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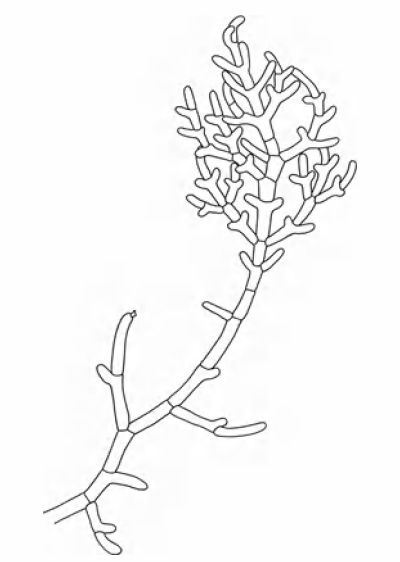
Taxonomic and phylogenetic studies in the Cladophorophyceae (Chlorophyta)



Frederik Leliaert

Proefschrift ingediend tot het behalen van de
graad van Doctor in de Wetenschappen (Biologie)
Academiejaar 2003-2004

Promotor: Prof. Dr. Eric Coppejans

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Promotor: Prof. Dr. Eric Coppejans

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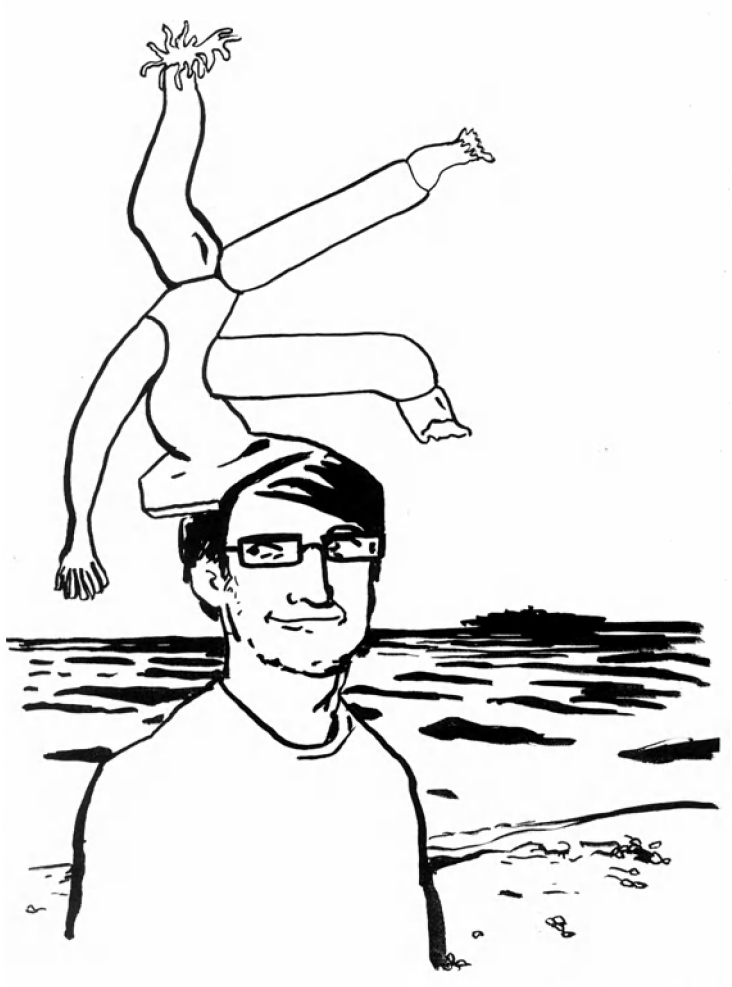
***Cladophoropsis composita* complex**



Peter Lagast 2004

Contents

Chapter 1

Introduction and objectives

The Cladophorophyceae

The Cladophorophyceae nom. nud. (van den Hoek *et al.* 1995) encompass a class of siphonocladous (coenocytic) Chlorophyta and include both orders Cladophorales Haeckel and Siphonocladales Oltmanns. A total of 78 genera have been described in the class (Farr *et al.* 1979, 1986), only about half of which are recognized to date. The monophyly of the Cladophorophyceae has been demonstrated by ultrastructural, morphological as well as molecular evidence (van den Hoek *et al.* 1995) but its position within the Chlorophyta is still not completely resolved. Phylogenetic studies based on partial SSU and LSU nrRNA suggest the Bryopsidophyceae and/or Dasycladophyceae to be the sister groups of the Cladophorophyceae (Zechman *et al.* 1990, 1999). The relationship between the Cladophorophyceae and Dasycladophyceae was later confirmed by Watanabe *et al.* (2001) based on complete SSU rRNA, but no members of the Bryopsidophyceae were included in this study. The class is distributed from tropical to arctic regions and includes mainly marine species as well as some freshwater and terrestrial representatives (van den Hoek 1984). Thallus organization ranges from unbranched or branched uniseriate filaments to more complex architectural types such as parenchymatous thalli, thalli composed of inflated cells, stipitate plants, blade-like thalli, and reticulate plants composed of anastomosing filaments.

Systematic history of the orders Cladophorales and Siphonocladales

The history of both orders has been reviewed in great detail by J. Feldmann (1938b), Egerod (1952), Jónsson (1962), van den Hoek (1984) and Olsen-Stojkovich (1986), and is represented in a diagram in Fig. 1.

Schmitz (1879) created the Siphonocladaceae (as Siphonocladiaceae) to accommodate chlorophytes with multinucleate, septate thalli and chloroplasts forming a continuous parietal layer, and included his new genus *Siphonocladus* Schmitz along with *Valonia* C. Agardh, *Anadyomene* Lamouroux, *Microdictyon* Decaisne, *Cladophora* Kützing, *Chaetomorpha* Kützing, *Pithophora* Wittrock, *Botrydium* Wallroth (currently placed in the Xanthophyta), and, provisionally, *Struvea* Sonder. A slightly different taxonomy was proposed by Blackman & Tansley (1902) who established the Siphonales in which they recognized two suborders: the Siphoneae (nonseptate forms) and the Siphonocladeae (septate forms, including the Gomontiaceae, Cladophoraceae, Sphaeropleaceae and Valoniaceae). Oltmanns (1904) created the order **Siphonocladales** (as Siphonocladiales) in which he placed Schmitz' (1879) Siphonocladaceae, and distinguished five families: Cladophoraceae, Siphonocladaceae, Valoniaceae, Sphaeropleaceae (now Ulotrichales) and Dasycladaceae (now Dasycladales). The order Siphonocladales was accepted by Børgesen (1913) who initially recognized three families: Cladophoraceae, Valoniaceae [including the "subfamilies" (erroneously with the tribe ending –eae) Anadyomeneae, Valonieae, Siphonocladeae and Boodleae] and Dasycladaceae. The Dasycladales were later excluded and the subfamilies of the Valoniaceae raised to family level by Børgesen (1948).

A major taxonomic reorganisation was proposed by Fritsch (1935) who accepted the Valoniaceae and, in agreement with Blackman & Tansley (1902), placed it in the Siphonales. However, whereas Blackman & Tansley recognized the suborder Siphonocladeae to

accommodate the septate, coenocytic families, Fritsch removed the Cladophoraceae to the **Cladophorales** of Haeckel (1894), which had been resurrected by West (1904).

Since then, most of the taxonomic controversy has centered on whether or not the Siphonocladales and Cladophorales have to be separated. In most traditional taxonomies two separate orders have been recognized (Børgesen 1948, Egerod 1952, Papenfuss 1955, van den Hoek 1978, Lee 1980, Womersley 1984, Bold & Wynne 1985, Sartoni 1992, Leliaert *et al.* 1998): genera with a complex or specialized thallus architecture (including *Anadyomene*, *Apjohnia* Harvey, *Boergesenia* J. Feldmann, *Boodlea* Murray & De Toni, *Chamaedoris* Montagne, *Cladophoropsis* Børgesen, *Dictyosphaeria* Decaisne ex Endlicher, *Ernodesmis* Børgesen, *Microdictyon*, *Siphonocladus*, *Struvea*, *Struveopsis* Rhyne & Robinson, *Valonia*, *Valoniopsis* Børgesen and *Ventricaria* Olsen & West) were placed in the order Siphonocladales, whilst genera with a more simple, less specialized construction were ranged under the Cladophorales (including *Cladophora*, *Chaetomorpha*, *Rhizoclonium* Kützing and some smaller, mostly freshwater genera, *Basicladia* Hoffmann & Tilden, *Wittrockiella* Wille, *Pithophora*, *Arnoldiella* Skvortzow, *Gemiphora* Skabichevskii, *Chaetonella* Schmidle, *Chaetocladiella* Meyer & Skabichevskii, *Cladophorella* Fritsch, *Cladostroma* Skuja and *Dermatophyton* Peter) (van den Hoek 1984). These classifications all recognized the Valoniaceae, Siphonocladaceae and Boodleaceae within the Siphonocladales, and the Cladophoraceae in the Cladophorales, but differed in the placement of the Anadyomenaceae which was either placed in the Siphonocladales (Egerod 1952; Leliaert *et al.* 1998) or Cladophorales (Papenfuss 1955; Womersley 1984). The Siphonocladales were thought to differ from the Cladophorales by a peculiar way of cell division termed "segregative cell division". This means cleavage of the protoplast into rounded and walled portions which later expand into new cells and branches (Børgesen 1905, 1913; Egerod 1952) (see below). However, well organized segregative cell division has been indisputably demonstrated in only a small number

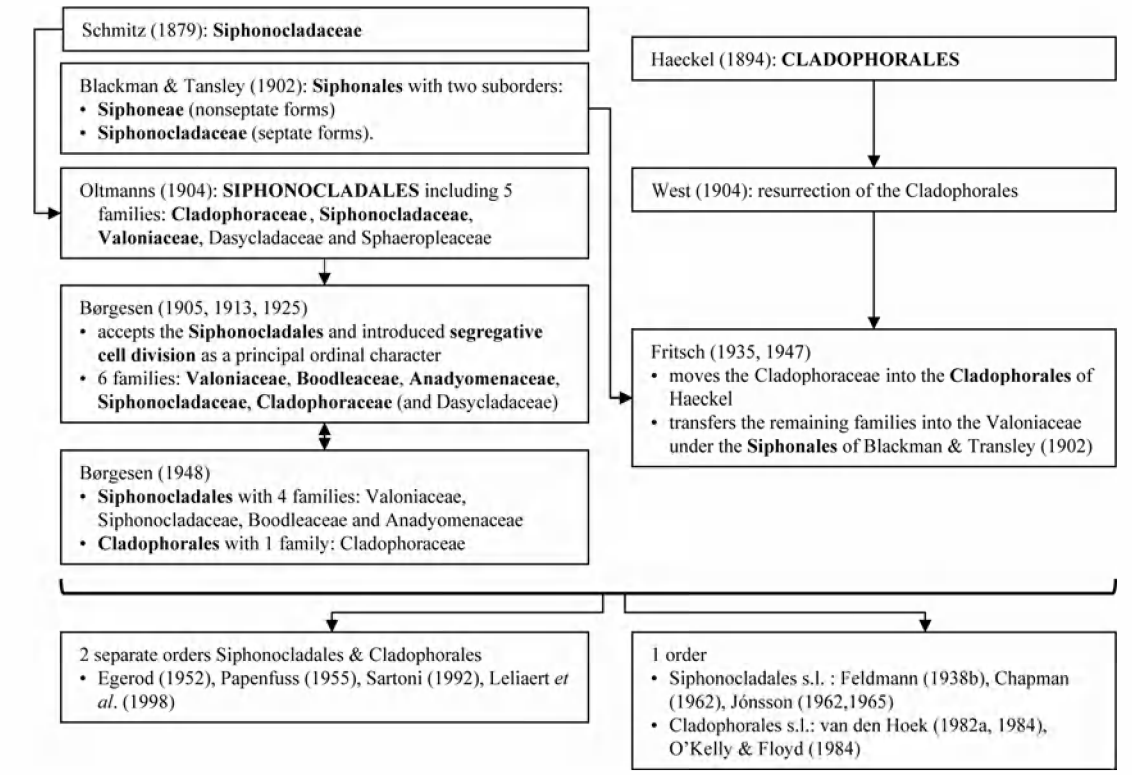


Fig. 1. Diagram showing the taxononomic history of the orders Siphonocladales and Cladophorales.

of genera (e.g. *Dictyosphaeria*, *Siphonocladus*, *Struvea* and *Ventricaria*) (Egerod 1952, van den Hoek 1984, Olsen & West 1988, Kraft & Wynne 1996).

The rationale for placing all genera in a single order, Siphonocladales *s.l.* (Børgesen 1913, 1925; Chapman 1962, J. Feldmann 1938b; Jónsson 1962, 1965), was the apparent homogeneity of thallus organization, chloroplast morphology and cell wall structure in the group. In later circumscriptions by van den Hoek (1984) and O'Kelly & Floyd (1984), a single comprehensive order is recognized based on the similarities in chloroplast morphology, ultrastructural characters (pyrenoids, zoids and mitosis), life history and cell wall composition. An additional ground against separating simple thalli in one order (Cladophorales) and complex thalli in another order (Siphonocladales) is formulated by van den Hoek (1982a, 1984) who hypothesized that complex and specialized genera have been derived from simple architectural types within *Cladophora*, supporting the inclusion of these genera in one and the same order (see below).

