) considered the above proposal to be premature. A V-shaped arrangement of tetrasporangia had been observed earlier in several species of *Pterocladia* (e.g. *P. americana*, *P. bartlettii*) and *Gelidium* (*G. pusillum*, *G. planiusculum*). Unless more critically applied, it was concluded, presence of stichidia with tetrasporangia arranged in V-shaped rows was of little use for segregating *Gelidiella* from either *Gelidium* or *Pterocladia*.

In 1992, Guiry and Womersley described a small gelidiacean alga collected in Victoria, Australia. It had total absence of rhizines, irregularly cruciately divided tetrasporangia occurring in terminal stichidia

and uniporate, unilocular cystocarps with carposporangia in chains of 2–3 formed from gonimoblasts radiating from the region of the axial cell. *Gelidiella minima*, as the species was named, differed from other species in the genus by its diminutive size, its largely prostrate axis and by the presence of gametangia and cystocarp. The authors also noted that the cystocarp found was very similar to that previously reported from *Pterocladia melanoidea* (Frederiksen & Ruess, 1990) and for *P. capillacea* (Bornet & Thuret, 1876; Fan, 1961; Santelices, 1991a).

Later (see note added to the proof), Guiry & Womersley (1992) found rhizines in the lower erect axes and in the stolons of *Gelidiella minima*, indicating that the taxonomic position of this species required further investigation. In spite of the presence of rhizines, they concluded that the diminutive size and largely creeping axes of *G. minima*, were characters more in conformity with a number of species currently placed in *Gelidiella*.

The presence of a *Pterocladia capillacea*-type cystocarps in *Gelidiella minima* later prompted its transfer to *Pteroclatiella* (Santelices & Hommersand, 1997). However, the correlation of *P. capillacea*-type cystocarps and tetrasporangia in V-shaped rows was interpreted (Hommersand & Fredericq, 1996; Rico & Guiry, 1997) in the sense that other species, now placed in *Gelidiella*, with unknown cystocarps but with tetrasporangia in regular V-shaped rows may belong with *Pteroclatiella*. Current data (Table 3) do not support this prediction. In both *Pterocladia* and *Pteroclatiella* there are species with and species without stichidium-like sporophylls.

The species of *Pteroclatiella* may or may not exhibit spores arranged in V-shaped rows (Table 3). The character seems to be ontogenetically variable as the V-shaped arrangement of spores observed in some species such as *P. capillacea* or *P. bartlettii* is lost by growth of the sporophyll or by additional spore production. Thus, as anticipated (Frederiksen & Ruess, 1990; Santelices, 1990; Freshwater et al., 1995) the character seems too variable to be useful for generic level recognition.

Recently male plants of *Gelidiella acerosa*, the type species of *Gelidiella*, have been found (Santelices, 1997b). This finding confirms the expectation (Sreenivasa Rao, 1971; Kapraun et al., 1994) of a sexual generation in *Gelidiella* and contradicts one of the two characters (lack of sexual generation) used by Fan (1961) to distinguish the family Gelidiellaceae from Gelidiaceae. However, the shape, pattern of di-

vision, size and way of differentiation of the male sorus of *Gelidiella acerosa* is unique among equivalent structures so far described for other members of the Gelidiales (Santelices, 1997b) and questions the relationship between the type species and other members currently placed in the genus *Gelidiella*. Many of these species have been assigned to the genus because of absence of rhizines and presence of tetrasporangial stichidium. Reexamination of previous collections, additional searches of field materials or culture of different life stages would allow knowing their cystocarpic structure and generic position. Such a finding also should help to elucidate whether or not a *Pteroclatiella*-type cystocarp may occur in species of *Gelidiella* which lack rhizines in all plant parts and life stages. In turn this should help to evaluate the validity of rhizines as a character for family segregation as well as to compare taxonomic affinities between *Gelidiella acerosa* and other, *Pteroclatiella*-like species included in *Gelidiella*.

Pteroclatiella and *Gelidium*

At present, there are several species of small gelidioids, which based solely on vegetative or tetrasporic materials, are placed in the genus *Gelidium*. As with the case of species of *Gelidiella*, additional searches of field materials or culture of different life stages would eventually yield cystocarpic structures to determine the generic position of these species. The recent description of *Gelidium maggsiae* (Rico & Guiry, 1997) constitutes an example. Gametophytes, bisexual and protandrous, were found only in cultured materials. Early development of the nutritive tissues in relation to the median plane defined by the central axis and secondary filaments, and the morphology of the cystocarps were considered to be characters of primary importance. Based on the biloculate cystocarp and the gonimoblast development this species was assigned to *Gelidium* rather than to *Pteroclatiella* or *Pterocladia*, in spite of the arrangement of the tetrasporangia in stichidia. Previous studies (e.g. Santelices & Hommersand, 1997) had determined that nutritive cells in *Pteroclatiella* grow centripetally forming a cylinder of tissue around the central axis while the nutritive cells of *Gelidium* form a network of short chains around each segment of the second order filaments.

It should be considered, however, that although the main differences between *Pteroclatiella* and *Gelidium* are based on the developmental patterns of nutritive cells and cystocarps, *Gelidium* is far from being a ho-

monogeneous group. Studies on apical architecture (Rodríguez & Santelices, 1987), cystocarp structure (Santelices, 1991b), and medullary structure (Rodríguez & Santelices, 1996) all suggest the existence of several subgroups within the genus. Such intrageneric heterogeneity is supported by sequence analysis of the *rbcl* gene of species of Gelidiales (Freshwater et al., 1995). Although the species groupings obtained from morphological studies are similar to those obtained with molecular biology techniques, the groupings are not identical. It is clear now that the definition of the genus *Gelidium* should be revised so as to clearly set boundaries in order to illuminate monophyletic relationships, as illustrated by Santelices and Hommersand (1997) for *Pterocladia*. A re-evaluation of the relationships among small gelidioids now being placed in *Pterocladia*, and those in the new groupings within *Gelidium* will be needed. For the time being, the differing ways in which cystocarps are constructed in *Gelidium* and *Pterocladia* assure generic recognition. The future challenge is to seek stable secondary features that will permit species discrimination in the two taxa. An evaluation of vegetative development must accompany reproductive studies, since a large number of specimens in these two genera are collected in the sterile condition.

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