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In honour of
Professor T. V. Desikachary
on the occasion of
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Vegetative and reproductive development of *Pterocladia capillacea* (Gelidiales, Rhodophyta) from La Jolla, California

by

M.H. Hommersand and S. Fredericq

With 31 figures

Abstract. The vegetative and reproductive development of *Pterocladia capillacea* has been investigated in material from La Jolla, California. Cystocarps were observed to develop differently in *P. capillacea* than in either *P. lucida*, the type species of *Pterocladia*, or *Gelidium*. Nutritive filaments originate from the four basal cells of third-order filaments borne on second-order filaments flanking the axial cell and grow towards the axial filament forming a central core. Gonimoblast filaments spread over the surface of this core and link to nutritive cells by means of tubular processes. Some gonimoblast cells unite to cells in the floor of the cystocarp attaching it to one side, while the rest radiate into the cystocarp cavity and bear carposporangia in chains. Cystocarps having this pattern of development are typically triangular in cross section with the carposporangia radiating on three sides from a central core that contains the axial filament and are typically inflated and bear ostioles only on one surface. So far, this pattern of development has been seen in *P. capillacea*, *P. caerulescens*, *P. melanoidea*, and in *Gelidiella minima*. It is suggested that these and other species having this type of cystocarp belong in a new genus.

Key words. Developmental morphology, Gelidiaceae, Gelidiales, *Pterocladia*, Rhodophyta.

Introduction

The genus *Pterocladia* was established by J. Agardh (1851, p. XI) to include a single species, *P. lucida* (Turner) J. Agardh (1852, p. 482–484) from Australia and New Zealand. Agardh separated *Pterocladia* from *Gelidium* on the basis that the cystocarp is unilocular in *Pterocladia* with a single placental surface bearing carposporangia and is bilocular in *Gelidium* with two placental surfaces bearing carposporangia on opposite sides of a longitudinal septum. In 1876 Bornet and Thuret discovered cystocarpic plants in a species previously known as *G. corneum* var. *capillaceum* or as *G. corneum* var. *pinnatum* and proposed the combination *Pterocladia capillacea* (Gmelin) Bornet & Thuret.

Bornet and Thuret investigated cystocarp development in many specimens of *Pterocladia capillacea* and reported that, whereas some were bilocular with a longitudinal septum and discharged spores through ostioles on both surfaces as in *Gelidium*, this behavior was exceptional. In most cases, the placenta tended to adhere to one side of the pericarp and was inflated and released spores from the opposite side. They noted that, in contrast to *Gelidium* in which the carpospores are solitary, the carpospores are borne in moniliform chains in *Pterocladia capillacea*. Their reexamination of *Pterocladia lucida* showed that the carpospores are also formed in chains in that species. While transferring *Gelidium capillaceum*

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(Gmelin) Kützing (1868) to *Pterocladia*, Bornet and Thuret (1876) commented that the distinction between *Pterocladia* and *Gelidium* is weak.

Fan (1961) investigated cystocarp development in *Pterocladia lucida* and in his new species, *P. lindaueri* from New Zealand. Topotype material of this latter species is indistinguishable from *P. capillacea* (Adams 1994). *Pterocladia lindaueri* was described as having cystocarps with two locules, with one more strongly developed than the other. As Bornet & Thuret (1876) had shown earlier, this behavior lies within the range of morphological variation of *P. capillacea*, and there appears to be no morphological basis for maintaining *P. lindaueri* as a separate species. Fan pointed out that the development of the female organs and cystocarps in *P. lucida* and *P. capillacea* (as *P. lindaueri*) represent two contrasting types. In the former, carpogonia develop only on one surface, nutritive filaments are produced only on the side on which the carpogonial branches have formed, and elongation of inner cell walls produces a cavity on only one side. In the latter, carpogonia are produced on both surfaces in the fertile depression, nutritive filaments are formed on both sides, and two locules may form, with one more strongly developed than the other. Fan confirmed that carposporangia are borne in short chains in both species.

Recently, Santelices (1991 a) investigated structural heterogeneity in the mature cystocarps in five *Pterocladia* and six *Gelidium* species and described six morphologically different types. Asymmetric cystocarps were found in several of them, including some species placed in *Gelidium*. Three of the cystocarp types, including a *lucida*-type, a *bulbosa*-type, and a *capillacea*-type, are represented among species presently placed in *Pterocladia*. In another paper, Santelices (1991 b) suggested that the combined morphological evidence favored separating *Pterocladia capillacea* and other species having similar unequally developed locules from *Pterocladia* and the erection of a new genus to accommodate them.

Vegetative characters have sometimes been used for separating *Pterocladia* from *Gelidium*. These include the location of rhizines (Okamura 1934), basal bending of lateral branches (Stewart 1968), the shape and disposition of cortical cells (Akatsuka 1981, 1986), and the special relationship between the apical cell of main axes and the initials of lateral branches (Rodríguez & Santelices 1987). All of these characters have been found to be unreliable or to require further investigation (Rodríguez & Santelices 1988, Santelices 1990), and Norris (1992) has recommended that the species of *Pterocladia* should be returned to *Gelidium* for this reason. For a review and description of species currently placed in *Pterocladia*, see Felicini & Perrone (1994).

In this study we compare cystocarp development in *P. capillacea* from La Jolla, California with that seen in *P. lucida*, the type species of *Pterocladia*, and with that found in typical species of *Gelidium*. Each possess a unique type of cystocarp characterized by the developmental pattern and distribution of the nutritive filaments and their interactions with the gonimoblast filaments. Our observations contribute further evidence in support of the establishment of a new genus to contain *Pterocladia capillacea* and related taxa.