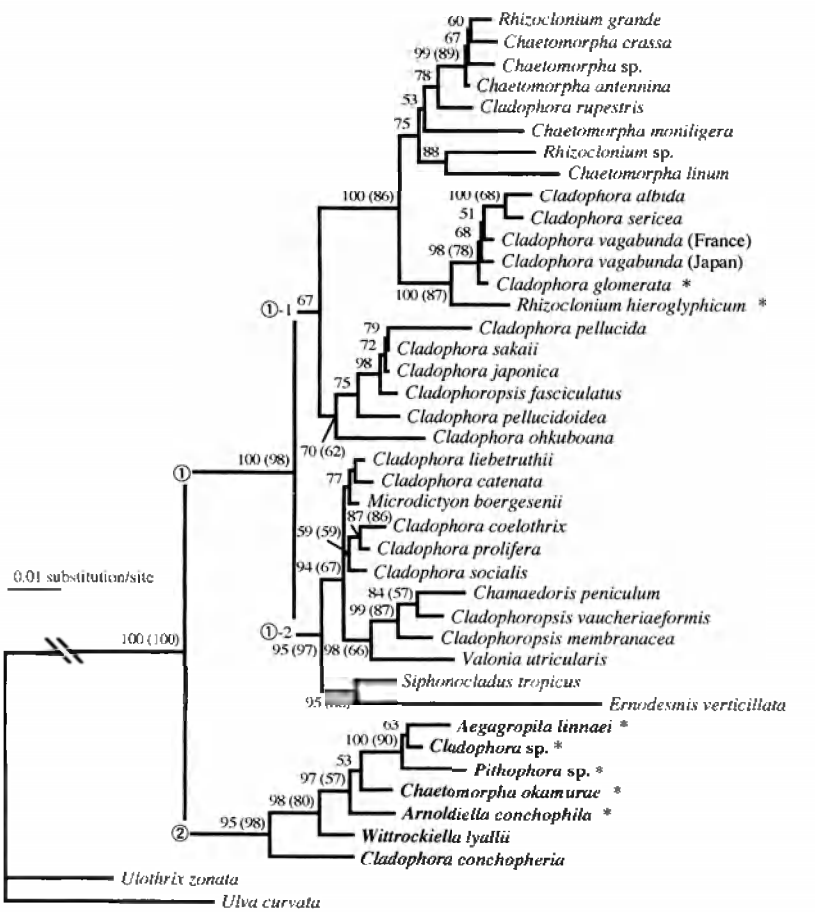


Fig. 2. A phylogenetic tree of the Cladophorophyceae (maximum likelihood tree) inferred from SSU nrRNA gene sequences. Asterisks show freshwater species. (From Hanyuda *et al.* 2002).

The idea of evolutionary homogeneity has been confirmed by phylogenetic studies based on nuclear SSU rRNA sequence analyses (Bakker *et al.* 1994, Hanyuda *et al.* 2002). The first study, based on sequences of 20 species, demonstrated that neither the Cladophorales nor the Siphonocladales forms a monophyletic group and that there is no basis for the independent recognition of both orders. This phylogeny supports two main lineages, one containing predominantly tropical members (including almost all siphonocladalean taxa and a number of

Table 1. Some examples of different proposed taxonomies, illustrating the confusing and variable family circumscriptions (genera presently excluded from the Cladophorophyceae are not included; genera which are currently reduced to synonymy of other genera have also been omitted) (partly after Wysor 2002).

	Anadyomenaceae	Boodleaceae	Cladophoraceae	Siphonocladaceae	Valoniaceae
Børgesen (1925, 1930, 1934, 1936, 1939)	*Anadyomene*, *Microdictyon*, *Valoniopsis*	*Boodlea*, *Cladophoropsis*	*Chaetomorpha*, *Cladophora*, *Rhizoclonium*	*Chamaedoris*, *Ernodesmis*, *Siphonocladus*, *Struvea*	*Dictyosphaeria*, *Valonia*
Børgesen (1940, 1946, 1948, 1952)	*Anadyomene*	*Boodlea*, *Cladophoropsis* (1940, 1946), *Microdictyon*, *Spongocladia*, *Struvea*	*Chaetomorpha*, *Cladophora*, *Rhizoclonium*	*Boergesenia*, *Chamaedoris*, *Cladophoropsis* (1948), *Ernodesmis*, *Siphonocladus*	*Dictyosphaeria*, *Valonia*
Egerod (1952)	*Anadyomene*, *Microdictyon*	*Boodlea*, *Struvea*		*Chamaedoris*, *Cladophoropsis*, *Siphonocladus*	*Dictyosphaeria*, *Valonia*
Taylor (1928)			*Chaetomorpha*, *Cladophora*, *Cladophoropsis*, *Microdictyon*, *Rhizoclonium*		*Anadyomene*, *Chamaedoris*, *Dictyosphaeria*, *Ernodesmis*, *Siphonocladus*, *Struvea*, *Valonia*
Taylor (1950, 1960)			*Chaetomorpha*, *Cladophora*, *Rhizoclonium*		*Anadyomene*, *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Microdictyon*, *Siphonocladus*, *Struvea*, *Valonia*, *Valoniopsis*
Womersley & Bailey (1970)	*Anadyomene*	*Boodlea*, *Struvea*	*Chaetomorpha*, *Cladophora*, *Rhizoclonium*	*Boergesenia*, *Cladophoropsis*	*Dictyosphaeria*, *Valonia*, *Valoniopsis*
Silva *et al.* (1996)	*Anadyomene*, *Microdictyon*		*Apjohnia*, *Chaetomorpha*, *Cladophora*, *Rhizoclonium*	*Boergesenia*, *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Dictyosphaeria*, *Siphonocladus*, *Struvea*, *Struveopsis*, *Ventricaria*	*Ernodesmis*, *Valonia*, *Valoniopsis*
Kraft (2000)	*Phyllodictyon*		*Boodlea*, *Chaetomorpha*, *Cladophora*, *Cladophoropsis*, *Microdictyon*, *Rhizoclonium*, *Spongocladia*	*Dictyosphaeria*	*Valoniopsis*, *Ventricaria*

Cladophora species), the other consisting of mostly warm- to cold-temperate species of *Cladophora*. The second study (Hanyuda *et al.* 2002) extended the previous phylogeny with 21 additional species. This analysis reveals a new sister clade (which they termed the *Aegagropila*-clade), comprising a mixture of marine and freshwater genera with a simple, *Cladophora*-type architecture (*Aegagropila* Kützing, *Arnoldiella*, *Cladophora*, *Pithophora* and *Wittrockiella*) (Fig. 2).

Traditional circumscription of the families

Four families (Anadyomenaceae, Cladophoraceae, Siphonocladaceae and Valoniaceae) are traditionally recognized within the Cladophorophyceae, mainly based on differences in thallus architecture and mode of cell division. Børgesen (1925) recognized a fifth family, Boodleaceae. The family circumscriptions are rather vague and variable, and consequently the included genera have changed frequently in the course of time (see Table 1). Moreover, some of the families have not been accepted by a number of authors. Taylor (1928, 1950, 1960) for example only recognized two families, Cladophoraceae and Valoniaceae, and Womersley (1984), amongst others, did not accept the Boodleaceae. A number of other families (Microdictyaceae, Dictyosphaeriaceae, Wittrockiellaceae and Pitophoraceae) have been proposed but have never gained wide acceptance. We refer to Silva (1980) for nomenclatural notes on the families.

The **Anadyomenaceae** was erected by Kützing (1843: 302, 311, 'Anadyomeneae') to accommodate the foliose genus *Anadyomene* (Fig. 3A, B). The genus *Microdictyon* (Fig. 3C-E) was included by Børgesen (1925) based on its blade like, astipitate thalli. Later, Børgesen (1930, 1934, 1940) regarded the flabellate branching mode as the principle character of the Anadyomenaceae and therefore he also included *Willeella* and *Valoniopsis*; *Microdictyon* on the other hand was excluded from the family and placed in the Boodleaceae based on the more irregular way of branching. Setchell (1929) placed *Microdictyon*, toghether with *Boodlea* and *Struvea*, in a family Microdictyaceae, based on similarities in anastomosis by tenacular cells (although different in type), resulting in open meshes, as opposed to *Anadyomene* where the cells join by lateral cohesion, resulting in solid blades. The family Microdictyaceae however has never been widely accepted. The traditional circumscription of the Anadyomenaceae as circumscribed by Børgesen (1925) and Egerod (1952) – uniseriate filaments, branching in a single plane and anastomosing by lateral coalescence or by annular or crenulate adhesion pads on the tips of cells – is still widely accepted to date and includes both *Anadyomene* and *Microdictyon*.

The **Valoniaceae** was erected by Kützing (1849: 507, 'Valonieae') to accommodate a heterogeneous assemblage of genera characterized by inflated cells, including *Valonia*, *Chamaedoris*, *Acrocladus* Nägeli, *Ascothamnion* Kützing (a genus originally assigned to the algae, but now considered to belong to the Bryozoa), and five genera which are currently placed in the Dasycladales. Wille (1890, 1910) even extended the circumscription of the family and recognized four subfamilies (erroneously with the tribe ending –eae): Valonieae (including *Apjohnia*, *Blastophysa* Reinke, *Dictyosphaeria*, *Halicystis* Areschoug and *Valonia*), Chaetosiphonales (*Chaetosiphon* Huber), Siphonocladeae (*Chamaedoris*, *Petrosiphon* Howe, *Siphonocladus*) and Anadyomeneae (*Anadyomene*, *Boodlea*, *Microdictyon*, *Rhipidiphyllon* Heydrich and *Struvea*). Børgesen (1925), J. Feldmann (1938b) and Egerod 1952) narrowed the family circumscription and only included the genera *Valonia* and *Dictyosphaeria*, characterized by cushion-like thalli composed of inflated cells and a similar mode of cell division (Egerod considered the lenticular mode of lateral formation in *Valonia* comparable to the segregative mode of cell division in *Dictyosphaeria*). *Dictyosphaeria* was placed in a separate family

Dictyosphaeriaceae by Kützing (1849: 512, 'Dictyosphaeriae') (*nom. rej.*, Silva 1980) but this name has never been widely accepted. In more recent classifications (e.g. Silva *et al.* 1996) the Valoniaceae include *Valonia* (Fig. 4), *Ernodesmis* and *Valoniopsis* (Fig. 5), all characterized by inflated cells and lenticular cell division.

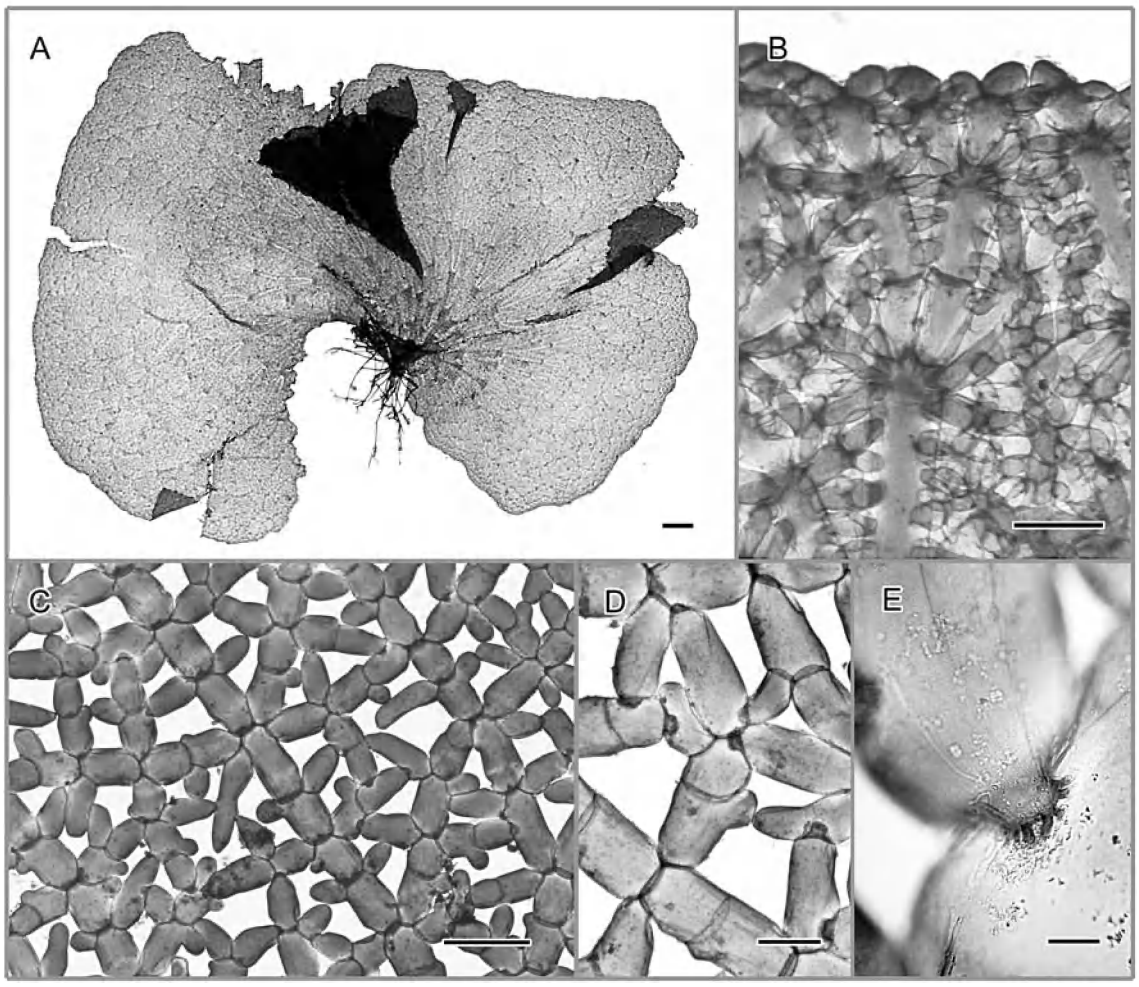


Fig. 3. A, B. *Anadyomene wrightii* Harvey ex J.E. Gray: fanshaped blade composed of flabellate branching filaments, interstitial spaces filled with small (interstitial) cells (HEC 9765, Bawe Island, Zanzibar, Tanzania). C-E. *Microdictyon okamurae* Setchell: reticulate blade composed of flabellate or opposite branching filaments, anastomosis by crenulate wall thickenings at the tip of apical cells (SEY 687, Alphonse Atoll, Seychelles). Scale bars: A = 1 mm; B, D = 200 µm; C = 500 µm; E = 20 µm.

