

Delineation of the Genera *Struvea* Sonder and *Phyllocladon* J. E. Gray (Cladophorales, Chlorophyta)

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SUMMARY

Plants of the stalked, net-forming green alga *Struvea plumosa* Sonder, the type species of the genus *Struvea*, divide segregatively at every stage of their multicellular differentiation. The segregative process results in virtually simultaneous internal cleavage of the cytoplasm of parent axes or laterals into uniseriate series of nearly identically sized daughter cells in which intercalary cross-wall formation never takes place. Several branch orders result through a repeated process by which each daughter cell produces a pair of opposite protrusions at its distal end; the protruded arms subsequently undergo segregative divisions themselves after reaching a sufficient length. *Struvea elegans* Børgesen is seemingly the only other member of the genus in which the thallus divides by this segregative process. The remaining species appear to lack segregative cell division, their septation resulting from non-synchronous, centripetal wall ingrowths that divide parent cells into more or less equal halves. Intercalary cell divisions are common, this process being easily seen in the most widely distributed member of the genus, *Struvea anastomosans* (Harv.) Picc. et Grunov ex Picc. *Phyllocladon* J. E. Gray, based on *Phyllocladon pulcherrimum*, is currently considered a synonym of *Struvea* but should be reinstated to accommodate those former species of *Struvea* that have *Cladophora*-type, as opposed to segregative, cell division. Although the two genera thus differ substantially in their modes of cytokinesis and are assumed to represent independent developmental lines, both *Struvea* and *Phyllocladon* are assigned to the Cladophorales on the basis of molecular studies by others showing that recognition of the separate order Siphonocladales renders the Cladophorales paraphyletic.

Key words: Chlorophyta, Cladophorales, *Phyllocladon*, segregative cell division, Siphonocladales, *Struvea*, *Struveopsis*, taxonomy

INTRODUCTION

The genus *Struvea* was created by Sonder (1845) for the Western Australian *Struvea plumosa*, but it was only

with the appearance of Harvey's color lithographs (Harvey 1858, pls 7, 32) that botanists could begin to appreciate the intricacy of these striking plants. Over the years, 16 additional species have been described in or transferred to *Struvea*, but the exact number that should be recognized today is debatable. Egerod (1952) credited the genus with about a dozen species, Womersley (1984) indicated around six, and Olsen-Stojkovich (1986) straddled the field with an estimate of 6–16.

In virtually all substantive studies of *Struvea*, including accounts of cytology (La Claire 1982; Bodenbender and Schnetter 1990), developmental morphology (Okamura 1908, as *Struvea delicatula*; Børgesen 1912; Egerod 1952, 1971; Chihara 1958, as *S. delicatula*) and molecular biology (Kooistra *et al.* 1993), observations have not involved the type species but have been based wholly or largely on the pantropical *Struvea anastomosans*. Details of basic processes such as cell division in the type species have not been published.

Fronds of *Struvea* species are composed of single or clustered, mostly simple (occasionally ramified), erect stalks that give rise distally to distichous, 1–4-times pinnately branched, uniseriate filaments that form a meshwork through the attachment of the various branch orders to one another by the crenulate, adhesive end-processes of small, modified terminal segments called 'tenaculæ'. The interconnected branch orders form a single layer that lies largely in one plane, resulting in an expanded blade of great intricacy, beauty, and (in some species) size. Agardh (1887) called attention to what he considered the remarkable resemblance of the ramification in a thallus of *Struvea* to the venation pattern of an entire leaf of a higher plant.

Egerod (1952) used the presence of tenaculæ to separate the family Boodleaceae (order Siphonocladales), in which she placed *Struvea*, from the Anadyomenaceae, the reticulate members of which lack tenaculæ. In the opinion of Womersley (1984), however, such differences may be generically significant but are of doubtful value in defining families. He thus placed

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Struvea, along with *Microdictyon*, in the Anadyomenaceae of the order Cladophorales.

The distinguishing cytological feature that traditionally has determined membership of coenocytic multicellular Chlorophyta in the order Siphonocladales rather than the Cladophorales is the presence of consistent segregative cell division. Where the cell division process consists of the separation of daughter cytoplasts by the centripetal ingrowth of fibrillar material to form a cross-wall, organisms are placed in one of several families of the Cladophorales. This latter process is particularly well illustrated at the light-microscopical level in *Microdictyon* by Enomoto and Hirose (1971), and close attention to this detail led Papenfuss and Chihara (1975) to transfer the genus *Apjohnia* from the Siphonocladales to the Cladophorales.

The term 'segregative cell division' was introduced by Børgesen (1912, 1913) to describe multicellular thallos differentiation in *S. elegans* Børgesen. Arnoldi (1913) soon afterwards reported a comparable phenomenon in *Dictyosphaeria*, but the process is best displayed by the genus *Siphonocladus* (Egerod 1952). Segregative division begins when the cytoplasm in a parent cell rounds up into numbers of roughly spherical vesicles, which then begin laying down fibrillar walls while expanding *in situ*. The sibling cytoplasts fill the parent cell, abut and become confluent with one another, and either protrude as lateral outgrowths from the parent wall, as in *Siphonocladus* (Egerod 1952), or expand within the confines of the parent cell, rupturing it in *Dictyosphaeria* (Enomoto and Okuda 1981; Enomoto *et al.* 1982) and eventually causing it to slough off (Womersley 1984, fig. 74H).

Womersley (1984) disputed the interpretation of Børgesen's (1913) illustration that led Børgesen to claim segregative cell-division for *S. elegans* and *S. anastomosans*. Womersley suggested the greater likelihood that cross-walls develop by peripheral ingrowths in all the species of *Struvea*, as takes place in the anatomically similar genera *Microdictyon* (Enomoto and Hirose 1971) and *Boodleia* (Olsen-Stojkovich 1986), as well as in *Anadyomene* (Enomoto and Hirose 1970) and members of the Cladophorales generally. Olsen-Stojkovich (1986) reported that cell divisions in the central erect axis and first-order laterals of *Struvea plumosa* are accomplished by centripetal wall invaginations, whereas second- and third-order laterals undergo 'segregative division *sensu stricto*' (Olsen-Stojkovich 1986). There is thus some dispute as to how cytokinesis actually takes place in the various species of *Struvea*.

The type localities of both *Struvea plumosa* and *S. anastomosans* are in the Perth region of Western Australia. Recent collections of the two species from this area by Dr John M. Huisman reveal that the former displays a programmed sequence of segregative divisions throughout all erect parts, whereas the latter does not appear to divide segregatively at any stage. They thus

differ significantly in their modes of cell division and should be regarded as distinct genera. For *S. anastomosans* and other current members of *Struvea* that lack segregative division, it has thus been necessary to determine if there is an earliest valid generic name that could be applied to them.

MATERIALS AND METHODS

Photographs of liquid-preserved specimens were made on a Wild 400 Photomakroskop, the material either unstained when taken under dark-field illumination or mounted in a dilute iodine solution when examined under bright-field. Dried specimens were rehydrated in a dilute detergent mixture warmed to 70°C. Vouchers are housed at the Melbourne University Herbarium (MELU) and the Herbarium, University of Michigan (MICH).