Materials and methods

Material examined in this study was fixed and preserved in 5–10% Formalin/seawater. Transverse, longitudinal and periclinal sections were stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted in 1:1 Hoyer's mounting medium : water according to the procedure of Hommersand et al. (1992), or stained with 1% aniline blue and mounted in 50% Karo® corn syrup. Photographs were taken with a Zeiss photomicroscope III using T-MAX film.

Collection data for the taxa illustrated in Figs. 2–27 and 29–31 are: *Pterocladia capillacea* (Gmelin) Bornet & Thuret, lower intertidal, Coast Boulevard near Seal Rock, La Jolla, San Diego Co., California, USA, 16.7.88, M.H.

Hommersand; *Pterocladia lucida* (Turner) J. Agardh, subtidal, 1–2 M, Goat Island, Leigh, North Island, New Zealand, 21.3.75, M.H. Hommersand.

Results

Habit

Plants of *Pterocladia capillacea* consist of one to several erect axes arising from a prostrate system of entangled stolons. Erect axes are regularly to irregularly distichously branched with up to five orders of branchlets, often of decreasing length giving the thallus a pyramidal outline, or they may be densely entangled and matted. Branches and branchlets taper to a constricted base and are typically compressed or flattened above and at the tips (Fig. 1, Dawson 1953, Abbott & Hollenberg 1976, Felicini & Perrone 1994). Plants of *Pterocladia lucida* are typically larger, up to 60 cm tall from a holdfast of prostrate, flattened branches with sucker-like attachments, and with main axes flattened, up to 5 mm wide, sometimes with a midrib, and with the tips of branchlets often flattened and broadly rounded (Fig. 28, Adams 1994, Felicini & Perrone 1994).

Vegetative development

Growth of the thallus in *Pterocladia capillacea* is initiated by concavo-convex division of a dome-shaped apical cell. Each intercalary cell cuts off two periaxial cells laterally, one on each side, which function as initials of lateral cell rows of the second order. Filaments of the second order lie in a series of arcs behind the apical cell (Fig. 5). Transverse periaxial cells are absent (Fig. 7). Each cell in cell rows of the second order divides obliquely cutting off two cells, one towards each surface, which become initials of cell rows of the third order. Cell rows of third and higher orders contribute to thallus thickness (Fig. 7). Secondary pit connections are ultimately formed between adjacent cells obscuring primary thallus organization.

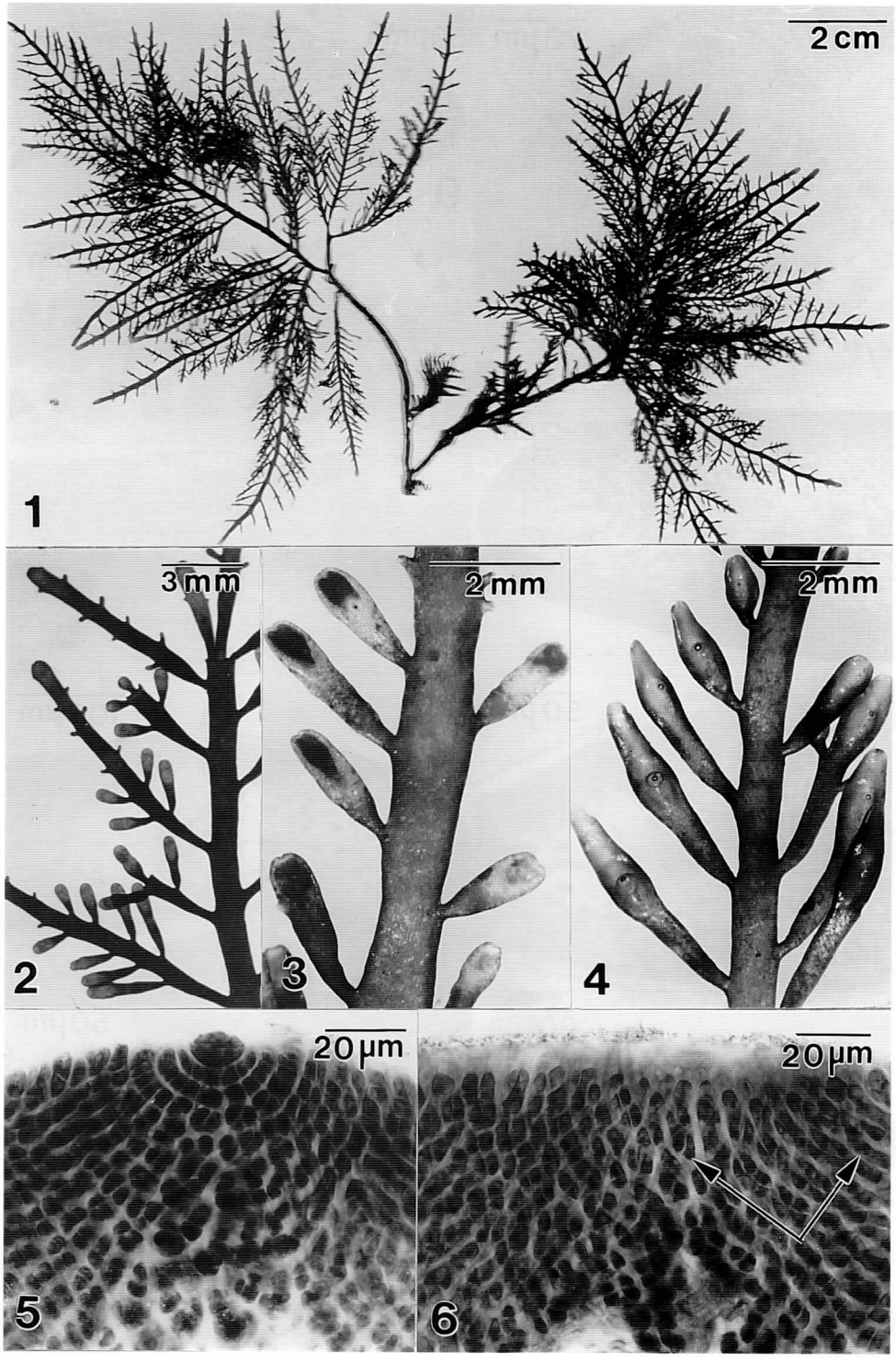
Surface cortical cells are generated in groups of fours by repeated anticlinal divisions that are perpendicular to one another (Figs. 6, 7). The first division is oriented towards the apical cell and the second in the direction of the arc of a second-order filament (Figs. 5, 6). Surface cells, which are quadrangular in shape while still meristematic, become rounded, pyriform, elliptical or elongate in surface view at maturity (Akatsuka 1981, 1986, Stewart 1992).