The original delineation of the **Siphonocladaceae** (Schmitz 1879: 20, 'Siphonocladiaceae') was very cryptic and the family included a heterogeneous assemblage of genera (*Anadyomene*, *Botrydium*, *Chaetomorpha*, *Cladophora*, *Microdictyon*, *Pithophora*, *Siphonocladus* and *Valonia*). Børgesen (1925) and J. Feldmann (1938b) assigned the presence of clavate cells with basal annular constrictions as the principle character of the family and included *Boergesenia*, *Chamaedoris*, *Ernodesmis*, *Siphonocladus* (Fig. 6) and *Struvea*. The present circumscription of the Siphonocladaceae has become very general and the family apparently serves to classify all genera which do not fit in any of the other families (see for example Silva *et al.* 1996).

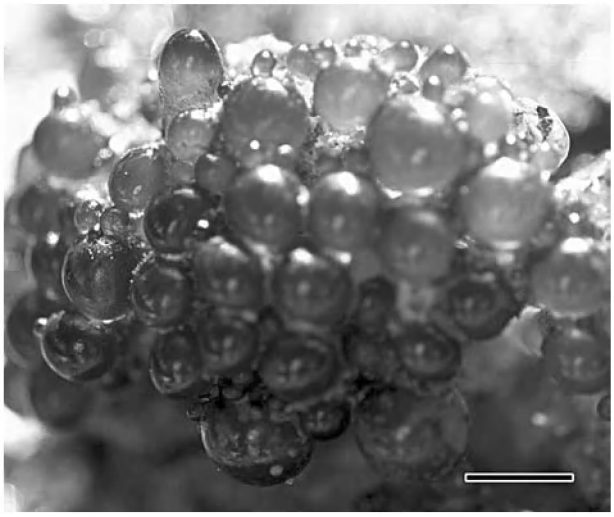


Fig. 4. Thallus of *Valonia macrophysa* Kützing composed of branching inflated cells (KZN 551, Bhanga Neck, KwaZulu-Natal, South Africa). Scale bar = 1 cm.

The **Cladophoraceae** was erected by Wille (*in* Warming, 1884: 30) to accommodate genera characterized by simple thalli, composed of branched or unbranched, uniseriate filaments. The family originally included *Aegagropila*, *Chaetomorpha*, *Chaetonella* Schmidle, *Cladophora*, *Cladophoropsis*, *Pithophora*, *Rhizoclonium*, *Spongocladia*, *Acrosiphonia* J. Agardh and *Urospora* Areschoug (Wille 1890, 1911). The latter two genera also have a siphonocladous thallus organization but have been excluded from the Cladophorophyceae and are currently placed in the Acrosiphoniales (Jónsson 1962, 1999) or Codiolales (van den Hoek *et al*. 1995) based on different cell wall composition, chloroplast structure and life cycle. J. Feldmann (1938b) already pointed out the numerous morphological similarities between various *Cladophora* species and other genera in different families (e.g. *Apjohnia*, *Boodlea*, *Chaetomorpha*, *Cladophoropsis*, *Rhizoclonium* and *Willeella*); this viewpoint was later adopted and elaborated by van den Hoek (1982a, 1984) (see below). The family names Confervaceae Dumortier and Pitophoraceae Wittrock have been rejected in favour of Cladophoraceae, and Wittrockiellaceae Wille is considered as a synonym of Cladophoraceae (van den Hoek 1980).

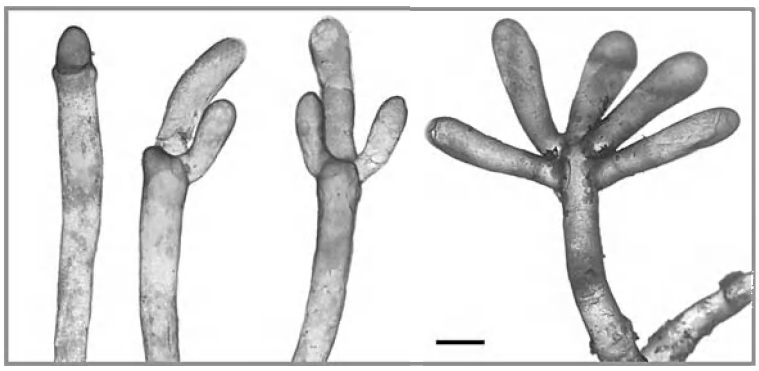


Fig. 5. Lenticular cell division and formation of laterals in *Valoniopsis pachynema* (G. Martens) Børgesen (SOC 46, Rhiy di-Qatanhin, Nogid, S coast of Socotra). Scale bar = 1 cm.

The family **Boodleaceae** was described by Børgesen (1925: 19) to accommodate *Boodlea* and *Cladophoropsis*, characterized by delayed cross wall formation and irregular branching. In later circumscriptions Børgesen (1940, 1946) also included *Spongocladia* and *Microdictyon* but J. Feldmann (1938b) questioned the position of the latter. Egerod (1952) redefined the family as "thalli forming reticulate blades or cushions composed of oppositely branching filaments (at least in early thallus development), and anastomosing by small hapteroidal cells, termed

tenacula (or tenacular cells), formed at the tips of the apical cells", and included only *Boodlea* and *Struvea*. Based on similarities in the formation of laterals, Egerod (1952) allied *Cladophoropsis* with *Boodlea* and considered the first as a transitional genus between the Boodleaceae and Siphonocladaceae.

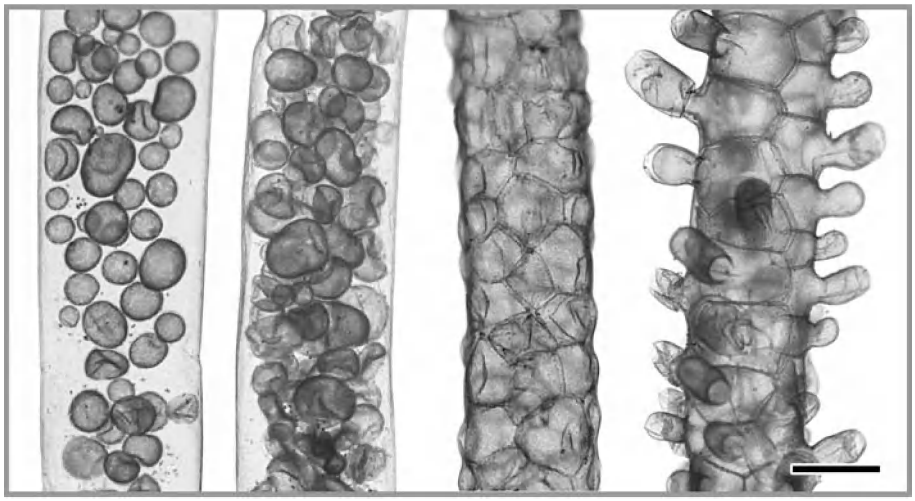


Fig. 6. Segregative cell division in *Siphonocladus tropicus* (P.L. Crouan & H.M. Crouan) J. Agardh (SOC 186, Bindar Fikhah, N coast of Socotra). Scale bar = 500 μm.

Circumscription of the Cladophorophyceae

Ultrastructural and molecular evidence have demonstrated that the Cladophorales s.l. form a monophyletic group, which stands apart from all other Chlorophyta to such an extent, that the status of a class under the name Cladophorophyceae was proposed for it (van den Hoek *et al.* 1995). The class is distinguished by a number of principle characters being the siphonocladous organizational level (i.e. thallus composed of multinucleate cells); the numerous chloroplasts forming a parietal reticulum or closed layer; the crystalline cellulose-I cell walls with a crossed fibrillar pattern; the isomorphic diplohaplontic life history of sexually-reproducing species; the zoids having two or four flagella with basal bodies exhibiting a similar ultrastructure (Floyd *et al.* 1985); a similar type of mitosis and cytokinesis (type VI as defined by van den Hoek *et al.* 1995: 332); vegetative cell division being uncoupled from mitosis; and the cytoplasm which does not stream. We refer to van den Hoek (1984) and van den Hoek *et al.* (1995) for a detailed review of the above characters.

The life cycle of sexually reproducing species are diplohaplontic and isomorphic. The haploid gametophytes produce biflagellate gametes while the diploid sporophytes produces quadriflagellate meiospores. Some species reproduce, either additionally or exclusively, by means of asexual, biflagellate or quadriflagellate zoospores. Cultural as well as karyological evidence of sexual reproduction is available for species of the genera *Cladophora*, *Chaetomorpha*, *Rhizoclonium*, *Anadyomene*, *Microdictyon*, and cultural evidence only for species of *Boergesenia*, *Boodlea*, *Chamaedoris*, *Dictyosphaeria*, *Siphonocladus*, *Struvea*, *Valonia* and *Ventricaria* (Bentlich *et al.* 1990; Bodenbender & Schnetter 1990; Chihara 1955; Enomoto & Okuda 1981, Hori 1994).

Most members of the Cladophorophyceae have bilenticular pyrenoids; that is, each pyrenoid consists of two hemispheres, separated by a single thylakoid and each hemisphere is capped by a bowl-shaped starch grain. The pyrenoid structure was initially thought to be uniform within the class (Jónsson 1962, van den Hoek 1984, van den Hoek *et al.* 1995), however several exceptions to this pattern have been reported recently. Matsuyama *et al.* (1998) and Miyaji (1999) recognized four pyrenoid morphologies among 15 *Cladophora*, *Chaetomorpha* and *Rhizoclonium* species: bilenticular, zonate (a variant of bilenticular with two intrapyrenoidal thylakoids), simple polypyramidal, and complex polypyramidal (radially subdivided pyrenoids covered by a number of radially arranged starch grains; the complex type is characterized by a higher number of thylakoids and starch grains). Hanyuda *et al.* (2002) demonstrated that all taxa in the *Aegagropila*-clade of a SSU nrRNA phylogeny share polypyramidal pyrenoids while species in the two main lineages possess bilenticular pyrenoids.

In most members of the Cladophorophyceae, cell division takes place through the ingrowth of a diaphragm-like cross wall (centripetal invagination of the cell wall, CI) (Enomoto & Hirose 1971). A few members exhibit a different mode of cell division which has been termed segregative cell division (SCD). Here the protoplasm cleaves into rounded, walled portions, which later expand into new vegetative cells (Fig. 6). A detailed description of segregative cell division in *Dictyosphaeria* has been provided by Enomoto *et al.* (1982) and Okuda *et al.* (1997a). Olsen-Stojkovich (1986) distinguished two types of segregative cell division. In segregative division sensu stricto (SDSS), occurring in *Dictyosphaeria*, *Siphonocladus* (Fig. 6) and *Struvea* (*sensu* Kraft & Wynne 1996), multinucleate aggregates of cytoplasm form walled spheres that remain in the parent cell, expand and rupture old parental cell walls. SDSS may result in parenchymatous thalli (*Dictyosphaeria*), branched, filamentous thalli (*Struvea*), or branched clavate cells (*Siphonocladus*). In a second type, termed modified segregative division (SDM), occurring in *Ventricaria* and *Boergesenia*, the cytoplasmic spheres are released from the parent cell and grow into new thalli. In various other members of the Cladophorophyceae (e.g. *Cladophoropsis*), cell wounding induces a reaction which resembles segregative cell division: after mechanical damage, cells contract their protoplasts into balls which produce new cell walls (La Claire 1982; O'Neil & La Claire 1984). Both segregative cell division and this typical type of wounding reaction only occur in tropical representatives of the Cladophorophyceae. van den Hoek & Chihara (2000: 23) suggested that these might be an adaptation to grazing pressure in tropical waters. Olsen-Stojkovich (1986) recognized a fourth type of cell division, lenticular cell division type (LC), occurring in *Valonia*, *Valoniopsis* (Fig. 5) and *Ernodesmis*, in which a convex septal disc is formed along the cell-wall, followed by elongation of a new lateral. This mode of cell division was considered as a special case of segregative cell division by Egerod (1952) while van den Hoek (1984) considered LC essentially similar to CI.

All members of the Cladophorophyceae have a siphonocladous level of organization (i.e. septated thalli are composed of multinucleate cells). The size of the multinucleate cells is highly variable, ranging from micrometers [e.g. *Cladophora globulina* (Kützing) Kützing] to centimeters [e.g. *Ventricaria ventricosa* (J. Agardh) Olsen-Stojkovich]. A wide variation of thallus architectures occurs in the class. The most simple thalli are composed of branched (e.g. *Cladophora*, *Cladophoropsis*, *Wittrockiella*) or unbranched (*Chaetomorpha*, *Rhizoclonium*) uniseriate filaments. More complex architectural types include parenchymatic thalli (*Dictyosphaeria*), thalli composed of inflated cells (e.g. *Valonia*), giant, unbranched unicells (*Ventricaria*), stipitate plants with conspicuous annular constrictions (e.g. *Chamaedoris*, *Struvea*), blade-like thalli (e.g. *Anadyomene*), and two- or three-dimensional reticulate plants composed of anastomosing filaments (e.g. *Microdicyton*, *Boodlea*).