The following material was examined:

(1) *Struvea plumosa* Sond. Australia, W. Aust. 'Cosy Corner' of Hamelyn Bay: 3 m deep, (J. Huisman, 14.xii.1991. MELU, A42201). Rottneest Island: 5–10 m deep, (G. Kraft and R. Ricker, 1.xii.1980. MELU, A42199); 20 m deep seaward of Green Island (G. Kraft and R. Ricker, 4.xii.1980. MELU, A42200); 9–12 m at Point Clune (J. Huisman, 2.xii.1980. MELU, A41794). Point Peron: 1 m deep, (G. and C. Kraft, 8.iii.1978. MELU, K6539). Ocean Reef Marina: 6 m deep (G. Kraft and P. Gabrielson, 9.xii.1980. MELU, K7296). Port Denison: 6–12 m deep (G. Kraft and B. Allender, 10.viii.1979. MELU, K7039a); (G. Kraft and R. Ricker, 11.xii.1980. MELU, A42202 and MICH). Kalbarri, Red Bluff: 6–10 m deep (G. Kraft and R. Ricker, 15.xii.1980. MELU, A42203).

(2) *Struvea anastomosans* (Harv.) Picc. et Grunov ex Picc. Australia, W. Aust. Ravn Reef, Rottneest Island: 15 m deep (Huisman, 15.i.1993. MELU, A42,198). Queensland. Wistari Reef, Capricorn Group, southern Great Barrier Reef: 24 m deep (G. Kraft and C. O'Brien, 18.iii.1985. MELU, K16112). Philippines. Ernie Loveland's *Eucheuma* farm, Zamboanga, Mindanao: 1.5 m deep (G. Kraft, 2.vi.1968. MELU, K831). Hawaii. In front of the Natatorium, Waikiki Beach, Oahu: shallow subtidal (G. Kraft, 10.viii.1967. MELU, A41894).

(3) *Phyllodictyon pulcherrima* J. E. Gray. USA, North Carolina. Onslow Bay: 40 m deep (R. Searles, 23.vi.1970. MICH); 35 m deep (C. Schneider, 25.vi.-1971. E-17330 [Herb. C. W. Schneider, Trinity College, Hartford, CT]). Florida. Off Singer Island, Palm Beach Co.: 25 m deep (M. Hall and S. Blair, 1.iv.1980. HBOM, 4932); 58 m deep (N. Eiseman and S. Blair, 23.vi.1980. HBOM, 5266). Bermuda. Argus Bank: 64 m deep (J. Frederick, 22.viii.1960. MICH). Challenger Bank: 55 m deep (W. R. Taylor, 7.iv.1961. MICH). Netherlands West Indies. near Aruba: 43 m deep (W. R. Taylor, 10.iv.1939. MICH).

RESULTS

Struvea plumosa Sond.

The anatomy of young and mature plants is described and illustrated by Womersley (1984). Thalli occur from low tide levels to depths of at least 33 m (Womersley 1984) either in clumps (Fig. 1) or as isolated individuals and growing on limestone. Turgid clavate axes displaying varying degrees of regularly spaced basal annulations (Fig. 2) can reach 10 cm in length as unicells (Fig. 1) before the first stages in cytoplasmic cleavage take place to initiate the distal net of the frond. Although anchored by a primary hapteral holdfast, horizontal rhizoids issuing from the frond base commonly give rise to secondary erect axes (Fig. 2). The rhizoids are irregularly septate, but whether by segregative or by *Cladophora*-type cell divisions could not be determined.

Septation of the initially unicellular axes (Figs 1, 2, 7) appears to be strictly segregative. Some 6–30 rounded vesicles form in a linear series (Fig. 3), at first expanding radially until contact is made with the parent wall, then lengthening in poleward directions until contact is firmly established with contiguous sibling cells (Fig. 4). The distal one-quarter to one-third of the parent cell thus becomes fully occupied by the segregation products, resulting in a series of horizontal cross-walls and the overlapping of the parental and lateral daughter cell walls (Fig. 5). Each of the cellular units then expands distally to form a distichous series of shoulders (Fig. 6), which progressively differentiate into a pair of opposite lateral primordia (Figs 7–9, 12). The segregative-division process is then repeated in each of the primary laterals, beginning at the basal laterals and progressing acropetally (Fig. 10). Tenacular cells terminate each of the primary laterals (Fig. 11) and may appear either before (Fig. 13) or after (Fig. 10) the remainder of the segregative septation of the first-order branches takes place. The apices of the first-order laterals arch toward the frond apex (Figs 9–11; Womersley 1984, fig. 73C), and their tenacular cells attach to the acropetally adjacent primary lateral (Figs 11, 13). Tips of the second-order laterals fuse in a similar fashion to cells of the most closely adjacent first-order laterals (Figs 13, 14). The apical cell of each primary lateral behaves like a secondary lateral in regard to the timing of its own internal segregative divisions. It is in this cell that the second-order lateral segregative process begins at the base of the frond (Fig. 14), and its tendency to produce distal protrusions from the segregation products unilaterally (Fig. 15; Womersley 1984, fig. 73C) gives the frond margins a smooth but undulating contour (Fig. 11). Segregative divisions proceed in a relatively ordered fashion to produce linear series of roughly equal-sized daughter progeny acropetally (Fig. 15). With age, a further one or two branch orders are produced segregatively, and the frond contour becomes coarser and

less ordered (Harvey 1858, pl. 32; Womersley 1984, fig. 73B, C).

Struvea anastomosans (Harv.) Picc. & Grunov ex Picc.