Medullary cells elongate longitudinally, obscuring the central axis a short distance behind the apex. Rhizoidal filaments (rhizines) are initiated from the lower sides of inner cortical cells and medullary cells, eventually filling in the intercellular spaces. They are easily seen in cross sections, owing to their fine diameters and comparatively thick walls (Fig. 8, Felicini & Perrone 1986, Fig. 1).

Reproductive development

Male, female and tetrasporangial plants are morphologically similar, with the reproductive structures formed near the apices of ultimate branchlets. Often these are unbranched lateral pinnules (Figs. 2–4, 24), but they may be compound branchlets (Stewart 1968, Figs. 6, 7). Spermatangial sori form colorless patches just behind the apex, here stained darkly with aniline blue (Fig. 3). Young female pinnules expand laterally forming broad, median depressions on both sides (Fig. 4). At maturity the cystocarps are unilocular and inflated on only one side. One to several ostioles may form; however, in our material the protruding wall with its ostiole(s) arises from only one side of the thallus in each cystocarp (Fig. 4).

Fig. 1. Habit of *Pterocladia capillacea* (NCU) from La Jolla, California (Dawson, 1.6.1946). – Figs. 2–27. *Pterocladia capillacea* (NCU) from La Jolla, preserved in 5% Formalin/seawater (Hommersand, 16.7.88). – Fig. 2. Branching pattern of a tetrasporangial plant. – Fig. 3. Fertile pinnules of male plant showing spermatangial sori stained with aniline blue. – Fig. 4. Fertile pinnules