In several species, reinforcement of the thallus is achieved by interweaving of the filaments (e.g. *Cladophora* sections *Repentes*, *Aegagropila* and *Boodleoides*, and *Cladophoropsis*), often combined by anastomosis of adjacent cells by rhizoids or tenacular cells (e.g. *Boodlea*, *Microdictyon*, *Valonia*). Olsen-Stojkovich (1986) distinguished four types of tenacular cells: type-1 tenacular cells: unspecialized cells with crenulate or annulate apices (e.g. *Microdictyon*); type-2 tenacular cells: minute hapteroid cells, formed laterally between adjacent vesicular cells (e.g. *Dictyosphaeria* and *Valonia*); type-3 tenacular cells: small hapteroid cells formed at the distal ends of branches and anastomosing to neighbouring filaments (e.g. *Boodlea* and *Struvea*); and type-4 tenacular cells: small hapteroid cells formed intercellularly between septa (e.g. *Apjohnia*). Many tropical representatives produce adventitious, intercalary rhizoids in any part of the thallus (e.g. *Cladophora* section *Repentes*, *Boodlea*, *Cladophoropsis*, *Anadyomene* and *Microdictyon*) which may attach to the substratum or occasionally realize anastomosis of adjacent filaments. Intercalary rhizoids also promote the formation of dense tufts loaded with sediments and sand that are unattractive to herbivores. Intercalary rhizoid formation might therefore be an adaptation to the intensive grazing pressure (mainly by fish and sea urchins) in tropical regions (van den Hoek & Chihara 2000: 23).

Thallus growth in the Cladophorophyceae generally occurs through apical or intercalary cell division, cell elongation and enlargement, and formation of laterals. Some species or genera are restricted to diffuse or intercalary growth only (e.g. *Chaetomorpha*, *Dictyosphaeria* and *Rhizoclonium*), while others are almost exclusively apical, resulting in an acropetal thallus organization (e.g. *Apjohnia*, *Ernodesmis* and the *Cladophora* sections *Rugulosae* and *Longi-articulatae*). Most species, however, exhibit a combination of both growth types. Based on the phylogenetic studies of Olsen-Stojkovich (1986) and Bakker *et al.* (1994), van den Hoek & Chihara (2000) argue that the acropetal architecture is the ancestral "Bauplan" of the Cladophorophyceae.

The genus *Cladophora* is by far the largest genus of the Cladophorophyceae. Notwithstanding the simple thallus architecture of its representatives, at least 12 architectural types can be distinguished, representing the sections of *Cladophora* as conceived by van den Hoek (1963, 1982a). Based on a comparison of morphology, van den Hoek (1982a, 1984) hypothesized that numerous reduction and specialization events have occurred independently several times in different *Cladophora* sections, resulting in the various reduced and specialized morphologies (genera). These reductions and specializations were circumscribed in eight hypothetical morphological transformations or tendencies: (1) planification of the thallus (tendency to blade formation), (2) interweaving of filaments by hapteroid rhizoids or tenacular cells in upper thallus parts to strengthen blades or other structures, (3) lateral coalescence of filaments to strengthen blades, (4) replacement of succedaneous initiation of branches on one node by simultaneous or nearly simultaneous initiation of branches, (5) increase of the number of branches per node, (6) inflation of cells, (7) differentiation between axis and branches, and (8) reduction or suppression of branches. Fig. 7 illustrates the morphological relationships between six of the twelve sections of *Cladophora* and a number of other genera of the Cladophorophyceae, discussed in detail by van den Hoek (1982a, 1984). For example, one of the morphological series leads from the *Cladophora* section *Repentes*, over the genera *Cladophoropsis* and *Boodlea* to *Struvea* (or *Phyllodictyon* J.E. Gray) by the four morphological tendencies 1, 2, 4 and 7. Another morphological series leads from the *Cladophora* section *Longi-articulatae*, over the genus *Ernodesmis* to *Chamaedoris* by the morphological transformations 2, 5 and 7. Immunological studies (Olsen-Stojkovich 1986) and SSU nrRNA phylogenies (Bakker *et al.* 1994, Hanyuda *et al.* 2002) confirm in general the above morphological derivations.

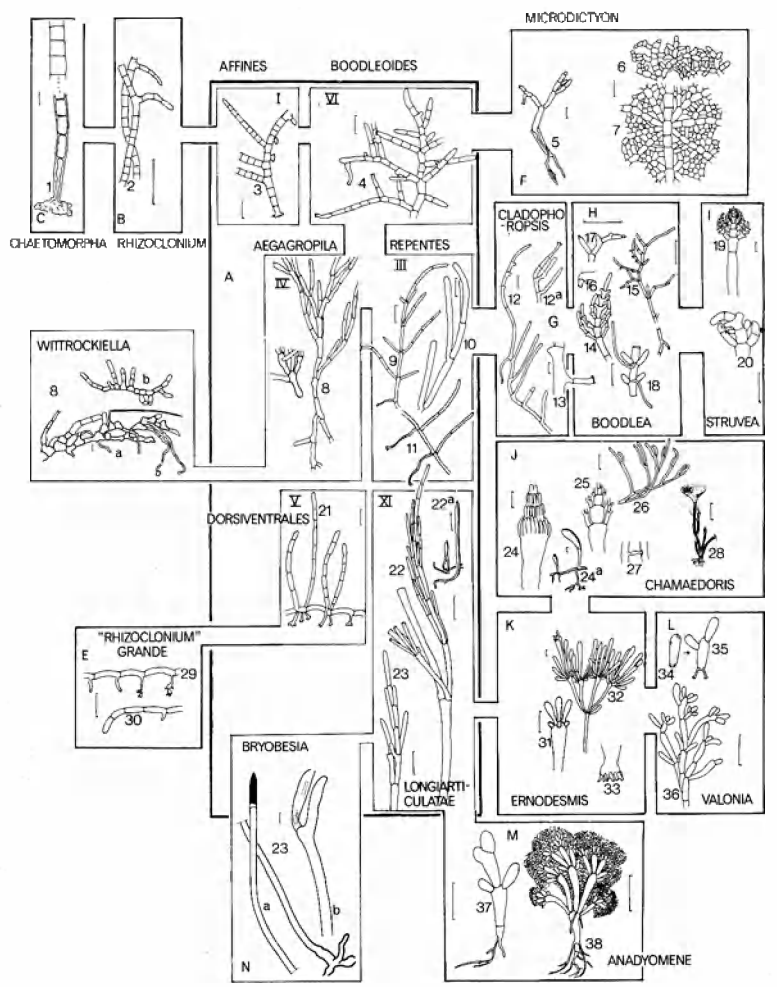


Fig. 7. Morphological relationships between sections of the genus *Cladophora* and other genera of Cladophorophyceae (from van den Hoek 1984).

The exact number of species in the Cladophorophyceae is uncertain and estimates range from 200 (van den Hoek & Chihara 2000) to 420 (van den Hoek *et al.* 1995). The highest number of taxa has been described in the genus *Cladophora* (over 1000 names, Index Nominum Algarum). In his revision of the European species of *Cladophora*, van den Hoek (1963) reduced the number of European species from circa 900 to 37. This tremendous reduction came about mainly through the assessment of ecologically induced morphological variability (phenotypic plasticity) in the species of the genus. *Cladophora* has been well studied in the Northern Atlantic, Southern Australia and Japan (Söderström 1963, van den Hoek 1963, 1982a, van den Hoek & Womersley 1984, van den Hoek & Chihara 2000) but the tropical and subtropical representatives remain poorly known. Other species-rich genera include *Anadyomene* (24 described species), *Chaetomorpha* (ca. 200 described species), *Cladophoropsis* (39 described species), *Microdictyon* (27 described species), *Rhizoclonium* (ca. 130 described species) and *Valonia* (36 described species) (Index Nominum Algarum). The taxonomy of most of these genera, in particular the tropical representatives [with the exception of *Anadyomene* (Littler & Littler 1991) and *Microdictyon* (Setchell 1929)], remains poorly studied. Determining the true number of species in the Cladophorophyceae has become even more complicated through the detection of cryptic species in molecular phylogenetic and phylogeographic studies (Bakker *et al.* 1995b, van der Strate *et al.* 2002).

The age of the Cladophorophyceae remains doubtful. The only fossil evidence is provided by Butterfield *et al.* (1988) who found *Cladophora*-like forms in a submarine Proterozoic shale of Spitsbergen, suggesting that cladophoralean species are 800-700 Ma years old. The age of the Cladophorophyceae can also be derived indirectly by evaluation of the sister group, which according to Zechman *et al.* (1990), is either the Bryopsidophyceae or the Dasycladophyceae. Both groups are Precambrian lineages of tropical marine green algae that have maintained a relatively consistent body plan throughout their 600-570-million year evolutionary history (Berger & Kaever 1992), and this could therefore be also the minimum age of the Cladophorophyceae (van den Hoek & Chihara 2000).

Ecology and Geographical distribution

Most of the Cladophorophyceae are restricted to marine habitats while a small number of species and genera have successfully invaded fresh-water and even terrestrial habitats. Hanyuda *et al.* (2002) demonstrated that the evolution of freshwater species has occurred at least twice independently. Marine species grow from the supralittoral fringe (e.g. *Rhizoclonium africanum* Kützing) to the deep subtidal [e.g. *Phyllodictyon pulcherrimum* J.E. Gray which has been found down to 90 m depth (Littler & Littler 2000)] and are generally epilithic or epiphytic, but may also occur epizoic or endophytic (e.g. *Wittrockiella paradoxa* Wille). One species, *Cladophoropsis vaucheriiformis* (Areschoug) Papenfuss typically grows in symbiosis with a sponge (see chapter 5). Several species typically grow loose-lying on the substratum or are free-floating. Some marine species have a very narrow ecological range and are, for example, restricted to deep subtidal habitats (e.g. *Cladophora vandenhoekii* J.N. Norris & J.L. Olsen), while other species have a very wide ecological range and occur both intertidally and subtidally [e.g. *Dictyosphaeria cavernosa* (Forsskål) Børgesen], or penetrate into estuaries and brackish water [e.g. *Cladophora coelothrix* Kützing and *C. vagabunda* (Linnaeus) van den Hoek]. A number of *Cladophora*, *Chaetomorpha* and *Rhizoclonium* species are restricted to brackish or freshwater habitats where they grow in oligotrophic to eutrophic streams or stagnant waters. Some smaller genera like *Arnoldiella* and *Pithophora* comprise exclusively freshwater species. *Cladophorella calcicola* Fritsch (1944) is the only known terrestrial representative, found on limestone rocks in the tropical greenhouses of the Cambridge Botanical Gardens.

Worldwide patterns in distribution of seaweeds have been shaped by historical events such as paleogeographical (continental drift) and paleoclimatic change (Lüning 1990, van den Hoek *et al.* 1990). Within this historical background, present day geographical distribution of seaweeds depends on prevailing environmental and ecological conditions and dispersal capacity of particular benthic algal species. van den Hoek (1982b) proposed that the geographic distribution boundaries of seaweed species can be defined according to temperature constraints, either for survival, growth or reproduction. These hypothetical temperature boundaries have been extensively tested for a wide array of *Cladophora* species with various distribution patterns (Cambridge *et al.* 1984, 1987, 1990a, b c, 1991; Breeman *et al.* 2002). In general, these studies demonstrate that species with a narrow geographical distribution [e.g. the Australian endemic species *Cladophora feredayi* Harvey and *C. valonioides* (Sonder) Kützing] have stenothermal responses, while widespread species (e.g. *Cladophora vagabunda*, or at least some clades or within this species complex) are eurythermal. However, many species could be expected to extend beyond their present known range on the basis of their temperature responses and seawater temperatures (Cambridge *et al.* 1991). Although temperature is generally accepted to be the most important factor for establishing large-scale boundaries of

algal distribution pattern, other environmental and ecological factors (Lüning 1990) in combination with dispersal capacity (van den Hoek 1987; Norton 1992) are also responsible for determining distribution pattern.

Based on phylogenetic studies, it is currently assumed that the Cladophorophyceae are an originally tropical clade with numerous species having successfully invaded warm- to cold-temperate zones (Bakker *et al.* 1994; van den Hoek & Chihara 2000).

Taxonomy, phylogenetic systematics and species concepts

Taxonomy aims to classify organisms into natural categories. Long before the idea of evolution was firmly established, natural historians had realized that some animal and plant species shared similar characters and could be grouped based on a variety of shared similarities. In the 1700's a Swiss botanist named Carolus Linnaeus developed a system for classifying animals and plants into a hierarchical series of categories. At the top of the hierarchy were the most inclusive categories: kingdoms (Linnaeus recognized two of these: plants and animals), while at the bottom was the species: organisms that were essentially 'the same' kind. In grouping organisms, Linnaeus was not recognizing any evolutionary connection between them, rather, he was trying to uncover the underlying organization of God's creation. The importance of the fundamental works of Linnaeus (1753, 1758), selected by international agreement (International codes for botanical and zoological nomenclature) is not so much the listing of animal and plants that Linnaeus gave, but the establishment of a simple scheme for naming organisms and for presenting classification lists (Benton 2000). From the works of Linnaeus stem three principles: the binomen, priority, and the hierarchical categories. The Linnaean system of classification is still used today under a recent, statistical, incarnation: phenetics or numerical taxonomy (Sneath & Sokal 1973). Numerical taxonomy does not try to reflect evolutionary relationships, instead it is based on overall similarities among organisms. In other words, in phenetic analyses, no distinction is made between similarity due to real shared common ancestry (homology, synapomorphy) and similarity due to convergent ancestry (analogy, homoplasy). Numerical taxonomy is especially appealing because of its objectivity and easy computer implementation.