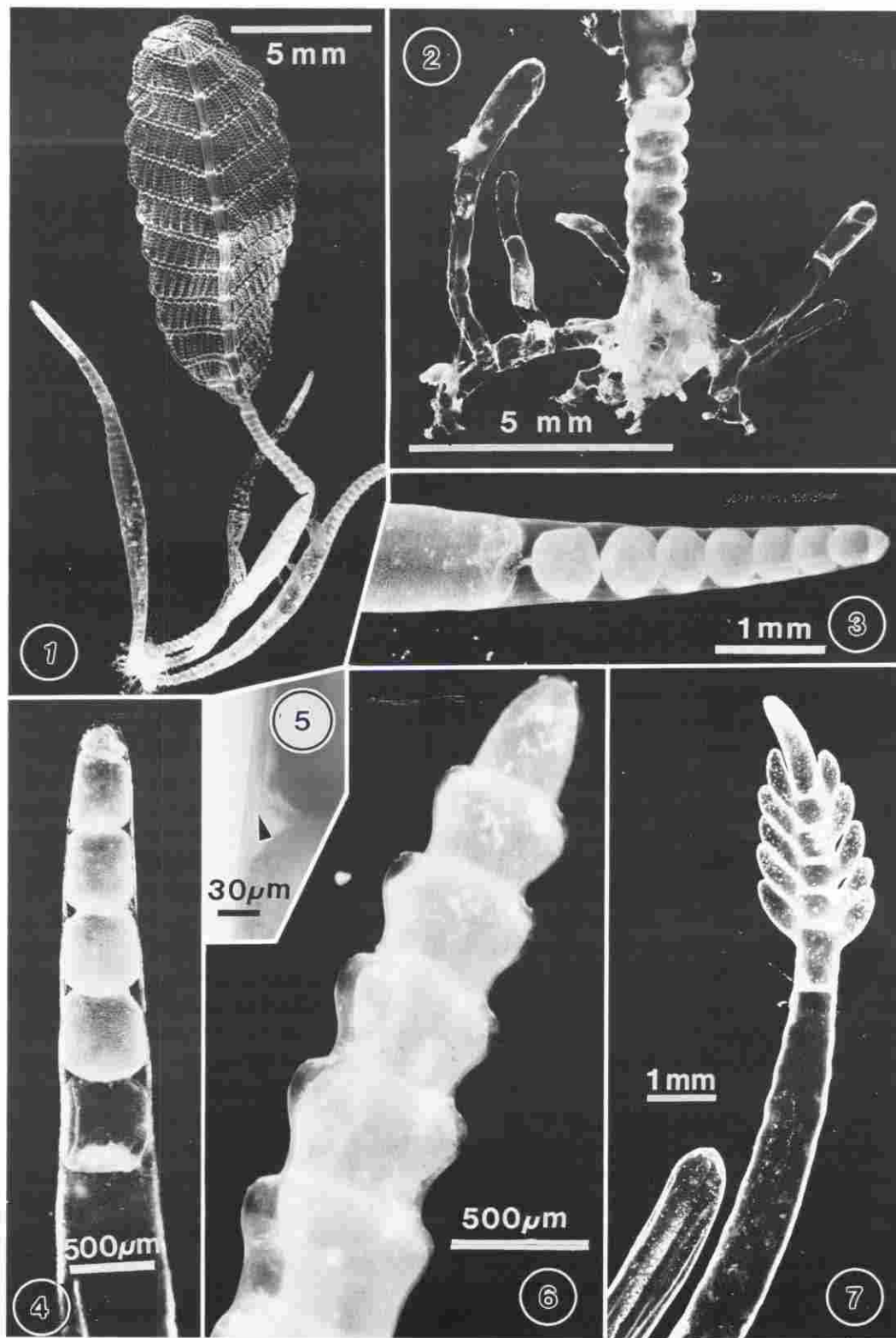
Recorded from warm-temperate and tropical waters worldwide, the thalli of this species tend to occur as scattered and isolated individuals, although clusters are also encountered. In contrast to *S. plumosa*, the outline of the frond meshwork is highly irregular, the apical cells of primary laterals neither curving in on the margins nor regularly forming tenacular attachments (Fig. 16). The stalks are non-annulate (Fig. 17). Although cells of the reticulate frond can superficially resemble those of *S. plumosa* in regard to their regularly opposite shouldered protrusions (Fig. 18), even at early stages differences are apparent. Septation is not a coordinated process, as it is present throughout some second-order laterals and absent in others (Figs 18, 19). Cross-walls at different stages of formation are commonly seen at points where opposite laterals first become cut off from the parent cell (Figs 18, 19), and are particularly noticeable in intercalary cells of first-order laterals (Fig. 20). The cross-walls grow centripetally from the periphery of the parent cell, as evidenced by the continuity of the cytoplasm during their development (Fig. 21), and are non-synchronously produced even in opposite laterals of the same age (Figs 18, 19, 22). Tenacular cells differentiate at the apices of second- and third-order laterals (Figs 19, 21, 25). Where they make contact with a cell of an adjacent branch order, a flared, crenulate tip (Fig. 23) often effects adhesion.

Intercalary cell divisions begin in the main axis and first-order laterals (Figs 16, 20, 25) and spread to higher-order laterals. Mature fronds display numerous intercalary cell divisions that are irregularly distributed even on adjacent branches of the same order (Fig. 19).

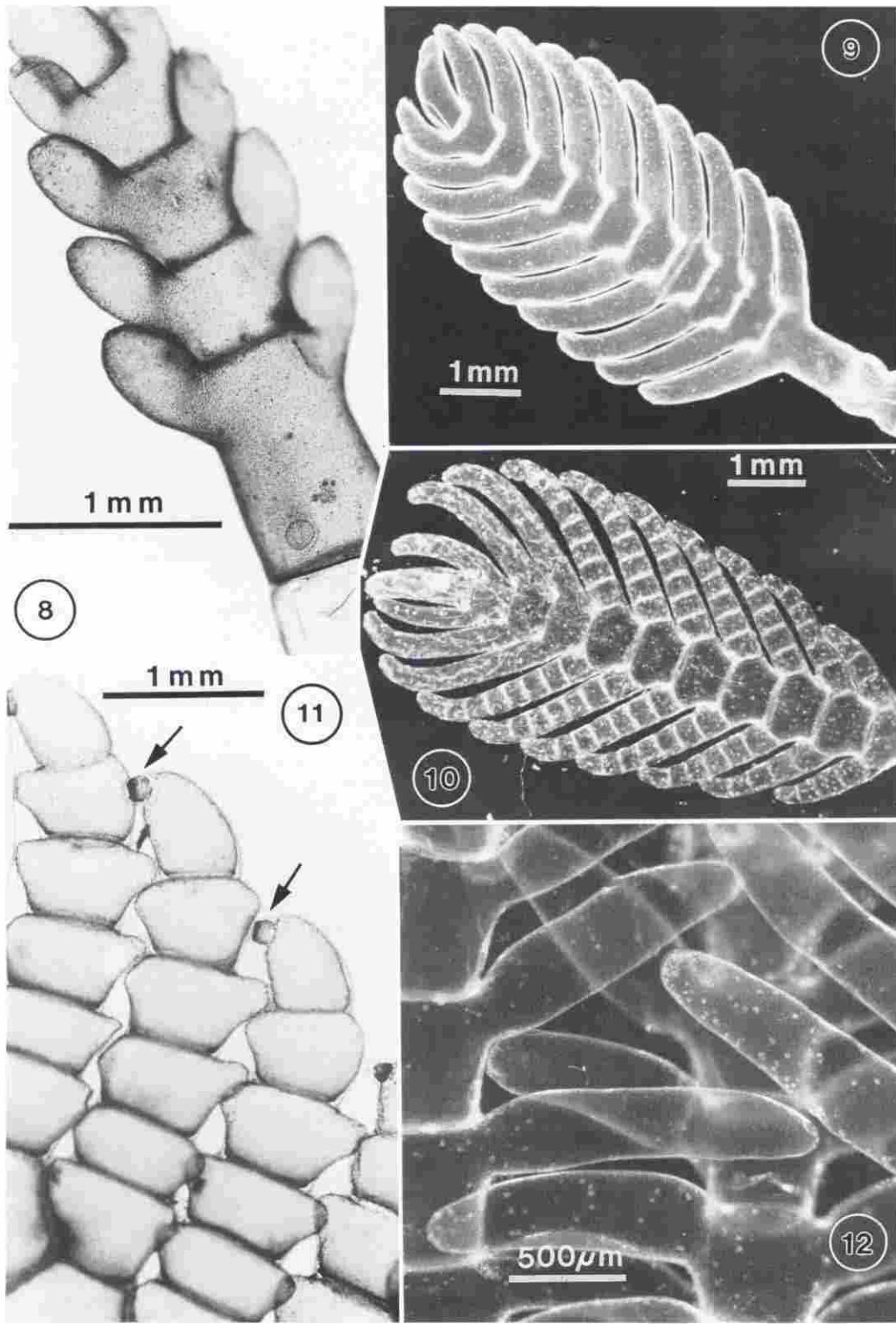
At scattered locations on most fronds are cells in which the cytoplasm has rounded up in a superficially segregative fashion (Fig. 24). This may be the phenomenon used as evidence by various authors that the species undergoes segregative division (Børgesen 1913; Egerod 1952, fig. 4g), for entire branch tips can take on the appearance. As pointed out by Olsen-Stojkovich (1986), however, the rounding up of cytoplasm is a common wound or damage response in the septate, siphonous greens and a process that may be associated with either segregative or *Cladophora*-type cell division. In *S. anastomosans* this phenomenon occurs sporadically and uncoordinatedly rather than globally and uniformly, as in the case of true segregative division.