of female plant. Young pinnules above with median depressions. Older pinnules below with raised pericarps and ostioles on one side. – Fig. 5. Apical cell of vegetative axis with second-order filaments forming a series of arcs behind apical cell. – Fig. 6. Surface cortical layer of tip in Fig. 5. Cell divisions of surface cells in groups of four with divisions oriented at right angles toward apical cell and along arc of second-order filaments (arrows). – Fig. 7. Longitudinal section of vegetative tip showing apical cell, axial cells linked by primary pit connections, and third and higher order filaments directed toward thallus surface. Surface cells curve slightly towards apex. – Fig. 8. Transverse section in mid-region of mature vegetative axis. Rhizoidal filaments abundant along margin to the right with only a few in the central medulla. – Fig. 9. Transverse section of male pinnule. Spermatangial sori on both sides of pinnule covered by a cuticle. – Fig. 10. Spermatangia (arrows) cut off singly to outside by transverse division of individual spermatangial parent cells. (Note eccentric position of nucleus above hyaline spermatangial vesicle.) – Fig. 11. Elongate spermatangial parent cells and spermatangia in another sorus. – Fig. 12. Longitudinal section of young female pinnule. Innermost cells of third-order filaments have extended forming cavity. Nutritive filaments (nf) situated alongside axial filament. – Fig. 13. Transverse section of young female pinnule showing nutritive filaments organized in a central core