During an entire century after Darwin's publication "*The origin of species*" and the rediscovery of Mendel's laws, taxonomy continued to be based on morphological similarities in which it was tacitly implied that evolutionary history was included (Mayr 1969). A new taxonomic approach, termed cladistics, was proposed by Hennig (1966), and uses evolutionary descent as the sole criterion for classification. Cladistics was also known as phylogenetic systematics, although today the latter include a broader range of methodologies. The basic idea behind cladistics is that members of a group share a common evolutionary history, and are closely related, more so to members of the same group than to other organisms. These groups, termed as monophyletic groups, are recognized by sharing unique features (shared derived characteristics or synapomorphies) which were not present in distant ancestors. The reconstruction of evolutionary history is done through the assessment of homology (similarity due to common ancestry) and the elimination or minimization of convergence (homoplasy). Determination of homology is achieved either by structure or position. In the case of morphological characters, structural comparisons are the most common, whereas in molecular data (e.g. DNA sequences) homology is assessed by sequence alignment. Most phylogenetic methods with morphological data operate on the principle of parsimony, but with the advent of

molecular data, numerous other phylogenetic methods have been proposed. The results of phylogenetic analysis may be depicted as a phylogenetic tree (cladogram or phylogram), a graphic illustration of the genealogical relationships between the entities under study.

Phylogeny reconstruction using morphological data is problematic in the Chlorophyta due to their relatively simple thallus architecture and limited number of phenotypic characters, and consequently, such studies are scarce (Littler & Littler 1990, 1991, 1992; Mishler *et al.* 1994; Woolcott *et al.* 2000). Recently, molecular phylogenetic studies in various green-algal groups have demonstrated that morphology is often incongruent with the evolutionary history, due to the highly convergent nature of most phenotypic characters (e.g. Famà *et al.* 2002; Kooistra 2002; Kooistra *et al.* 2002; Hayden *et al.* 2003; Olsen *et al.* 1994). Also in the Cladophorophyceae, phylogenies based on molecular data often contradict the classical generic concepts, which are primarily based on thallus architecture and mode of cell division (Kooistra *et al.* 1993; Bakker *et al.* 1994; Hanyuda *et al.* 2002).

Molecular phylogenetics

Molecular phylogenetics aims to reconstruct the evolutionary history of genes and species by unraveling the information stored within gene sequences. DNA sequences are valuable because they provide the most detailed information possible for any organism – the instructions for how each working part should be assembled and operate (Page & Holmes 1998). The underlying philosophy of molecular phylogenetics is based on the fact that organisms and genes sharing a common ancestor, have evolved from a single genome through accumulating mutations. It must be noted that species trees and gene trees can be quite different due to horizontal gene transfer, gene duplications, lineage sorting and coalescence (Slowinski & Page 1999). One of the most important contribution of molecular data to phylogenetic analysis is the possibility to examine evolutionary relationships among morphological identical or similar taxa (Avise 1994).

The most basic task in sequence analysis is to ask whether two or more sequences are similar and can be compared. Answering this question is done by aligning these sequences and subsequently deciding whether the alignment is biologically relevant (homologous) or whether the alignment occurred by chance and has no biological meaning. Nucleotides in different sequences are homologous if these sequences acquired that state directly from their common ancestor. Detecting homology in DNA or RNA sequences may not be immediately obvious because there are only four nucleotides [guanin (G), cytosin (C), adenin (A) and thymin (T) or uracyl (U)] in varying order along the sequence. Moreover, multiple substitutions can greatly obscure the actual evolutionary history of sequences. Molecular systematists generally rely on computers using multiple sequence alignment algorithms (see Phillips *et al.* 2000 for a review).

Several features of nuclear ribosomal DNA (nrDNA) (and their internal transcribed spacers, ITS1 and ITS2), make alignment particularly difficult because insertions and deletions, common in nrRNA sequences, require the placement of many gaps in sequence alignment. The alignment of these sequences by multiple sequence alignment algorithms requires assumptions about the evolutionary costs for gaps in the alignment that are indefinable when uniformly applied across the entire sequence (Kjer 1995). Some regions of nrRNA are extremely intolerant to changes in length while other regions vary without any apparent constraints. The function of nrRNA, as a component of the ribosome, is largely

determined by its complex secondary structure that includes both long-range hydrogen-bounded stems and local short-range hairpin stem-loops. The stem regions are dependent on Watson-Crick pairings and G-U base pairing. The general structure of nrRNA is universally conserved, even when sequences have diverged significantly (e.g., across kingdoms). Since, the conservation of nrRNA secondary structure exceeds that of its nucleotides, several authors recommended the use of secondary structures to guide decisions about the assignment of homologous positions in phylogenetic studies (Kjer 1995, Coleman & Mai 1997, Mai & Coleman 1997). Prudence is called for, however, since different secondary structure models can produce alternative phylogenies (Winnepenninckx & Backeljau 1996).

The application of secondary structure in aligning sequences involves "anchoring" of homologous positions. An initial alignment may be conducted by using a multiple alignment algorithm, and comparison with existing secondary structure alignments (Wuyts *et al.* 2001). In a following step, two-dimensional secondary structure models are constructed for the different sequences. Initial screening for the secondary structure of the sequences is conducted by folding the sequences, using computer programs which are based on a thermodynamic (energy minimization) methods (Mathews *et al.* 1999, Zuker *et al.* 1999). The resulting optimal and suboptimal secondary structures are then compared and screened for common motifs. The initial sequence alignment is refined in accordance to the common secondary structures. The new alignment is then searched for covariations or compensating base-pair changes (those positions that changed as to maintain base pairing), as supporting evidence for the true secondary structure and the identification of homologous stem regions. The approach is an iterative process in which possible structures are identified and repeatedly refined until the nucleotide sequences and covariation data and structures are in agreement (Mai & Coleman 1997). The alignment editor DCSE (Dedicated Comparative Sequence Editor) may be used to aid the incorporation of secondary structure information in the sequence alignment (De Rijk & De Wachter 1993).

Numerous methods have been developed for constructing phylogenetic trees from molecular data. They can be classified into two general categories: distance methods (e.g. neighbour-joining), and discrete data methods, also known as tree searching methods (e.g. parsimony, maximum likelihood and Bayesian methods). Literature on phylogenetic construction is extensive and the advantages and disadvantages of different methods are frequently debated. The last few years, much effort went to the study of specific models explaining the evolutionary change of the molecules. If the 'true' evolutionary process could be described quite accurately by a certain model of substitution, trees inferred on the basis of that model would suffer less from systematic errors (see further). Although most methods produce unrooted tree topologies, most trees are represented as rooted by including one or more, a priori known outgroup sequences. The most commonly used methods are explained by Swofford *et al.* 1996, Page & Holmes (1998), Nei & Kumar (2000) and Baldauf (2003). **Distance methods** try to fit a tree to a matrix of pairwise evolutionary distances (Felsenstein, 1988). For every two sequences, the distance is a single value based on the fraction of positions in which both sequences differ, defined as dissimilarity. Usually, this dissimilarity is an underestimation of the true evolutionary distance, because of the fact that some of the sequence positions are the result of multiple events. Therefore the number of substitutions that have actually occurred is estimated by applying a specific substitution model. One of the most used distance methods is neighbour-joining (NJ) which combines computational speed with uniqueness of result (Saitou and Nei 1987). These two attributes (i.e. getting a single tree, fast) have made it very appealing. The algorithm of NJ is somewhat complicated and is explained in detail by Nei & Kumar (2000). Apart from computational speed, the advantage of distance methods in general is that a substitution method can be applied allowing to correct for multiple

mutations. The major disadvantage is the fact that phylogenetic information is reduced to a single number. **Maximum parsimony** (MP) was among the first methods for inferring phylogenies. The central idea is that the preferred evolutionary tree requires the smallest number of evolutionary changes (i.e. nucleic acid substitutions). In MP analysis, only sites at which there are at least two different kinds of nucleotides, each represented at least twice, are used (parsimony-informative sites). Other variable sites are parsimony-uninformative, although they may be informative for distance and maximum-likelihood methods. In practice it is usually not possible to evaluate all possible tree topologies and therefore a heuristic approach has to be applied, reducing the number of tree topologies that are evaluated. In MP analyses it is very common to find different tree topologies that have the same number of steps ('equally parsimonious'). In such cases, the results of the phylogenetic analysis are usually represented as a consensus tree (e.g. strict consensus). The advantages of MP methods are the fact that sequence information is not reduced, and the possibility to study and compare alternative tree topologies. Disadvantages are that the method is slow for large datasets, that no substitution model can be applied, and the sensitivity to unequal rates of evolution in different lineages. **Maximum likelihood** (ML) analyses consists of three parts. First a model of evolutionary change for nucleotides is specified (see below). Then, based on this model, different hypotheses about the evolutionary history are evaluated in terms of the probability that the hypothesized history would give rise to the observed data. Finally, the evolutionary tree with the highest probability is selected. ML often yields estimates with a lower variance than other methods, and it is frequently the estimation method least affected by sampling error (Swofford *et al.* 1996). The major drawbacks of ML methods is that they are computationally very expensive, and that the outcome is dependent on the evolutionary model used.

As already mentioned above, models of nucleotide acid evolution play an essential role in the analysis of molecular sequence data. They are a tool to reduce the enormous complexity of the biological mutation process to a comparatively simple pattern that can be described by a small number of parameters. These models specify a modus of substitution for nucleotides at a given site (substitution rates), indicate base frequencies and proportion of invariable sites, and give a prescription how the rate of substitutions is distributed over different positions in a sequence (rate heterogeneity). Phylogenetic methods based on explicit models of evolution (e.g. ML) should explore which is the model that fits the data best, justifying then its use. This can be done by testing the goodness of fit of models by hierarchical likelihood tests (LRT) or the Akaike Information Criterion (minimum theoretical information criterion, AIC) (Posada & Crandall 1998). In general, phylogenetic methods may be less accurate when the wrong model of evolution is assumed (Posada & Crandall 2001). However, some authors have questioned the utility of complex models in phylogenetic analysis and the appropriateness of using objective criteria for choosing a substitution model (Takahashi & Nei 2000, Xia 2000).

Different techniques, including bootstrap and decay analysis, have been developed for evaluating the reliability of branches in the inferred phylogenetic trees. The bootstrap method (Felsenstein 1985) involves a random resampling of characters from the data set. Then, for each reproduced (artificial) data set, a tree is constructed, and the proportion of each subset of taxa among the bootstrap replicates is computed. Decay analysis or Bremer support (Bremer 1988) is used to test the reliability of MP trees. Support for a clade is expressed as the number of extra steps that are needed in order to collapse that clade.

The use of LSU nrRNA in phylogeny reconstruction

Eukaryotic nrDNA genes occur as tandem repeats and their primary transcripts include the small-subunit (SSU), 5.8S, and large-subunit (LSU) rRNA separated by internal transcribed spacers (ITS) regions (Fig. 8). All of the nrDNA genes are known to be a mosaic of conserved and divergent regions (Hillis & Dixon 1991). SSU nrDNA genes are the most widely used nuclear sequences for phylogeny reconstruction at higher taxonomic levels in plants and algae. However, due to a conservative rate of evolution, SSU nrDNA alone sometimes provides too few phylogenetic informative characters to resolve relationships adequately. Numerous studies have suggested the potential of LSU nrDNA for phylogeny retrieval at taxonomic levels comparable to those investigated with SSU nrDNA and the chloroplast gene *rbcL* (e.g. Rousseau *et al.* 1997, 2001; Kuzoff *et al.* 1998; Stefanović *et al.* 1998; Hopple & Vilgalys 1999; Jovelin & Justine 2001). The conserved regions of LSU nrDNA show great similarity in secondary structure even between prokaryotes and eukaryotes (Hassouna *et al.* 1984). In contrast, the divergent regions vary greatly, even between closely related lineages, and it is primarily within these regions that phylogenetic information from LSU nrDNA has been found (Michot *et al.* 1990; Kuzoff *et al.* 1998).

Because nuclear ribosomal DNA (nrDNA) sequences are members of a multicopy gene family, it is possible that more than one haplotype occurs within a single organism, hampering phylogenetic reconstruction of species. Concerted evolution (Arnheim 1983), generally homogenizes such variation but nevertheless, intra-individual variation has been observed in for example the fast evolving ITS region in *Caulerpa* (Famà *et al.* 2000), affecting intra- and interspecific phylogenetic reconstruction.