Struvea pulcherrima (J. E. Gray) G. Murray et Boodle

Records of this rare and exclusively deep-water species range from North Carolina (Humm and Cerame-Vivas



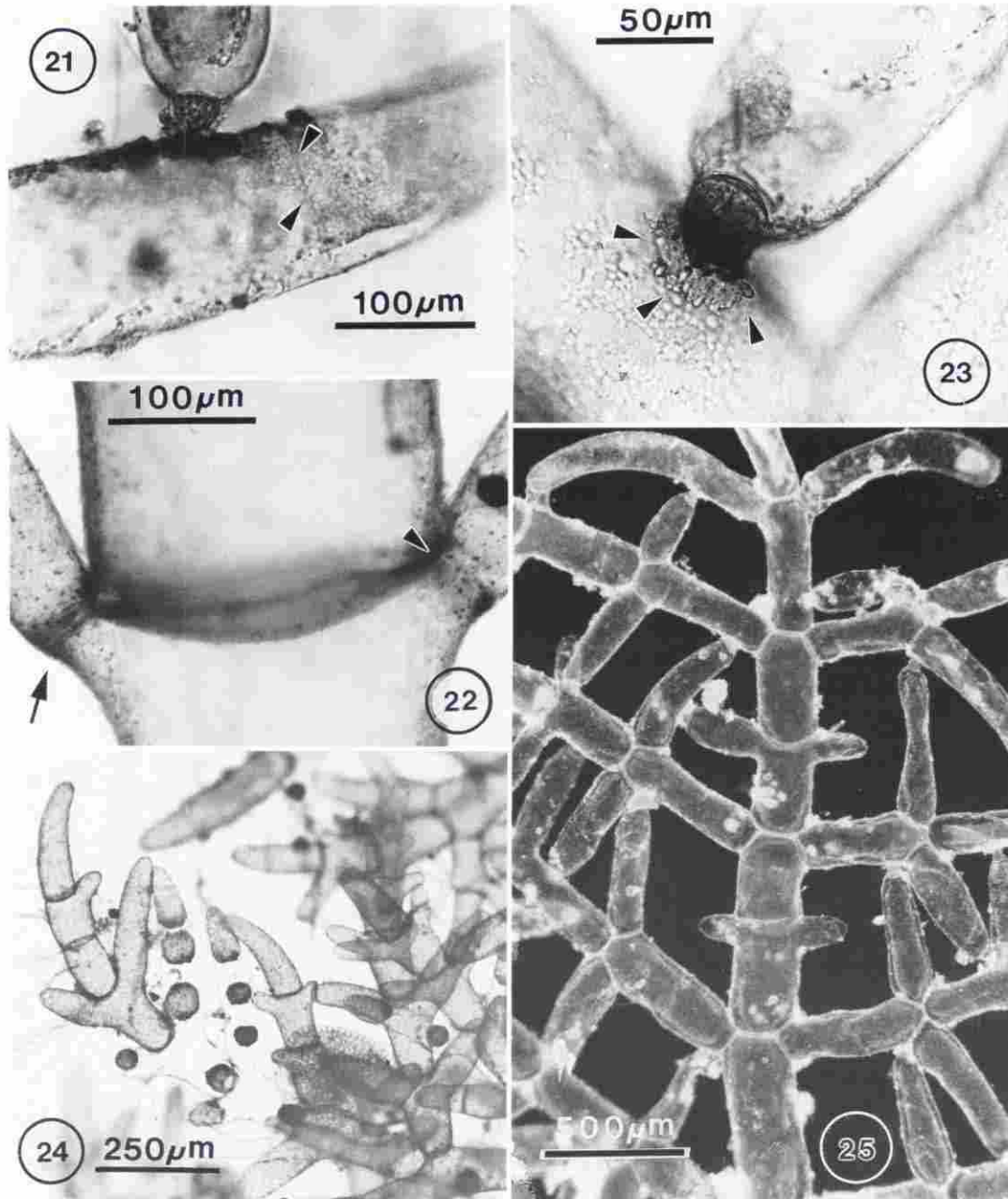
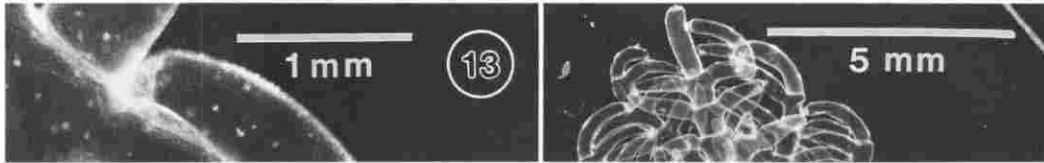
Figs 1-7. *Struvea plumosa* Sond. 1. Cluster of axes at pre and post net-forming stages. 2. Base of an annulate primary axis showing rhizoidal outgrowths on which secondary erect axes have arisen. 3. Segregative divisions within the distal portion of a primary axis into eight linearly arranged cytoplasts. 4. Expansion of segregatively derived cytoplasts to fill the parent axis. 5. Detail of the confluence of the parent cell wall and the wall of a segregatively derived daughter cell (arrowhead). 6. Early stage in the distal shouldering of the primary segregative-division products. 7. Apex of an undivided primary axis (left) and the distal portion of an axis in which distichous lateral primordia have arisen on the segregated sibling cells (right).



Figs 8–12. *Struvea plumosa* Sond. 8–9. Early and late stages in the production of distichous primary laterals prior to segregative septation. 10. Simultaneous cleavage of cytoplasm in proximal first-order laterals into cells of uniform lengths. 11. Tenacular cells (arrows) at the apices of first-order laterals, the proximal cells bearing distichous protrusions of impending second-order laterals. 12. Fully developed first-order laterals prior to the initiation of segregative divisions and the production of tenacular cells.

like in appearance, lacking a percurrent primary axis and consisting of major veins interspersed among a dense meshwork of narrower filaments representing the higher branch orders. Up to eight of the coarser fila-

tremely thin-walled, globose cells much constricted at their cross walls, with intercalary cell divisions being numerous (Fig. 27). Tenacular cells terminate the branches and are often narrowly elongate (Fig. 28).