around axial filament. Arrow points to developing ostiole. – Fig. 14. Transverse section showing organization of nutritive filaments. Individual nutritive filaments are derived from basal cells of third-order filaments (arrows) and branch toward axial cell at center. – Fig. 15. Multinucleate carpogonium (arrow) bearing gonimoblast filaments (g) which extend around nutritive filaments (nf). Aborted carpogonia are seen above (small arrows). – Fig. 16. Longitudinal section showing rectangular gonimoblast cells (g) external to nutritive filaments. Elongated lateral derivatives of some gonimoblast cells (arrows) have fused with cells of the nutritive filaments. – Fig. 17. Transverse section of nutritive filaments surrounding axial cell with overlying gonimoblast filaments (g). – Fig. 18. Gonibmoblast filaments (g) linked to nutritive filaments (nf). Individual cells of nutritive filaments are fusing through their primary pit connections. – Fig. 19. Longitudinal section of young cystocarp showing distended cystocarp cavity with two ostioles and nutritive filaments surrounded by gonimoblast filaments. – Fig. 20. Close-up of gonimoblasts with maturing carposporangia (ca) borne in chains. Most cells of the nutritive tissue have fused to form an interconnecting network. – Fig. 21. Transverse section of gonimoblasts bearing carposporangia (ca) in chains. Carposporangial chains are linked directly to network of fused nutritive filaments (arrows). – Fig. 22. Longitudinal section of cystocarp with maturing carposporangia and cystocarp