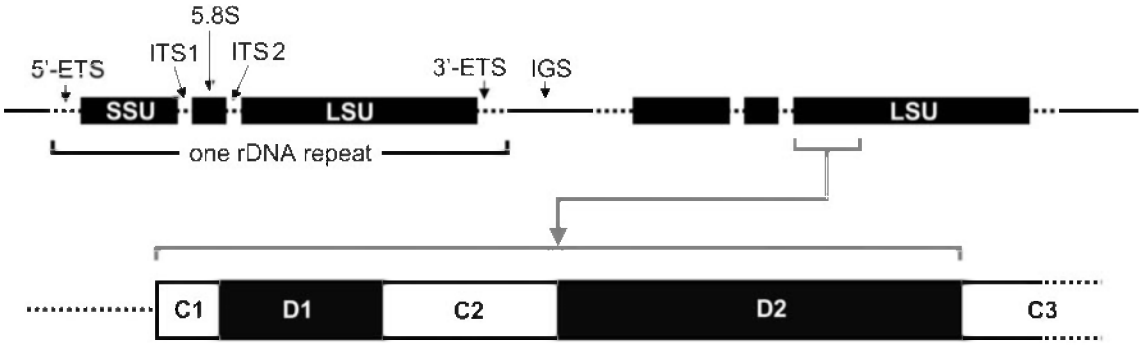


Fig. 8. Schematic representation of two nrDNA repeats and indication of the partial LSU rDNA region used in the present study. ETS = external transcribed spacer, IGS = intergenic spacer, ITS = internal transcribed spacer, LSU = large subunit, SSU = small subunit.

Species concepts

Although the literature on theoretical and practical species concepts is extensive, there is still no general consensus to date on what constitutes a species. A large number of species concepts has been proposed, including morphological, biological, palaeontological, evolutionary and phylogenetic, amongst others (see Hull 1997 and Mayden 1997 for reviews). Algal systematics has been dominated by the morphological species concept, a criterion which uses discontinuities in the pattern of morphological variation for distinguishing species (phenetic approach). New data on phenotypic plasticity, breeding compatibility and molecular analysis are clarifying

species concepts (John & Maggs 1997). Although life histories have been studied and sexual reproduction demonstrated in numerous representatives of the Cladophorophyceae (van den Hoek 1984), breeding studies (i.e. investigation of sexual compatibility) have not yet been used to explore the biological species concept (Mayr 1992) in the group. The phylogenetic species concept (in which species are defined as the smallest diagnosable monophyletic group) resembles the biological species concept in that it also applies to populations (Claridge *et al.* 1997). Molecular data have been used to test established species concepts (principally morphological) in *Cladophora* (Bot *et al.* 1989a, b, 1990; Bakker *et al.* 1995a, b) and *Cladophoropsis membranacea* (Kooistra *et al.* 1993; van der Strate *et al.* 2002). Both DNA-DNA hybridization studies and nrDNA ITS sequence analyses have demonstrated that the morphological species *Cladophora vagabunda*, occupying one huge continuous geographic area, represents at least four divergent lineages (Bot *et al.* 1990, Bakker *et al.* 1995). Depending on the interpretation of these molecular data, *C. vagabunda* can be seen as a single species or a cryptic species complex (multiple species). Cryptic speciation has also been recognized in *Cladophoropsis membranacea* based on ITS sequence analyses and amplification differences of microsatellite loci (van der Strate *et al.* 2002). As will be discussed in chapter 5, it is likely that also the *Boodlea composita* complex (which has been demonstrated to be closely related to *C. membranacea* by Kooistra *et al.* 1993) constitutes of a number of cryptic species (Wysor 2002). In this species complex, species boundaries might be furthermore obscured by ecological or developmental plasticity.

Objectives

This study has three main aims: (1) understanding of the evolutionary relationships within the Cladophorophyceae, focusing in particular on members of the Siphonocladales *s.s.*, (2) searching for congruence between morphology and phylogeny, and (3) re-assessing the taxonomy of the closely related genera of the *Cladophoropsis* complex, based on new phylogenetic and morphological evidence.

Different genera in the Cladophorophyceae are thought to be derived from the various architectural types in the genus *Cladophora* of which the subtropical, South African representatives are studied in **Chapter 2**. Of the 11 different architectural types distinguished world-wide, 7 occur along the subtropical South African East coast. Detailed descriptions and illustrations of twelve *Cladophora* species are presented.

In **Chapter 3** phylogenetic relationships within the Cladophorophyceae are investigated based on partial LSU nrRNA gene sequences of 37 species, representing 18 genera. The phylogenetic potential and the distribution of phylogenetic signal in the partial LSU sequences is explored and phylogenetic analyses are performed.

Crystalline cell inclusions have been relatively poorly studied in algae. Different morphological types of crystals are detected in various representatives of the Cladophorophyceae and their taxonomic value examined in **Chapter 4**.

In **Chapter 5** the closely related genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis* are reviewed based on phylogenetic insights and morphology. The grounds for the recognition of a single genus are discussed and detailed species descriptions and illustrations are provided.

Material

The extensive phycological collection of the herbarium GENT, including over 2500 specimens of Cladophorophyceae, formed the initial basis for the present study. The specimens were collected at various localities in the Mediterranean and Indo-Pacific region during the last three decades, mainly by E. Coppejans and co-workers, including T. Beeckman, O. Dargent, O. De Clerck, F. Leliaert, I. Vackier, H. Verstraete and T. Schils. The collection consists mainly of dried herbarium specimens, many of which are also preserved in formalin; recently, parts of specimens are also dried in silica gel for DNA extraction. The Mediterranean seaweeds were collected by E. Coppejans between 1974 and 1983, mainly from Corsica, Banyuls, Port Cros and Marseille. In 1980, E. Coppejans started fieldwork in Papua New Guinea, both along the South Coast (Port Moresby and vicinity) and the North Coast (Madang Province). The country was visited on several occasions, spread over a 10-year period, by E. Coppejans, W. Prud'homme van Reine and O. De Clerck; sets of duplicates of herbarium specimens are deposited in L, PNG and UPNG (Coppejans *et al.* 1995, Coppejans *et al.* 2001). The Indonesian seaweeds were collected by E. Coppejans, W. Prud'homme van Reine and F. Heys, during the oceanographic Snellius-II expedition in 1984; the main collection is deposited in L with duplicates in AMB, GENT and JAK. The siphonocladalean representatives from Papua New Guinea and Indonesia have been studied by Leliaert *et al.* (1998). The material from the Philippines was collected on three occasions by E. Coppejans, F. Leliaert, L. Liao and O. Dargent in 1998 and 1999. The specimens from the Maldives, Sri Lanka and Thailand were collected by E. Coppejans. Various projects dealing with the biodiversity of marine benthic algae along the tropical East African coast started in 1985. The majority of these collections are from Kenya (1985-1992), and Tanzania (1993-2003) (Coppejans *et al.* 2000); sets of duplicates are deposited in the Kenya Marine and Fisheries Institute, Mombasa and the Institute of Marine Sciences, Zanzibar respectively. The seaweeds from the subtropical East Coast of South Africa were mainly collected from 1998 onwards by E. Coppejans, O. De Clerck, F. Leliaert, H. Engledow, J. Bolton and R. Anderson in the framework of a bilateral project dealing with the biogeography of South African seaweeds (Bolton *et al.* 2004); duplicates are deposited in BOL (Leliaert *et al.* 2001). The material from the Seychelles was collected during the Dutch 'Oceanic Reef Expedition' from December 1992 to January 1993 by E. Coppejans, W. Kooistra and P. Audiffred; the main collection is deposited in L with duplicates in GENT and SEY (Coppejans *et al.* 1994). Some seaweeds from Réunion and Mauritius were collected by O. Dargent during a personal collecting trip in 1998. Specimens from Rodrigues were collected by E. Coppejans and D. Marie in September 2001 during the Shoals of Capricorn Programme (UK) (Coppejans *et al.*, accepted). The seaweeds from Madagascar (mainly from Fort Dauphin and Tuléar) were collected by E. Coppejans during an expedition in August 2002. The specimens from Saudi Arabia were collected in 1992 by O. De Clerck and E. Coppejans in the framework of the Jubail Marine Wildlife Sanctuary Project which aimed to asses the impact of the oil pollution following the 1991 Gulf War (De Clerck & Coppejans 1996). The seaweeds from Socotra (Yemen) were collected by F. Leliaert and T. Schils (in 1999 and 2000 respectively) in the framework of a UNDP/GEF project "Conservation and sustainable use of biodiversity of Socotra Archipelago". The collections from Masirah Island (Oman) were made by T. Schils in 2001, in collaboration with the Ardoukoba Association (France).

Apart from the collections in GENT, additional material from several herbaria (including AKU, B, BISH, BM, BR, GB, L, LD, M, MEL, MICH, NSW, NY, O, PC, S, SAP, UC, UPS and W) was examined. Herbarium abbreviations follow Holmgren *et al.* 1990).

A taxonomic database was developed (largely based on De Clerck 1999) to store taxonomic and specimen data. This database consists of three main indices or tables which are linked to one another. The main index (nomenclature table) includes all taxa involved in this study with reference to the original description, basionym and synonyms, and information on the type material. The second table includes citations of the species involved with indication of whether or not descriptions, illustrations or other information is provided. The third table includes all specimens examined with the correct name (identification) and information provided on the specimen labels (herbarium, collector, collection number and date, habitus and ecology). The database is stored in the library of the Research Group Phycology and is available on request.

— *Chapter 2* —

The marine species of *Cladophora* from the South African East Coast

Adapted from: Frederik Leliaert & Eric Coppejans. 2003. The marine species of Cladophora *(Chlorophyta) from the South African East Coast. Nova Hedwigia 76: 45-82.*

Abstract – Twelve species of the genus *Cladophora* occur along the South African East Coast. Detailed descriptions and illustrations are presented. Four species are recorded for the first time in South Africa: *C. catenata*, *C. vagabunda*, *C. horii* and *C. dotyana*; the last two are also new records for the Indian Ocean. A comparison of the South African *C. rugulosa* specimens with specimens of *C. prolifera* from South Africa and other regions have shown that these species are not synonymous as previously considered, leading to the resurrection of *C. rugulosa* which is probably a South African endemic.

Introduction

Cladophora Kützing is one of the largest green-algal genera and has a worldwide distribution. Within the class Cladophorophyceae the genus *Cladophora* is characterized by its simple thallus architecture: branched, uniseriate filaments of multinucleate cells. Eleven different architectural types (sections) are distinguished in the genus (van den Hoek 1963, 1982a; van den Hoek & Chihara 2000). Recent studies based on morphological and molecular data have proven that *Cladophora* is polyphyletic (van den Hoek 1982a; Bakker *et al.* 1994; Hanyuda *et al.* 2002). The available molecular data are not sufficient yet to confirm (or reject) van den Hoek's morphological sections. A phylogeny of the Cladophorophyceae based on 18S rRNA (Bakker *et al.* 1994) suggests two lineages in the class: one containing predominantly tropical species including siphonocladean taxa and some *Cladophora* species, the other one containing mostly warm- to cold-temperate species of *Cladophora*. The addition of several species by Hanyuda *et al.* (2002) revealed a new clade within the class, containing a mixture of marine and freshwater species of *Cladophora* and other genera. The revisions of van den Hoek (1963, 1982a), van den Hoek & Womersley (1984) and van den Hoek & Chihara (2000) are usually considered to represent the best taxonomic treatments of the genus *Cladophora*. Stegenga *et al.* (1997: 102-112, pls 20-23) studied the *Cladophora* species along the South African West Coast. Other papers dealing with the genus in South Africa are Levring (1938), Papenfuss (1940a, 1940b, 1943), Simons (1960, 1969, 1977), Seagrief (1967, 1980, 1988), and some of the earlier publications such as Chamisso (1821), C. Agardh (1824), Suhr (1834, 1840), Kützing (1849) and Martens (1868). Table 1 gives an overview of the *Cladophora* species recorded along the South and East Coast of South Africa (from Cape Agulhas to the Mozambican border) together with morphological characters, ecology and references to more detailed descriptions and illustrations. This paper presents a survey of the marine *Cladophora* species along the South African East Coast, with the emphasis on the flora of KwaZulu-Natal (KZN).

Table 1. *Cladophora* species recorded along the Indian Ocean coast of South Africa: type locality, morphological characters, ecology and references to more detailed descriptions and illustrations. Cell dimensions [from South African specimens measured and/or in literature if data was available; otherwise from other sources (see references)]: a = apical cell diameter (µm), m = main axis diameter (µm), b = basal cell diameter (µm), l/w = length-width ratio of the cells. Geographical distribution: uncertain records have been omitted, SA = distribution in South Africa, W = world distribution.