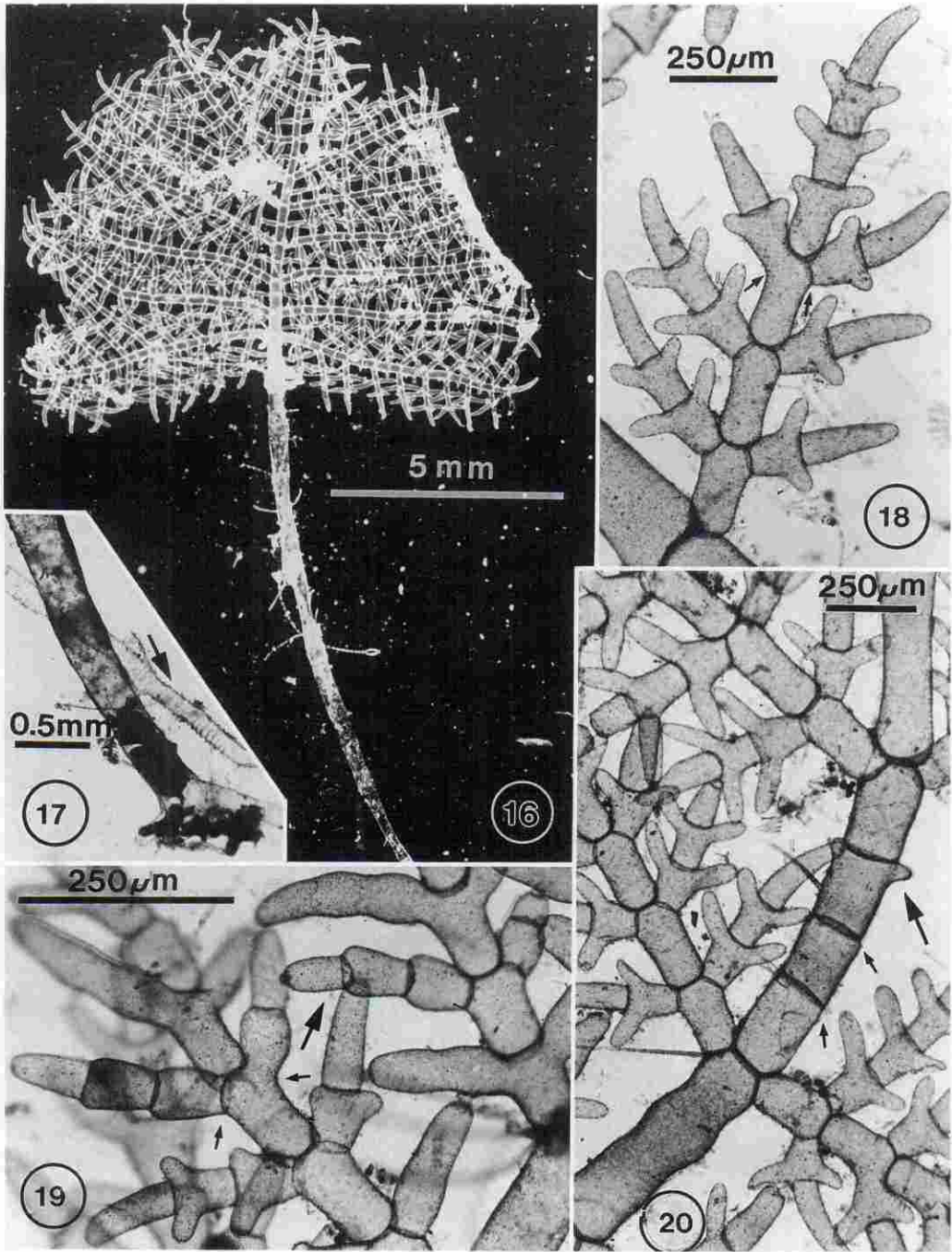


Figs 21–25. *Phyllodictyon anastomosans* (Harv.) Kraft et M. J. Wynne. 21. Early stage in the formation of a centripetally growing cross-wall (arrowheads) in a first-order lateral. The cytoplasm (arrow) is continuous through the site of incipient septation rather than segregatively segmented. 22. Opposite third-order laterals, one separated from its parent cell by a complete septation (arrow), the other in the initial stages of cross-wall formation (arrowhead). 23. A tenacular cell terminating a third-order lateral and attached to the cell of a second-order lateral by a crenulate adhesion pad (arrowheads). 24. Axes in which rounded cytoplasm, probably the result of mechanical injury, superficially give the appearance of segregative-division products. 25. Overview of first- to third-order laterals showing the mixed stages of branch development due to non-synchronous and intercalary cell divisions.

DISCUSSION

Several genera of net-forming marine Chlorophyta have been described, but most have been relegated to taxonomic synonymy with other genera or are inadequately known from sparse material. Gray (1866a, 1866b) proposed the new genera *Calomena*, *Cystodictyon*, *Grayemma*, *Macrodictyon*, *Phyllodictyon* and *Pterodictyon*

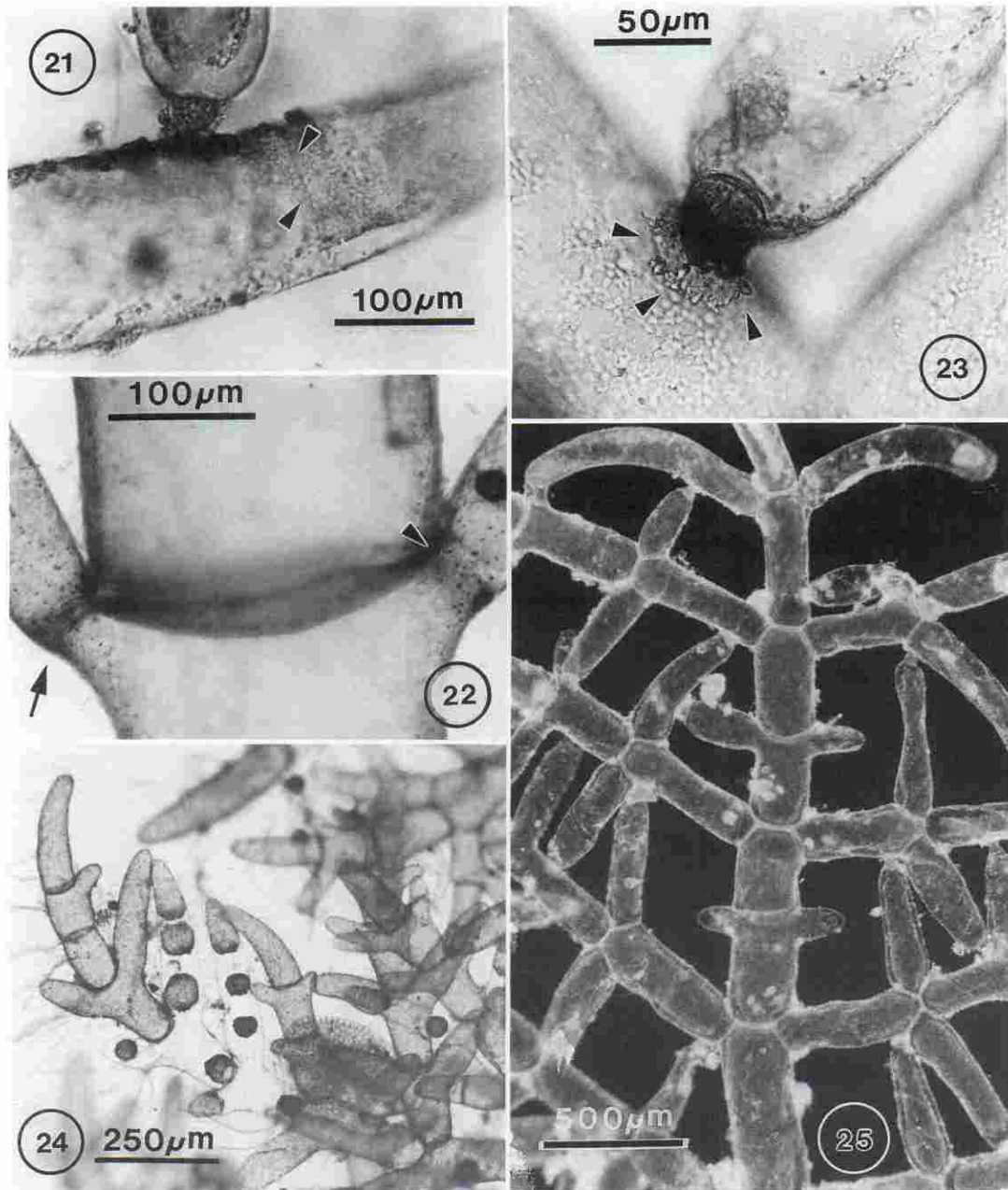
for a number of species from various Eastern and Western Hemisphere tropical regions. Of these, *Calomena*, *Cystodictyon* and *Grayemma* are presently treated as taxonomically equivalent to *Anadyomene* (Littler and Littler 1991); *Macrodictyon* is virtually unknown but appears from its description (Gray 1866b) to be a form of the widespread and highly variable *Microdictyon um-*