cavity with an ostiole (arrow). – Fig. 23. Transverse section of cystocarp with maturing carposporangia in chains and cystocarp cavity with an ostiole. – Fig. 24. Fertile pinnules of tetrasporangial plant. Small dark specks are tips of tetrasporangia. – Fig. 25. Stages in development of tetrasporangial initials. – Fig. 26. Longitudinal section of pinnule with tetrasporangia in various stages of development. – Fig. 27. Transverse section of pinnule with mature, cruciately divided tetrasporangia. – Fig. 28. Habit of *Pterocladia lucida* from the Coromandel Peninsula, New Zealand (Hommersand, 2.10.1974). – Figs. 29–31. *Pterocladia lucida*, female plant (subtidal, Leigh, North Island, New Zealand (Hommersand, 21.3.75). – Fig. 29. Longitudinal section showing carpogonia (arrows) formed on one side of thallus. – Fig. 30. Median periclinal section showing nutritive filaments (nf) in relation to the central axis and network of second order filaments. – Fig. 31. Cross section of mature cystocarp showing gonimoblasts linked basally to gametophytic cells and bearing carposporangia in chains.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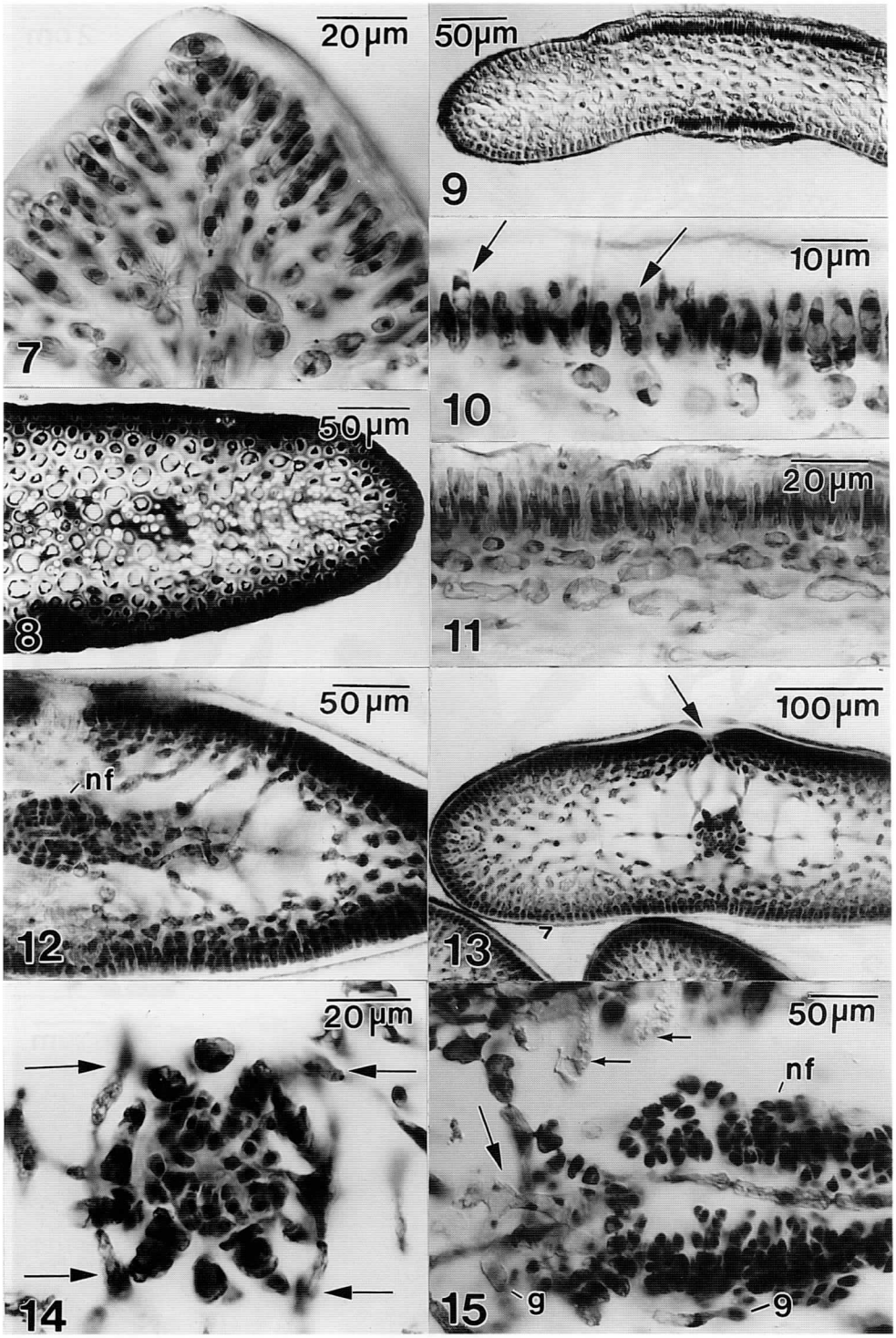
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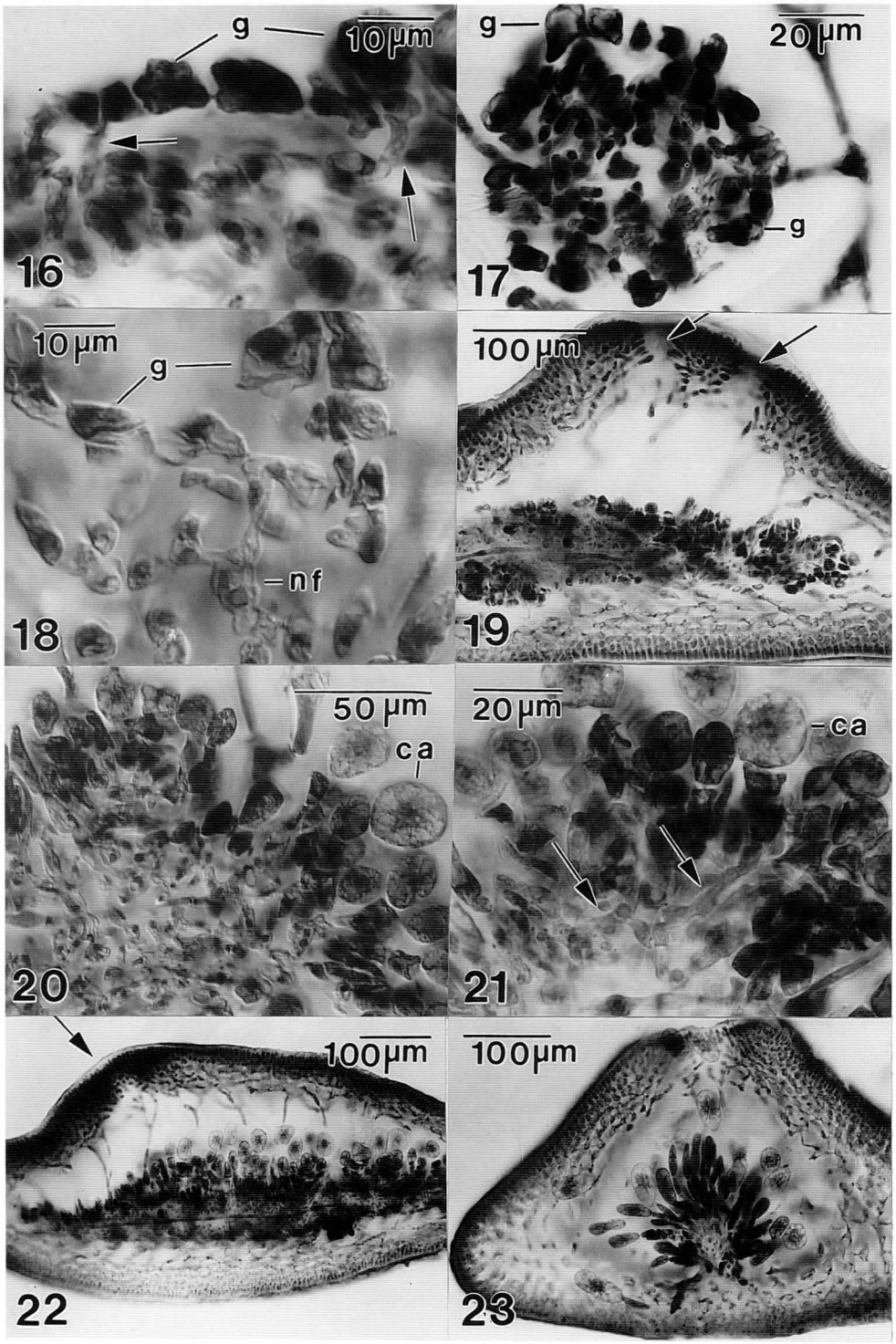
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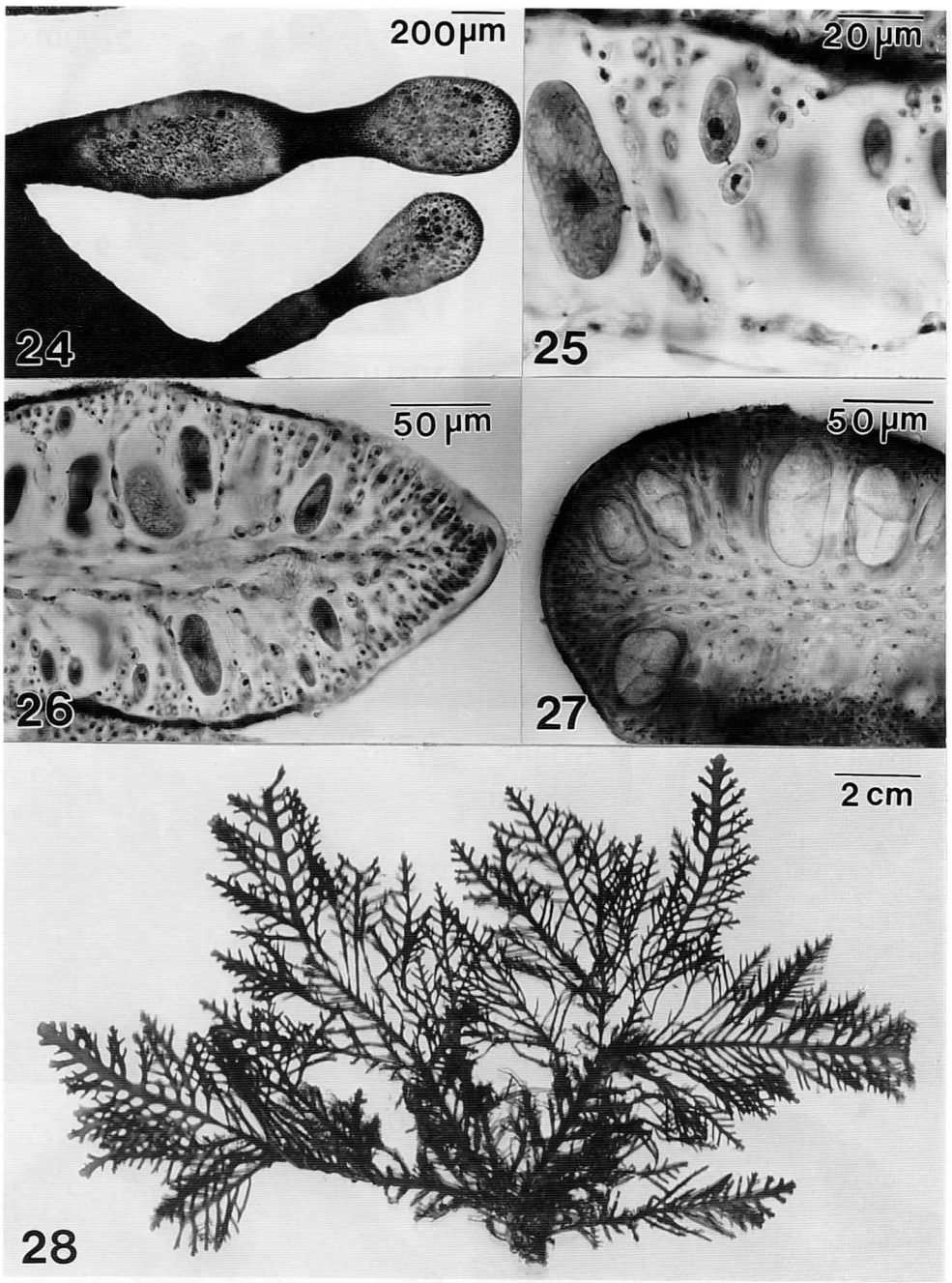
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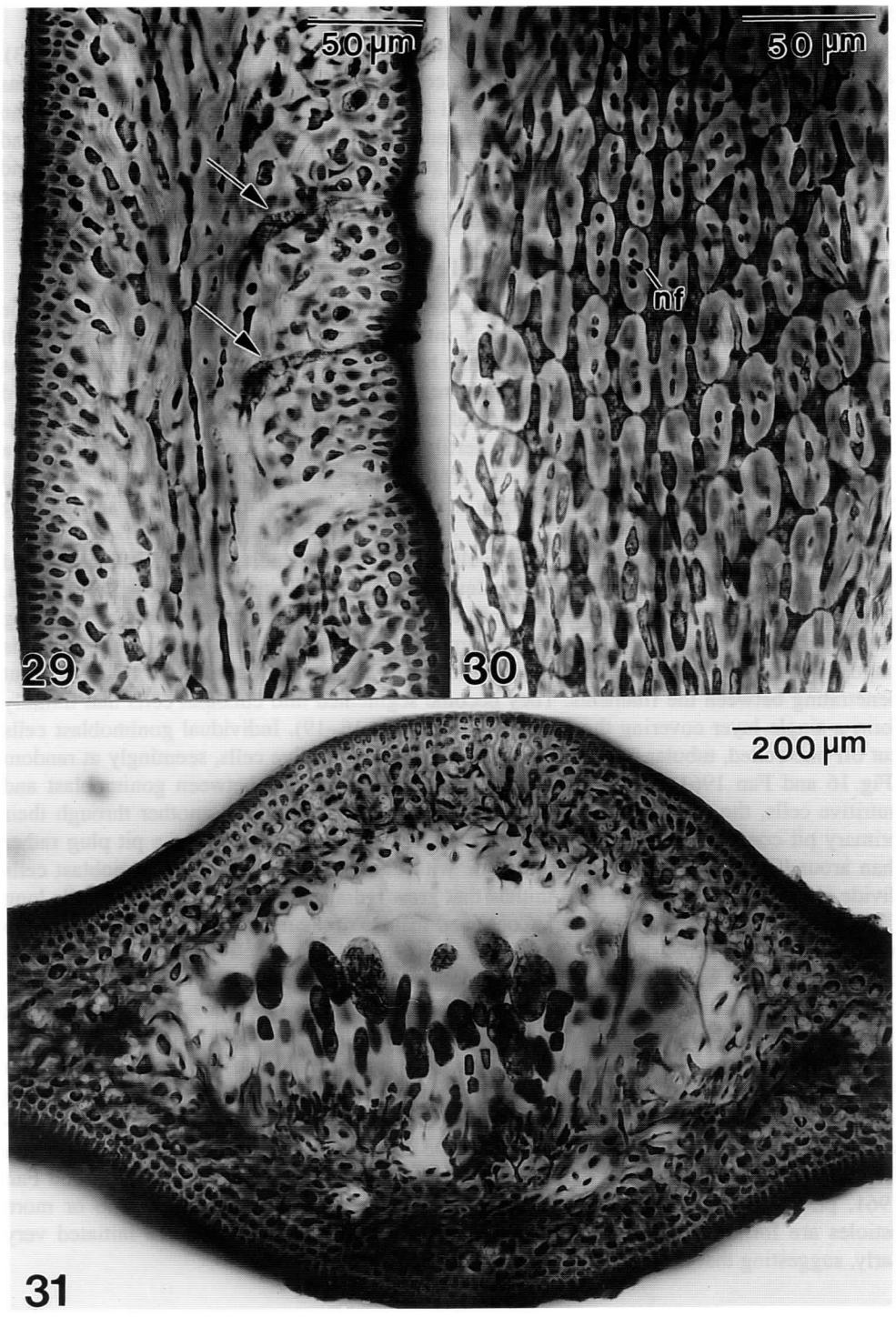
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Spermatangia