Species Type locality (T)	habit	cell dimensions (µm)	branching system	other characters	ecology	Reference(s)	Geographical distribution
C. aculeata (Suhr) De Toni, 1889: 353, *nom. illeg.* T: Algoa Bay, S coast South Africa	rigid erect, fastigiate filaments	unknown	fastigiate, verticillate		unknown	De Toni (1889: 353)	SA: South coast (Barton 1893: 56)
C. afra Kützing, 1849: 411 T: mouth of Knysna River S Coast, South Africa	free erect, flaccid filaments	a: 20-30 b: 70-90	spreading, pseudodichotomous	filaments often curved	unknown	Kützing (1849: 411; 1854: 11, pl. 53: fig. 1); De Toni (1889: 304)	SA: South coast (Barton 1893: 55)
C. albida (Nees) Kützing, 1843: 267 T: England	small (3 cm high) and spongy when exposed to wave action; large (50 cm) and erect in sheltered conditions.	a: 10-50, l/w 1-20 m: 20-80, l/w 1.5-8	dense, straight to refract, acropetally to irregular; growth mainly intercalary; 1-3 branches per cell		intertidal, wide ecological amplitude	van den Hoek (1963: 94-96, pl. 20-24 (p.p.); 1982a: 100-105, figs 133-137, 144); van den Hoek & Womersley (1984: 206-208, figs 66C, 68A-D)	SA: South Coast (Bolton & Stegenga 1990: 236) W: world-wide in temperate zones of northern and southern hemispheres (van den Hoek & Chihara 2000: 129)
C. capensis (C. Agardh) De Toni, 1889: 354. T: Cape of Good Hope, West coast of South Africa	free erect filaments, 30-50 cm tall	a: 65-80, l/w 3-4 m: to 250, l/w 1.5-4	irregular, acute angled; growth mainly intercalary; 1-4 branches per cell	apical cells tapered	lower intertidal and below, epilithic	Seagrief (1988: 40, fig. 5:2); Stegenga et al. (1997: 103, Pl. 20: 1)	SA: West coast (Stegenga et al. 1997: 103), South coast (Seagrief 1988: 40)
C. catenata (Linnaeus) Kützing 1843: 271 T: Bahamas	compact stiff cushions, composed of curved and intertwined branch systems	a: 300-360, l/w 7-25 m: 240-470, l/w 2-12	curved and intertwined, irregular; growth both apical and intercalary	very conspicuous long apical cells; filaments stiff and often curved; apical ends of decumbent axes often with terminal haptera	lower intertidal, surf-exposed rocky substrata	van den Hoek (1982a: 59-64, figs 41-68); this paper	SA: East Coast (this paper) W: tropical W-Atlantic and Pacific Oceans (van den Hoek 1982a: 58; van den Hoek & Chihara 2000: 45)
C. catenifera Kützing T: Cape of Good Hope, West coast of South Africa	*Cladophora catenifera* was proposed as a synonym of *C. pellucida* by van den Hoek (1982a: 178). Barton (1896: 193) proposed the conspecificity with *C. radiosa*.						South African West, South and East? coast (Delf & Michell, 1921: 93).
C. coelothrix Kützing, 1843: 272 T: Golfo di Genova, Italy	spherical tufts or compact moss-like or loose-lying mats	a: 57-75, l/w 5-15 m: 57-120, l/w 2.5-12	dense, irregular; 1 (-2-3) branches per cell; frequent intercalary cell division	many cells give off one rhizoid at their basal pole	intertidal to deep subtidal (-40 m) preferring shaded areas	van den Hoek (1963: 40-43, pl. 5-8 (p.p.); 1982a: 47-52, figs 11-29); van den Hoek & Womersley (1984: 190-192, figs 60C, 61C,D); this paper	SA: East Coast (Bolton & Stegenga 1987: 168; this paper) W: world-wide in tropical to warm-temperate seas (van den Hoek & Chihara 2000: 37)
C. connexta Levring, 1938: 8-9, figs 4A,B, pl. I: fig. 2 T: Port Nolloth, West coast of South Africa	dark green cushions, a few cm high, composed of densely interwoven branch system	a: 70-100, l/w 1-3 m: up to 150, l/w 1-3	irregular, main axes often with numerous short ramuli in long secund series, 1 (-2) branches per cell, apical systems more polystichously branched; growth mainly intercalary	apical cells tapering to acute; many cells of the main axes give off rhizoids	sandy substrata	Stegenga et al. (1997: 105, pl. 21: 1-3)	SA: West coast (Stegenga et al. 1997: 105); East Coast [1] (Farrell et al. 1993: 149).

Table 1. (continued).

C. dotyana Gilbert, 1965 T: Hokipa Park, East Maui, Hawaii	dark green, erect, coarse, stiff tufts	a: 250-290, l/w 3-6 m: 320-840	pseudodichotomously branching main axes; terminal branch systems acropetally to irregularly organized, 1-2 branches per cell.	one- or two-celled stipe	epilithic, subtidal (at -19 m)	Kraft (2000: 554, fig. 18A-C), van den Hoek & Chihara (2000: 88-91, figs 38-39).	SA: East coast (this paper) W: Hawaii, Japan and South Africa.
C. flagelliformis (Suhr) Kützing, 1849: 388 T: Cape of Good Hope, West coast of South Africa	erect thallus, up to 30 cm tall, forming dense tufts	a: 50-80, l/w 0.5-8 m: 60-150 (-205), l/w: 1-5	1-4 laterals per cell; distal parts of the laterals unbranched and flagelliform	fertile cells developing in long unbranched apical sections	epilithic in lower intertidal and rock pools	Stegenga et al. (1997: 109, pl. 20: 2, colour plate 26); this paper	SA: West coast (Stegenga et al. 1997: 109); East Coast (Farrell et al. 1993: 149 as *C. virgata*) W: Tristan da Cunha (Baardseth 1941: 11) doubtful record
C. hospita (Mertens ex Chamisso) Kützing, 1843: 271 T: Cape of Good Hope, West coast of South Africa	According to Papenfuss (1940: 5-6) this species is conspecific with *C. mirabilis* (C. Agardh) Rabenhorst in Hohenacker. *C. mirabilis* however has only been recorded along the South African West coast while *C. hospita* has been recorded in the (sub)antartic regions and South Africa. See Stegenga et al. (1997: 110, plate 22:1) for a description and illustration of the species.						SA: West and South coast (Barton 1893: 55) W: St. Paul Island (Reichardt 1871); Antarctic and subantartic (Papenfuss 1964)
C. horii, van den Hoek & Chihara, 2000: 67 T: Okinawa, Sesoko Isl., Japan	dense, erect, dark green tufts, up to 5 cm high	a: 60-90, l/w 1.4-5.5 b: up to 160, l/w 3-4	Branching more or less acropetally organized, small angle of ramification. 1-2 lateral per node.	The habit of this species has some likeness to small specimens of *C. prolifera*.	intertidal rockpools or shallow subtidal, epilithic or epiphytic	van den Hoek & Chihara (2000 : 67-68, fig. 28)	SA: East Coast (this paper) W: Japan (type locality)
C. hutchinsiae (Dillwyn) Kützing, 1845: 210 T: Bantry Bay, Ireland	plants up to 35 cm long, coarse texture	a: 90-195, l/w: 1-4 m: 240-400, l/w: 1-3.5	pseudodichotomously branching main axes, set with branches of different lengths; terminal branch systems irregular to slightly acropetal, growth mainly intercalary; 1-2(-3) laterals per node.		intertidal to subtidal (-20 m)	van den Hoek (1963: 60-66, pl. 12-14 (p.p.)); Burrows (1991: 157-158, fig. 46); Schneider & Searles (1991: 65)	SA: South coast (Seagrief, 1988: 40) W: NW-Atlantic (Schneider & Searles, 1991); NE-Atlantic, Mediterranean (van den Hoek 1963: 61); NE-Pacific (Scagel et al. 1989)
C. lehmanniana (Lindenberg) Kützing, 1843: 268. T: Helgoland, Germany	fastigiate tufts	a: (22-) 90-160, l/w 2-10 m: (90-) 140-330, l/w 2-10	pseudodichotomously branching main axes which end in often falcate, acropetally organized branch-systems.		intertidal and subtidal in shaded habitats	van den Hoek (1963: 122-128, pl. 29-30 (p.p.)) van den Hoek & Womersley (1984: 198-200, figs 64B, 65C,D) Burrows (1991: 160-161, fig. 47); Huisman (2000: 235, +fig.)	SA: South coast (Barton 1893: 55) as *C. spinulosa* and *C. nuda* (misapplied names *fide* Papenfuss notes). W: warm-temperate Atlantic and Mediterranean coasts of Europe (van den Hoek 1963: 125); S-Australia (van den Hoek & Womersley 1984: 198); tropical Indian Ocean (Silva et al. 1996: 776).
C. liebetruthii Grunow in Piccone, 1884: 53. T: Gran Canaria and Ionian Sea	dark green, compact matted tufts or entangled, reticulate masses.	a: 60-80; l/w 2-5 m: 70-95; l/w 1.5-4	irregular wide angled ramification without distinct main axes; intercalary growth resulting in typical long, unbranched stretches of filaments; 1-3 branches per cell	apical cells often terminating in short rhizoids	intertidal to deep subtidal, epilithic	van den Hoek (1963: 59, Pl. 12, figs 128, 129; 1982a: 69-72, figs 84-95); Kraft (2000: 564, fig. 22); this paper	SA: East Coast (this paper) W: tropical to warm-temperate Atlantic ocean (van den Hoek 1982a: 70); tropical Pacific Ocean (Kraft 2000: 566); Indian Ocean (Raghukumar 1986: 290)

Table 1. (continued).

C. ordinata (Børgesen) van den Hoek, 1982a. T: Dwarka, Okha Port, India	dark to medium green, bushy, fan-like tufts with distinct main axes	a: (27-) 30-45; l/w 2-3.5 m: (70-) 110-175; l/w 2-10	acropetally organized; opposite to flabellate; all branches typically in a single plane, 2-8 branches per cell.	conical apical cells	epilithic, intertidal rock pools to subtidal (to 37 m deep)	Børgesen (1934: 17, fig. 3); van den Hoek (1982a: 123-125, figs 231-237); van den Hoek & Chihara 2000: 219-224, figs 93, 94.	SA: East Coast (Papenfuss & Egerod 1957: 82-83). W: disjunct in the tropical to warm temperate Atlantic and Indo-Pacific Oceans.
C. prolifera (Roth) Kützing, 1843: 271. T: "in mare Corsicam"	thalli dark green, forming dense, coarse, stiff tufts of densely branched fasciculate filaments.	a: 90-130, l/w 2.5-5.5 b: up to 200, l/w 7-10	acropetally organized, growth only by division of apical cells; 1-3 branches per cell; small angle of ramification.	basal cells elongated and club-shaped, often with basal annular constrictions; old cells give off a rhizoid with annular constrictions, which grows down to the substratum	shallow intertidal, epilithic	*see text*	SA: South (?) and East Coast (this paper) W: widely distributed in the tropical to warm-temperate seas (van den Hoek & Chihara 2000: 54)
C. radiosa (Suhr) De Toni, 1889: 354 T: Algoa Bay, (near Port Elizabeth), South coast of South Africa	thallus dark green, bushy, erect, up to 50 cm high	a: 150-200, l/w 4-8 m: up to 600, l/w 25-70	acropetally organized branch-systems, growth mainly apical cell division; 1-2 laterals per node.	*C. radiosa* resembles *C. prolifera* but lacks annular constrictions in the basal cells	intertidal or subtidal, epilithic	Stegenga et al. (1997: 110-111, pl. 22: 2-3, colour plate 25)	SA: West Coast (Stegenga et al. 1997: 110); South coast (Simons, 1977: 17); East Coast (Farrell et al. 1993: 149) W: SE-Atlantic: Gough Island (Chamberlain, 1965).
C. rugulosa G. Martens, 1868: 112 T: Durban, East Coast of South Africa	thalli dark green, forming dense, coarse, stiff tufts of densely branched fasciculate filaments.	a: 105-285, l/w 2-8 b: 230-550, l/w 5-50	acropetally organized terminal branch systems, growth by apical cell division; up to 5 laterals per node.	basal cells club-shaped, with distinct annular constrictions. The basal poles of the old cells with distinct protuberances that attach to the parent cell below.	shallow intertidal and infralittoral fringe, epilithic	*see text*	SA: South and East Coast (see text)
C. sericea (Hudson) Kützing, 1843: 264. T: Isle of Sheppey, Kent, England	light to grass green, densely tufted plants up to 20 cm high	a: 15-70, l/w 3-16 m: 50-170, l/w 2-10	terminal branch systems acropetal to irregular; main axis pseudodichotomously branched; growth mainly by intercalary cell division.	apical cells tapering with an obuse tip	common in intertidal rockpools, able to penetrate in water with low salinity	van den Hoek (1963: 77-79, pl. 17-21 (p.p.); 1982a: 93, 95-100) van den Hoek & Womersley (1984: 210, figs 69A, 70A,B)	SA: South coast (Bolton & Stegenga 1990: 236) W: temperate N-Atlantic ocean, Mediterranean, N-Pacific, (van den Hoek 1982a: 96); South Australia (van den Hoek & Womersley 1984: 210)
C. socialis Kützing, 1849: 416 T: Tahiti	spongy or compact moss-like mats, or individual plants interwoven among other algae	a: 25-50; l/w 10-40 m: 35-55; l/w 3-20	branching dense, irregular; intercalary cell divisions frequent, 1-2 branches per cell	Many cells give off rhizoids at their basal poles. Differs from *C. coelothrix* by smaller cell diam.	intertidal, epilithic or epiphytic	van den Hoek (1963: 43, 46, 47, pls 8, 9 (p.p.); 1982a: 52-57, figs 30-40)	SA: East Coast (Bolton & Stegenga 1987: 168; this paper) W: world-wide in tropical to warm-temperate seas (van den Hoek & Chihara 2000: 42)
C. vagabunda (Linnaeus) van den Hoek, 1963 T: Selsey, Sussex, England	light green, lax tufts, densely branched, fascuculate terminal branch systems	a: (35-) 45-55, l/w 3.5-8.5 m: 180-210, l/w 4-10	terminal branch systems acropetally organized, (refracto-) falcate, 1-4 branches per cell		epilithic, intertidal to subtidal (to 6 m deep).	van den Hoek (1963: 144-148, pls 33, 36, 37, 39; 1982a: 137-138, figs 264-294).	SA: East Coast (this paper) W: wide-spread in tropical to warm temperate seas

[1] The SA East Coast records could not be verified since the voucher specimens are lost (Critchley pers. comm.).