Figs 16–20. *Phyllocladon anastomosans* (Harv.) Kraft et M. J. Wynne. 16. Frond habit. 17. Detail of holdfast and non-annulate basal stalk, the stalk overlying a hydrozoan tube (arrow). 18. Acropetal differentiation of second- and third-order laterals. Cross-wall formation at the base of opposite second-order laterals is not synchronous (arrows). 19. Non-synchronous cross-wall formation at the bases of third-order (small arrows) laterals. One septate branchlet (large arrow) is flanked on both sides by non-septate branchlets. 20. Three intercalary cell divisions in a first-order lateral. Two of the cells (small arrows) lack the distal second-order branch primordia of the third (large arrow).

at its greatest diagonal width, borne on a slightly annular stalk 25 mm in length that is trifurcate at its distal end (Fig. 26). The frond is particularly *Microdictyon*-like in appearance, lacking a percurrent primary axis and consisting of major veins interspersed among a dense meshwork of narrower filaments representing the higher branch orders. Up to eight of the coarser fila-

ments converge on and arise from scattered points on the blade surface (Fig. 26) in conspicuous stellate configurations. Higher-order filaments are composed of extremely thin-walled, globose cells much constricted at their cross walls, with intercalary cell divisions being numerous (Fig. 27). Tenacular cells terminate the branches and are often narrowly elongate (Fig. 28).

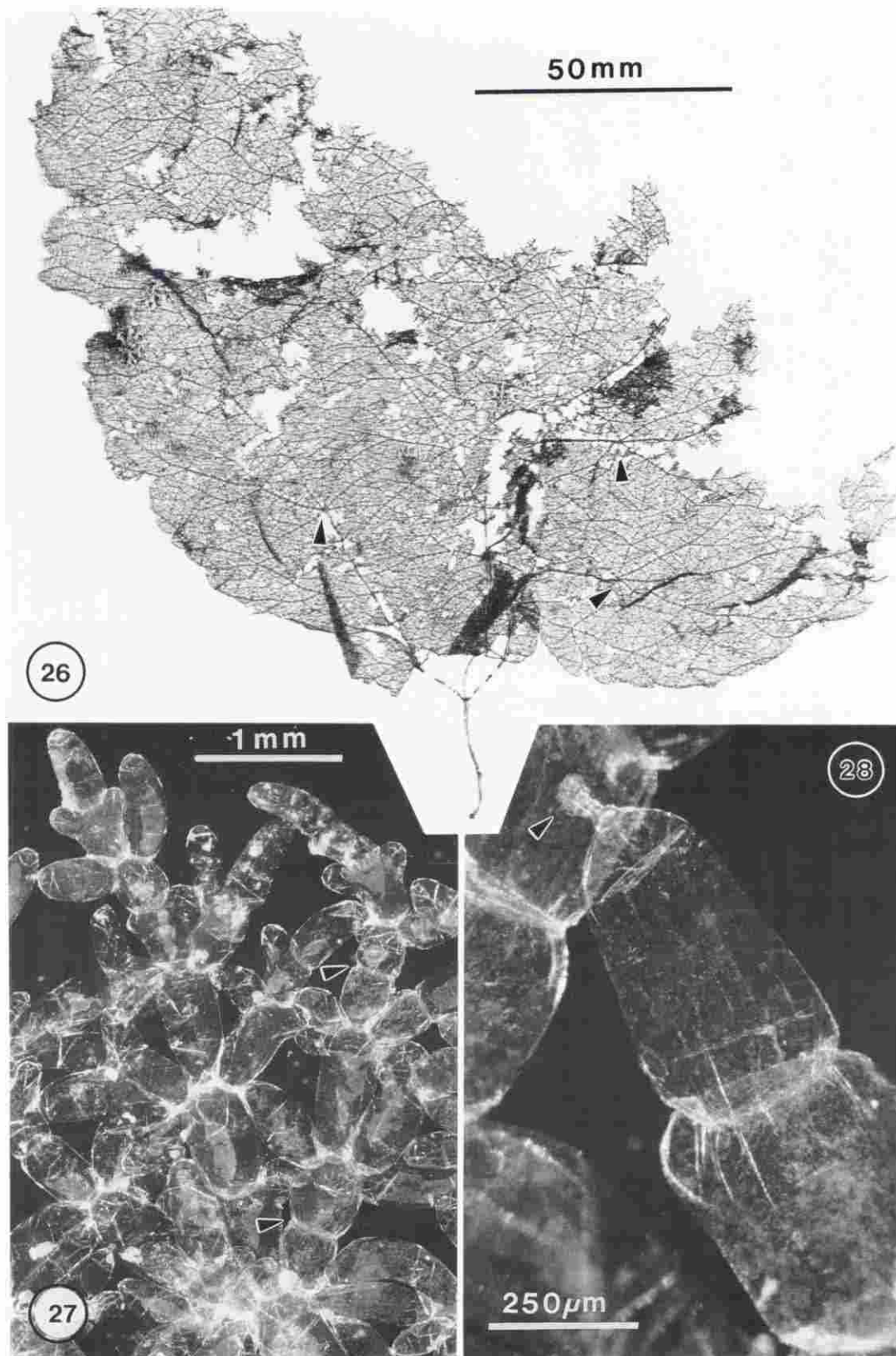


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Figs 26–28. *Phyllocladon pulcherrimum* J. E. Gray. 26. Habit showing characteristic stellate aggregations of first-order laterals (arrowheads) and lack of percurrent primary axes within the reticulate frond. 27. Second- and third-order laterals composed of thin-walled, bulbous cells and displaying two intercalary cell divisions (arrowheads). 28. A slender tenacular cell (arrowhead) at the apex of a third-order lateral.

billicatum. *Pterodictyon* and *Phyllodictyon* are based on species currently assigned to *Struvea* (Murray and Boodle 1888), but *Pterodictyon* is illegitimate because the name was used earlier by Unger (in Richter and Unger 1856) for a form-genus of fossil stem, possibly from a lycopod. The monotypic *Phyllodictyon* was based on *Struvea pulcherrima* but has never been adopted by anyone apart from its author.