Spermatangial sori develop immediately behind the apex in fertile branchlets (Fig. 3). According to Akatsuka (1973, figs. 1–4), outer cortical cells undergo two successive divisions giving rise to a group of four spermatangial parent cells, which are slightly taller than ordinary cortical cells. Each spermatangial parent cell divides transversely into two cells and the distal cell is transformed into a spermatangium. Mature spermatangia are colorless and uninucleate with the nucleus subtended by a hyaline spermatangial vesicle (Fig. 10). In some sori the spermatangial parent cells are especially elongate (Fig. 11).

Female gametophyte, carposporophyte, and cystocarp

Carpogonia are produced on both surfaces along the median fertile depression behind the apex of a fertile branchlet. A carpogonium is intercalary and is usually the second-basal cell of a cell row of the third order but may be the basal cell of a cell row of the fourth order as described by Fan (1961). Nutritive filaments are borne on basal cells in cell rows of the third order on both the upper and lower sides, and are restricted to the four basal cells of third-order filaments that flank axial cells in fertile regions (Figs. 13, 14). Each consists of a descending file that bears opposite branches from every segment. Lateral filaments grow and branch towards the axial filament forming a solid cylinder of nutritive tissue surrounding each axial segment (Figs. 13–14).

The carpogonium enlarges, becomes multinucleate and vacuolate after fertilization, and forms processes that give rise to uninucleate gonimoblast initials (Fig. 15). In addition, vegetative cortical cells attached to the fertilized carpogonium may fuse with it by widening their pit connections (Fan 1961). Remnant carpogonial trichogynes are sometimes seen at this stage (Fig. 15). Gonimoblast filaments grow over the surface of the nutritive tissue without penetrating between the filaments. They become segmented into cuboidal cells that initially form a single layer covering the nutritive tissue (Figs. 16–19). Individual gonimoblast cells cut off one-celled, tubular laterals that fuse with nearby nutritive cells, seemingly at random (Fig. 16 and Fan 1961, fig. 12c). Following these initial fusions between gonimoblast and nutritive cells, the cells of the nutritive filaments also fuse with one another through their primary pit connections (Fig. 18). Fusion proceeds through the center of the pit plug rather than around it. Once contact has been made with the nutritive filaments, gonimoblast cells divide obliquely cutting off several initials that grow radially forming chains three cells long (Figs. 20, 21, and Fan 1961, fig. 12c). Continued fusions of the nutritive filaments give rise to a reticulate fusion network (Figs. 20, 21, and Fan 1961, pl. 43). Nuclei remain intact, but the cells of the nutritive reticulum become vacuolate and lose their staining properties as gonimoblast cells differentiate into carposporangia (Fig. 20). Chains of carposporangia averaging three cells in length mature basipetally (Figs. 20–23).

Although carposporangial filaments begin to develop on all sides of a fertile pinnule in *Pterocladia capillacea* (Fig. 19, and Fan 1961, pl. 42), they mature only on the side facing towards the strongly developed locule (Fig. 22). In transverse section it is seen that carposporangial chains mature on all sides around the central axis except the most basal portion (Fig. 23). The cystocarpic wall is initially pushed up on both surfaces (Figs. 13, 19, and Fan 1961, pl. 42), but is more extensively elevated on one side than the other. One or more ostioles are formed only on the elevated side (Figs. 19, 22, 23). Ostioles are initiated very early, suggesting that they may form around collapsing trichogynes.

Tetrasporangia

Tetrasporangia occur scattered irregularly in spathulate sori (Fig. 24), beginning immediately behind the apex of a fertile branchlet (Fig. 26). In the La Jolla material, primary tetrasporangia are soon followed by the formation of secondary tetrasporangia and a mixture of sporangia of different sizes are commonly seen in surface views of the same sorus (Figs. 24, 26). A tetrasporangial inital is cut off laterally from the apical cell of a cortical filament by anticlinal division. The apical cell continues to divide and branch while the tetrasporangium elongates and enlarges (Fig. 25). Mature tetrasporangia are immersed within the cortex and are cruciately to irregularly divided into four tetraspores (Fig. 27).

Cystocarp development in *Pterocladia lucida*

Carpogonia bearing trichogynes and nutritive filaments are formed only on one side in a fertile region in *Pterocladia lucida* (Fig. 29, Santelices 1991 a, figs. 1, 2), although they may be produced on opposite sides in successive fertile areas or on different pinnules (Santelices 1991 a, figs. 9, 10). In a median periclinal section the small-celled, irregularly branched nutritive filaments are all seen borne on one side of the network of secondary filaments when viewed from below (Fig. 30). The gonimoblasts are linked through fusions to vegetative cells in the floor of the cystocarp and bear short chains of carposporangia on the opposite side that mature basipetally (Fig. 31, Fan 1961, pl. 41, Santelices 1991 a, figs. 7, 8).

Discussion

Apical growth of *Pterocladia capillacea* and early stages of spermatangial, carpogonial, and tetrasporangial development are typical for members of the Gelidiaceae. Apical cells are exserted in the youngest tips, rather than occurring in depressions in rounded tips as is characteristic of older thalli of *Pterocladia* (Rodríguez & Santelices 1987, 1988, Stewart 1992). Surface cells are arranged in tetrads aligned in arcs and radial rows, as probably occurs in very young tips of most Gelidiaceae. Differences in the shape and disposition of surface cells at maturity, changes in the anatomy of subcortical and medullary cells, and the formation of rhizines was not followed, and the reliability of vegetative characters for distinguishing *Pterocladia* from *Gelidium* was not tested.

Spermatangia, carpogonia, and tetrasporangia are initiated near the apex in reproductive pinnules of *Pterocladia capillacea*, much as in other Gelidiaceae. The tips of fertile pinnules broaden, becoming spathulate with the apical cell situated in an apical depression. Fertile female tips showing carpogonia directed towards both surfaces of the thallus have been illustrated previously by Fan (1961) for *P. capillacea* (as *P. lindaueri*) and by Santelices (1991 a) for *P. caerulescens*. This contrasts with their disposition on only one surface in *P. lucida* (Fig. 29, Santelices 1991 a).

The principal distinction between *Pterocladia capillacea*, *Pterocladia lucida*, and species of *Gelidium* lies in features of the early development of the nutritive tissues in relation to be median plane defined by the central axis and secondary filaments. In *P. lucida* nutritive filaments are produced primarily or exclusively on one side of this central plane, the same side as the carpogonia (Figs. 29–30, Fan 1961, Santelices 1991 a); in *P. capillacea* they originate exclusively from the basal cells of third-order filaments borne on second-order filaments situated alongside the central axis (Figs. 12–17); and in *Gelidium* they are derived mainly from basal cells of third-order filaments on opposite sides of second-order filaments flanking the central axis, except for those situated close to the thallus margin (Fan 1961,

Hommersand & Fredericq 1988, Santelices 1991a). Unlike in *Pterocladia lucida* or species of *Gelidium*, the nutritive filaments grow centripetally in *P. capillacea*, and form a virtually solid cylinder around the central axis.

Early stages of gonimoblast initiation in *P. capillacea* follow a pattern similar to that described by Hommersand & Fredericq (1988) for *Gelidium pteridifolium*, except that the gonimoblast filaments grow over the surface of the core of nutritive filaments, rather than weaving between them. Tubular protrusions from intercalary gonimoblast cells unite with nutritive cells which, in turn, fuse with one another forming a central nutritive network (figs. 16–21). The gonimoblasts completely surround the central core; however, gonimoblast cells on one side link to inner cortical cells on the lower side of the cystocarp and do not form carposporangia. The rest produce carposporangia in chains that mature basipetally and are released successively through the ostiole.

Because of the asymmetric development of the gonimoblasts, the cystocarp is usually attached on one side to the cystocarp floor and produces chains of carposporangia on the remaining three sides. This characteristic behavior typically yields a triangular-shaped cystocarp, as seen in cross section, that is inflated on one side with chains of carposporangia appearing to radiate from a core of filaments surrounding the central axis (Fig. 23). Similar structures have been illustrated in the past beginning with Bornet & Thuret (1876) for *Pterocladia capillacea* from Europe, Cordeiro-Marino (1978) for *P. capillacea* from Brazil, Santelices (1991a) for *P. caerulescens* from Hawaii, Fredriksen & Rueness (1990) for *P. melanoidea* from Mallorca, Spain, and Guiry & Womersley (1992) for *Gelidiella minima* from Australia. Variations in cystocarp anatomy that tend towards a bilocular configuration, such as those discussed by Santelices (1991b), are due to a failure of the gonimoblasts to attach properly to the floor of the cystocarp, or to secondary detachment in old cystocarps.

The inclusion of *Gelidiella minima* among the examples having a *Pterocladia capillacea*-type cystocarp raises the possibility that other species placed in *Gelidiella* that lack cystocarps, but have tetrasporangia arranged in regular rows (Maggs & Guiry 1987), also belong in the same genus as *Pterocladia capillacea*. This genus remains unnamed and undescribed. In agreement with Santelices (1991b), we suggest that a new name be proposed and that the characterization of the new genus be based on European material of *Pterocladia capillacea*.

Molecular evidence based on an analysis of plastid-encoded *rbc*L nucleotide sequences from diverse populations of Gelidiales (Freshwater et al. 1995) established the presence of ten well-resolved clades representing ten genera or species complexes. A clade containing nine populations of *P. capillacea* and one of *P. melanoidea* was one of these. This clade was well separated from the clade containing *P. lucida*, supporting the conclusion that the two belong in separate genera. Tetrasporangia are borne in chevron-like rows in *Pterocladia melanoidea* (Fredriksen & Rueness 1990) and *Gelidiella minima* (Guiry & Womersley 1992), and a similar arrangement has been seen in some populations of *Pterocladia capillacea* (Cordeiro-Marino 1978) but appears to be absent in our material of *P. capillacea* from La Jolla, California. The abundance and rapid formation of secondary tetrasporangia in the La Jolla material obscured the chevron-like arrangement seen in plants in which secondary tetrasporangia are few in number, or are lacking.

The material investigated in the present study corresponds to the type of *Pterocladia pyramidale* (Gardner) Dawson (1945) [Basionym: *Gelidium pyramidale* Gardner (1927)]. Stewart (1968) compared the morphological variation of seven Pacific species of *Pterocladia*, including *P. pyramidale*, with that of *P. capillacea* from Europe and concluded that all seven were synonymous with the European species. Two *Gelidium* species from the northern Gulf of California were later merged with *P. capillacea* by Stewart & Norris (1981). In the

molecular study of Freshwater et al. (1995), *rbc*L sequence divergences from nine populations from Atlantic and Pacific Oceans supported the opinion that *P. capillacea* is a cosmopolitan species that is widespread in warm-temperate and tropical waters. Sequence divergences for eight of the populations fell close to the range of error due to methodological factors (0.2–0.6%). The exception was the population from California that corresponded to typical *Pterocladia pyramidale*, which differred from the others by 1.1–1.4%. At the present time, there are no known morphological characters that clearly separate *P. pyramidale* from *P. capillacea*; however, in view of the large *rbc*L sequence divergence that characterizes the La Jolla material, a reinvestigation of the morphology and taxonomy of taxa referred to *P. capillacea* from southern California and Pacific Mexico seems warranted.

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Authors' addresses:

M.H. Hommersand, Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3280, USA; e-mail address: MHOMER.COKER@MHS.UNC.EDU

S. Fredericq, Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3280, USA; present address: Department of Botany and Laboratory of Molecular Systematics, MRC 166, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA; e-mail address: Frederic@onyx.si.edu