Nereodictyon Gerloff (1960) is an East African genus with habit similarities to *Boodlea* and *Microdictyon* but which lacks tenacular attachments, a feature that also defines the very similar if not taxonomically equivalent genera *Struveopsis* (Rhyne and Robinson 1969) and *Pseudostruvea* (Egerod 1975).

Comparison of *S. plumosa* with both *S. anastomosans* (the type species of the nomenclaturally illegitimate genus *Pterodictyon*) and *Struvea pulcherrima* (the type species of *Phyllodictyon*) shows that the latter two species differ substantially from the type species of *Struvea* in their primary mode of cell division. Cytokinesis patterns that differ by such a magnitude seem arguably strong grounds for the recognition of separate genera, and we recommend that *Struvea* be restricted to *S. plumosa* and the Caribbean species *S. elegans*. Although we have not examined fresh collections of the latter and have not been able to directly confirm Børgesen's claims that its cell division is segregative, herbarium specimens in MICH and Børgesen's illustration (1912, fig. 14c) strongly indicate that *S. elegans* closely resembles *S. plumosa* and is thus a true *Struvea*.

We have presented evidence based on the non-synchronicity of cross-wall formation, centripetal ingrowth of septa, and the presence of intercalary cell divisions that *S. anastomosans* does not undergo segregative cell division. Compelling molecular evidence that *S. anastomosans* and *S. elegans* are generically distinct has been provided by Kooistra *et al.* (1993), who show from analyses of rDNA-ITS nucleotide sequences and anatomical features in the two species that *Struvea* as presently constituted is polyphyletic. Anatomical similarities between *S. anastomosans* and *S. pulcherrima* suggest to us that both at least provisionally should be considered congeneric and distinct from *S. plumosa* and *S. elegans*, the name *Phyllodictyon* J. E. Gray being valid and available.

Struvea is usually assigned to the order Siphonocladales (e.g. Børgesen 1925; Feldmann 1938; Egerod 1952; Taylor 1960; Valet 1968; Dawes and van Breedveld 1969; Silva 1982), although Womersley (1984) placed it in the Cladophorales. Olsen-Stojkovich (1986) grouped *Struvea* with the genera *Boodlea*, *Chamaedoris* and *Cladophoropsis* based on cell division processes, the presence of tenacular cells, and immunological distance data, but she did not definitely assign it to either order. The genus is retained in the Siphonocladales by Kooistra *et al.* (1993). Bakker *et al.* (1994), however, analyzed 18S rRNA gene sequences in eight genera

(not including *Struvea*) of the Cladophorales/Siphonocladales complex and concluded that 'there is no basis for the independent recognition of the Cladophorales and Siphonocladales'. The data indicate that the Siphonocladales as traditionally circumscribed is polyphyletic, whereas the Cladophorales exclusive of the Siphonocladales is paraphyletic. We thus follow Bakker *et al.* (1994) in considering both *Struvea* and *Phyllodictyon* to be members of an order Cladophorales that encompasses former members of the Siphonocladales.

There are insufficient data at present to determine whether or not separation of *Phyllodictyon* and *Struvea* renders the former paraphyletic, but the indications of Kooistra *et al.*'s (1993) studies are that the two taxa are on separate developmental lines rooted in a distant common ancestry. Basic to such an hypothesis is the belief that although segregative cell division is probably a derived character, features such as annulated stalks, tenacular cells and reticulate frond architecture are unlikely to all be plesiomorphic conditions of a single struveoid clade. Our strong inclination for now would be to consider the many points of morphological similarity between *Struvea* and *Phyllodictyon* as probable examples of multiple convergences along independent lines.

Saunders and Kraft (1994) have argued in regard to red algae that the phylogenetically significant indications of molecular analyses can ideally direct the attention of morphologists to new or previously undervalued supporting observations at the anatomical level. In the present case, it appears that molecular and anatomical data are again complementary and mutually supportive of taxonomic and systematic conclusions. Although we have not examined all the species currently placed in *Struvea*, we have seen enough material to warrant, in our opinion, the transfer of most to the genus *Phyllodictyon*.

Taxonomic conclusions

Struvea Sonder (1845: 49) nom. cons., sensu stricto

Type species: *Struvea plumosa* Sond. (1845: 50). The type of *Struvea plumosa* is housed in MEL (502116). An isotype specimen is deposited in MICH ('Hb. Preiss n. 2486').

Synonym: *Struvea macrophylla* Harv. (1855: 564).

Records and distribution: Western Australia: Garden Island (type locality) and Rottneest Island (Sonder 1845); Champion Bay (Type locality of *Struvea macrophylla*) (Harvey 1855). Ranges from Kalbarari in the north, southward and eastward to near the Adelaide region of South Australia (Womersley 1984; Huisman and Walker 1990).

Additional species:

Struvea elegans Børgesen (1912), p. 264, figs. 13 and 14.

Records and distribution: St Thomas, US Virgin Islands, West Indies (type locality); Dry Tortugas, Florida, Gulf of Mexico (Taylor 1928); Seychelles Islands, Indian Ocean (Kalugina-Gutnik *et al.* 1992).

This species is apparently restricted to deep water and is similar to *S. plumosa* in its production of creeping filaments at the bases of primary stalks from which erect axes secondarily arise, percurrent axes, and an apparent lack of intercalary cell divisions. It differs in its proximally branched stalks, generally smaller overall size, and the nearly right-angled orientation of the first- and second-order branch primordia (Børgesen 1912, fig. 13; Taylor 1928, 1960). Taylor's (1960, pl. 9, fig. 1) depiction of an old blade shows lax, irregular branching very unlike anything seen in *S. plumosa*.

Phyllocladon J. E. Gray

Type species: *Phyllocladon pulcherrimum* J.E.Gray (1866a: 70).

Synonym: *Struvea pulcherrima* (J. E. Gray) G.Murray et Boodle (1888: 281). Dawes (1981, figs 5–17). Synonym: *S. anastomosans* var. *canariensis* Picc. (Piccone 1884) according to Børgesen (1925). Type locality: Gulf of Mexico, 1802 Menzies coll. (Gray 1886a).

Records and distribution: Jupiter Inlet, Florida, G. Hall coll. (Collins 1909); Florida, Gulf of Mexico, Barbados (Taylor 1928); Tampa Bay, Florida (Dawes 1974); North Carolina (Humm and Cerame-Vivas, 1964); Canary Islands (type locality of *Struvea anastomosans* var. *canariensis* Picc.).

Synonym: *Struvea ramosa* Dickie in J. D. Hooker (1875: 316). Type locality: Bermuda. Also recorded from Netherlands Antilles (Taylor 1960); Gulf of California, Mexico (Dawson 1966); Kenya (Isaac 1967); Philippines (Westerhagen 1974). Treated as a taxonomic synonym of *Struvea pulcherrima* by Schneider and Searles (1991).

Additional species:

(1) *Phyllocladon anastomosans* (Harv.) comb. nov.

Basionym: *Cladophora? anastomosans* Harv. 1859, pl. Cl. *Struvea anastomosans* (Harv.) Picc. et Grunov ex Picc. 1884: 20. Type locality: Fremantle, Western Australia. This species has been abundantly reported as occurring in tropical seas around the world, including the Caribbean Sea, West Africa, East Africa, and South Africa, the Indian Ocean, Red Sea, and the South Pacific. Representative records include Børgesen (1912, 1952), Dawson (1954), Steentoft (1967), Egerod (1971, 1975), Chang *et al.* (1975), Schnetter and Bula Meyer (1982), and Lawson and John (1982).

Synonym: *Struvea delicatula* Kütz. 1866: I, pl. 2. Type locality: New Caledonia. Considered a taxonomic synonym of *Struvea anastomosans* by Murray and Boodle (1888) and most subsequent workers, although not by Børgesen (1933).

Synonym: *Struvea multipartita* Pilger 1920: 2, figs 1–8. Type locality: Annobon Island, West Africa. Treated as a taxonomic synonym of *S. anastomosans* by Steentoft (1967) and Lawson and John (1982).

Synonym: *Struvea tenuis* Zanardini 1878: 39. Type locality: New Guinea. Treated as a taxonomic synonym of *Struvea anastomosans* by Cribb (1960).

The well documented pantropical distribution of this species is at least partly a result of so many taxa being synonymized with it. Collections in MICH and MELU, however, show a large range of habits, cell sizes, and mesh morphologies, suggesting that more than one species may ultimately be characterized for this large assemblage.

(2) *Phyllocladon gardineri* (A. Gepp et E. Gepp) comb. nov.

Struvea gardineri A. Gepp et E. Gepp 1908: 166, pl. 22, fig. 5. Type locality: Cargados Carajos, north of Mauritius, western Indian Ocean. Known only from the type locality.

(3) *Phyllocladon haterumensis* (Itono) comb. nov.

Basionym: *Struvea haterumensis* Itono 1973: 158, figs 15–20. Type locality: Hateruma I., at southernmost end of Ryukyu Is., Japan; and reported by Itono (1973) from Taketomi I., Ryukyu Is., Japan. Also recorded from Lord Howe Island, eastern Australia, at 24 m depth (G. Kraft, pers. obs.; Millar and Kraft 1994).

(4) *Phyllocladon intermedium* (C. F. Chang et E. Z. Xia) comb. nov.

Basionym: *Struvea intermedia* C. F. Chang et E. Z. Xia in Chang, Xia and Xia 1975: 43, fig. 14: 1–7, fig. 15: 1–9, pl. I, fig. 1. Type locality: near Shidao, Xisha Islands, Guangdong, China. Apparently endemic (Tseng 1983).

(5) *Phyllocladon japonicum* (Okamura et Segawa) comb. nov.

Basionym: *Struvea japonica* Okamura et Segawa in Segawa 1936: 178, figs 4 and 5. Type locality: Tozi, Izu Province, Japan. Dredged from 18–37 m. Known only from the type locality.

(6) *Phyllocladon orientalis* (A. Gepp et E. Gepp) comb. nov.

Basionym: *Struvea orientalis* A. Gepp et E. Gepp 1908: 167, pl. 22, figs 6–9. Type locality: Amirante

Is., west of the Seychelles. Known only from the type locality.

(7) *Phyllocladon tuticorinensis* (Børgesen) comb. nov.

Basionym: *S. tuticorinensis* Børgesen 1933: 3, pl. 1 and fig. 2. Type locality: Tuticorin, India, dredged from 12 m. Known only from the type locality.

The genera *Struveopsis* Rhyne et H. Rob. and *Pseudostruvea* Egerod

Very similar in morphology to *Phyllocladon* are the genera *Struveopsis* and *Pseudostruvea*. Rhyne and Robinson (1969) proposed the type species of *Struveopsis*, *Struveopsis chagoensis* Rhyne et H. Rob., plus a second species, *Struveopsis robusta*, based on *Cladophoropsis robusta* Setch. et N. L. Gardner (1924). They described fronds of their genus as small (to 2.75 cm tall in *S. chagoensis*; 2.5–3.5 cm tall in *S. robusta*), growing from a non-annulate lengthy stipe cell, and producing a flattened distal reticulum in which tenaculæ are completely lacking. Egerod (1975) described the genus *Pseudostruvea* in very similar terms to those of Rhyne and Robinson (1969), apparently unaware of their earlier publication. She also included *Cladophoropsis robusta* Setch. et N.L.Gardner in her genus, along with the type species, *Pseudostruvea siamensis* Egerod, which was described as 1–2 cm tall, with or without distinct annular constrictions at the bases of the prominent stalks, the stalks bearing distichous and opposite first-order branches and more irregularly arranged second- and third-order laterals. Again, tenaculæ were conspicuously missing.

We have seen specimens closely matching the descriptions of Rhyne and Robinson (1969) and Egerod (1975) from Lord Howe Island (G. Kraft, pers. obs.) and would agree with those authors that such plants are extremely *Struvea*-like in morphology in the sense that we now reserve for *Phyllocladon*. Cell divisions are of the *Cladophora*-type, and the lack of tenacular attachments between branch orders might make the separation of such plants from *Cladophora* itself appear questionable. That sort of decision obviously awaits more abundant collections of this rarely reported genus and analysis at the molecular level, but in the meantime it appears that in spite of minor inconsistencies the accounts of *Struveopsis* and *Pseudostruvea* are essentially the same. The inclusion of *Cladophoropsis robusta* as a second species by the authors of both genera seems further evidence of synonymy, in which case *Struveopsis* has priority over *Pseudostruvea*. As it is not possible to determine whether *Struveopsis chagoensis* and *Pseudostruvea siamensis* are the same or different species, we propose that the latter be at least provisionally transferred as:

Struveopsis siamensis (Egerod) Kraft et M. J. Wynne, comb. nov.

Basionym: *Pseudostruvea siamensis* Egerod 1975: 48, figs 12–14.

In conclusion, the salient features of the genera discussed in this paper can be summarized below:

Struvea: thallus consisting of stalked blades, borne singly or in clumps, attached by a monosiphonous stalk and constructed of a network of first- and higher-order distichously arranged laterals produced by a process of synchronous segregative cell division; tenacular cells terminating the laterals and fusing with adjacent laterals, resulting in a network of filaments lying essentially in one plane; intercalary cell divisions not occurring.

Phyllocladon: thallus consisting of stalked blades, borne singly or in clumps, attached by a monosiphonous stalk and constructed of a network of first- and higher-order distichously arranged laterals, produced by non-synchronous centripetal wall ingrowths that divide parent walls into approximately equal halves (*Cladophora*-type cell division); tenacular cells terminating the laterals and fusing with adjacent laterals, resulting in a network of filaments lying essentially in one plane; intercalary cell divisions commonly present.

Struveopsis: thallus consisting of a stalked, flattened frond, attached by a monosiphonous stalk and constructed of distichously arranged laterals lying essentially in one plane but the terminal segments of these laterals failing to attach themselves to other parts of the thallus (thus, tenacular cells lacking); cell divisions are of the *Cladophora*-type, i.e., produced by non-synchronous centripetal wall ingrowths that divide the parent cell into approximately equal halves.

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