Material and methods

Specimens examined were collected along the South African east coast on several occasions between November 1995 and February 2001. The collecting sites were located between Haga-Haga Mouth (north of East London) and Kosi Bay (northern KwaZulu-Natal) (Fig. 1). Specimens were processed as herbarium specimens in the field and preserved in 5% formalin in seawater. Voucher specimens are deposited in GENT and BOL. Herbarium abbreviations follow Holmgren *et al.* (1990).

Fig. 1. The South African East Coast, showing the sampling sites.

Results

Section *Repenites* Kützing

1. ***Cladophora coelothrix*** Kützing, 1843: 272 Fig. 2

Type locality: Golfo di Genova, Italy (leg. Meneghini, L 937/278/392).

Description:
Thallus dark green, forming cushion-like mats, composed of interwoven, densely branched filaments; loosely attached to the substratum by unbranched or branched, uni- or multicellular rhizoids developing from the basal poles of the short cells of the basal, stolon-like filaments. Basal filaments giving rise to the upright branch systems. Growth mainly by division of conspicuous apical cells, and by intercalary cell division lower down; cells becoming barely longer and broader in basipetal direction. Upright filaments either unbranched and composed of 3-5 cells, or branched with a branch system up to the 2nd order and a feebly acropetal organisation. Maximum of one lateral per cell; newly formed laterals often without cross walls at their base; in older laterals cross walls steeply inclined to the parent cell; angle of ramification 20°-50°; ultimate filaments and apical cells often curved. Apical cells cylindrical

with rounded tip, 57-75 µm in diam., l/w ratio 5-15; cells of ultimate filaments cylindrical, 57-93 µm in diam., l/w ratio 8-12; basal, prostrate cells cylindrical, 75-120 µm in diam.; l/w ratio 2.5-5. Cell walls ca. 1-3 µm thick in apical cells and ultimate filaments, up to 15 µm thick in basal cells.

Ecology: intertidal to subtidal (to 20 m deep).

Specimens examined: Adlams Reef, Sodwana Bay: KZN 321 (9/08/1999); Mabibi: KZN 2186 (13/02/2001).

Geographic distribution: *C. coelothrix* is widely distributed in the tropical to warm-temperate seas (van den Hoek & Chihara, 2000: 37). Along the East African coast it has been recorded for Somalia (Sartoni 1992), Mozambique (Coppejans *et al.* 2002) and South Africa (Transkei) (Bolton & Stegenga 1987: 168).

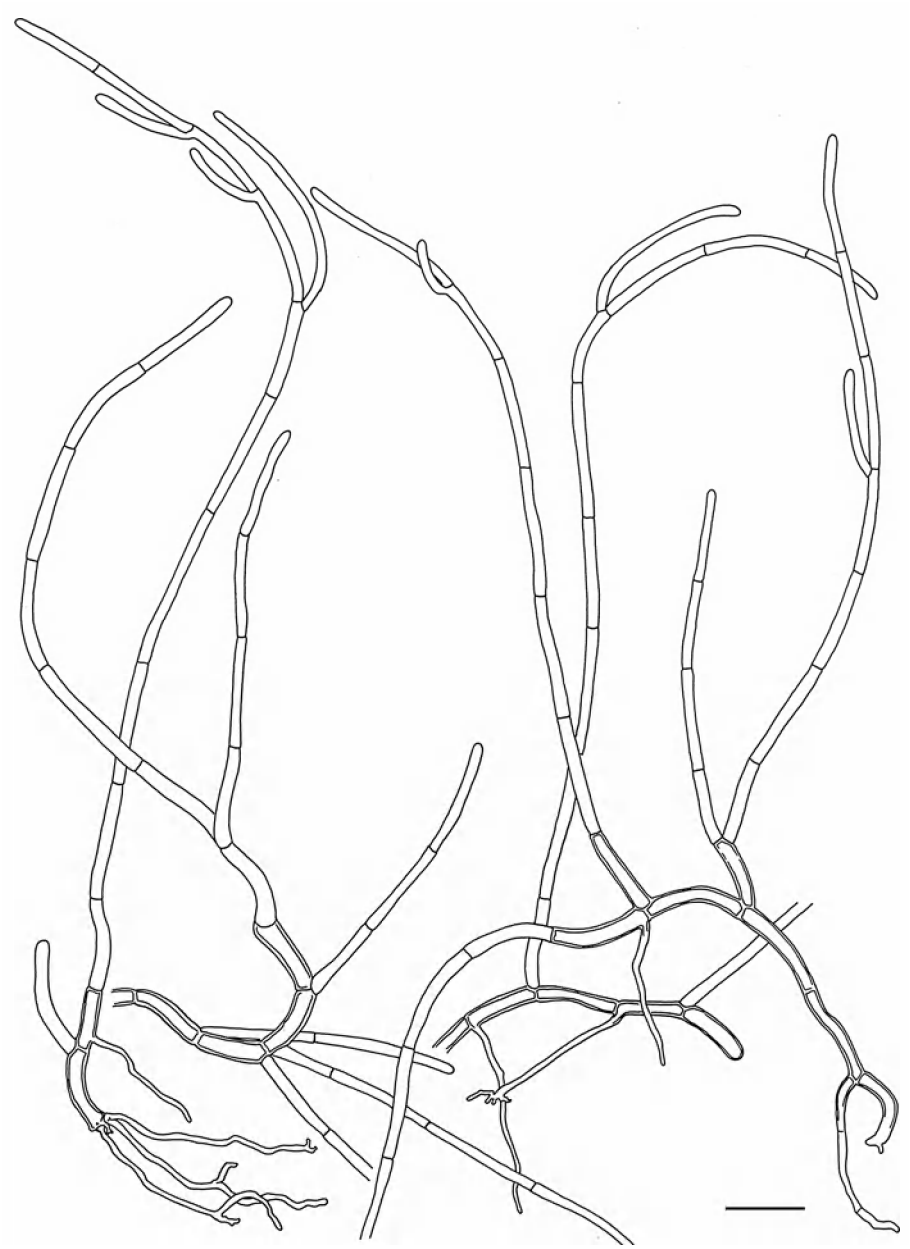


Fig. 2. *Cladophora coelothrix* (KZN 2186). Basal, stolon-like filaments giving rise to the upright branch systems. Scale bar = 500 µm.

Note: The possible absence of cross walls at the base of newly formed laterals is a result of the delay in their formation, a phenomenon also occuring in *C. socialis* and *C. catenata*. *C. coelothrix* may be confused with *Cladophoropsis sundanensis* Reinbold [recently recorded from South Africa (Leliaert *et al.* 2001)] due to similarities in growth form, presence of hapteroidal rhizoids, delayed cross wall formation and comparable cell dimensions. *C. sundanensis* can be distinguished by its light green thallus and cells which occasionally divide by segregative cell-division.

References: Børgesen (1939: 72-73, fig. 15); Sartoni (1992: 300, fig. 5B); van den Hoek (1963: 40-43, pl. 5, figs 55-67, pl. 6, figs 68-71, pl. 7, figs 72-77, pl. 8, fig. 78; 1982a: 47-52, figs 11-29); van den Hoek & Chihara (2000: 36-40, fig. 14).

2. ***Cladophora socialis*** Kützing, 1849: 416 Fig. 3

Type locality: Tahiti (L 937/253/440).

Description:
Thallus medium to dark green, forming 0.5-1 cm thick prostrate mats, composed of interwoven, densely branched filaments. Thallus loosely attached to the substratum by branched or unbranched, uni- or multicellular rhizoids arising from the basal poles of the short cells of the stolon-like filaments. These basal filaments give rise to the upright, terminal branch systems. Growth by division of apical cells, and by intercalary cell division lower down; cells in basipetal direction becoming barely longer and broader. Terminal branch systems feebly acropetal to irregular, wide-angled (45°-90°), with occasional rhizoids from the basal poles of the cells. Laterals mostly one (rarely two) per cell. Newly formed laterals often without cross walls at their base; in older laterals cross walls steeply inclined to the parent cell. Filaments of basal and terminal branch systems sometimes attached to one another by terminal hapteroidal holdfasts at the tips of the apical cells. Apical cells cylindrical with rounded tip, 25-50 µm in diam., l/w ratio 10-40; cells of terminal branches cylindrical, 35-55 µm in diam., l/w ratio 3-20; basal cells cylindrical, 60-120 µm in diam.; l/w ratio 3-5. Cell walls ca. 1 µm thick in apical cells, up to 8 µm in basal cells.

Ecology: intertidal sand covered rock, loosely attached to the substratum.

Specimens examined: Mabibi: KZN 2185 (13/02/2001); Rabbit Rock, Bhanga Nek: KZN 548 (13/08/1999).

Geographic distribution: *C. socialis* is widely distributed in tropical to warm-temperate regions of the Atlantic and Indo-Pacific Oceans, and has previously been collected in the Transkei (Bolton & Stegenga 1987: 168).

Note: *C. socialis* closely resembles *C. coelothrix* from which it only differs by its smaller cell diameter.

References: Børgesen [1940: 36-37, fig. 12 (as *C. patentiramea* (Montagne) Kützing forma *longiarticulata* Reinbold *in* Weber-van Bosse)]; Egerod (1974: 137-138, figs 17-21); Jaasund [1976: 9, fig. 17 (as *C. patentiramea* f. *longiarticulata*)]; Sartoni (1986: 361, 363, fig. 4A; 1992: 302-304, figs 6A,B); van den Hoek (1963: 43, 46-47, pl. 8, figs 79-85, pl. 9, figs 86-91; 1982a: 52-57, figs 30-40); van den Hoek & Chihara (2000: 40-42, fig. 16).

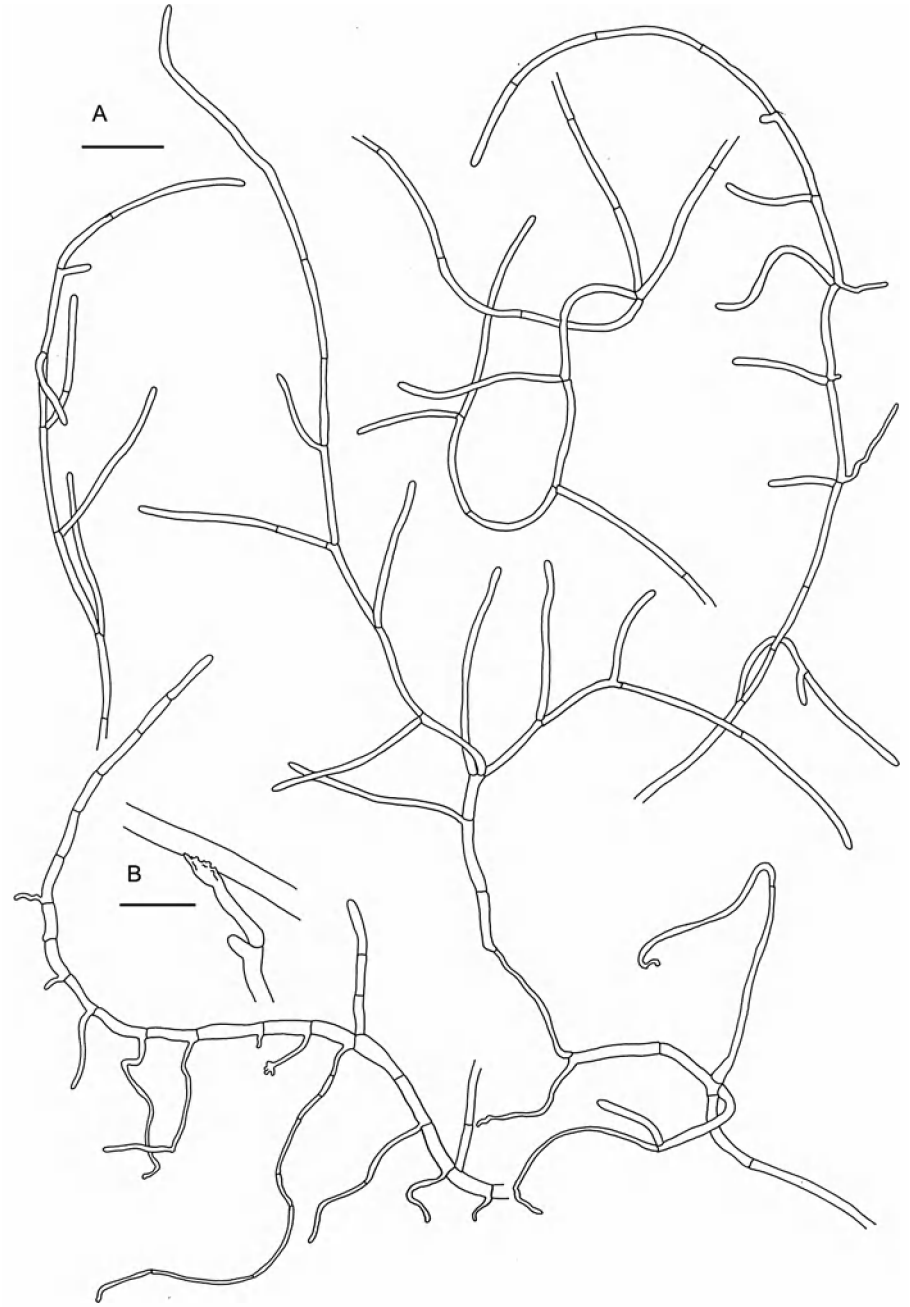


Fig. 3. *Cladophora socialis* (KZN 2185). A. Basal, stolon-like filaments giving rise to the upright branch systems. Scale bar = 500 µm; B. Attachment of filaments with one another by terminal hapteroidal holdfasts at the tips of the apical cells. Scale bar = 100 µm.

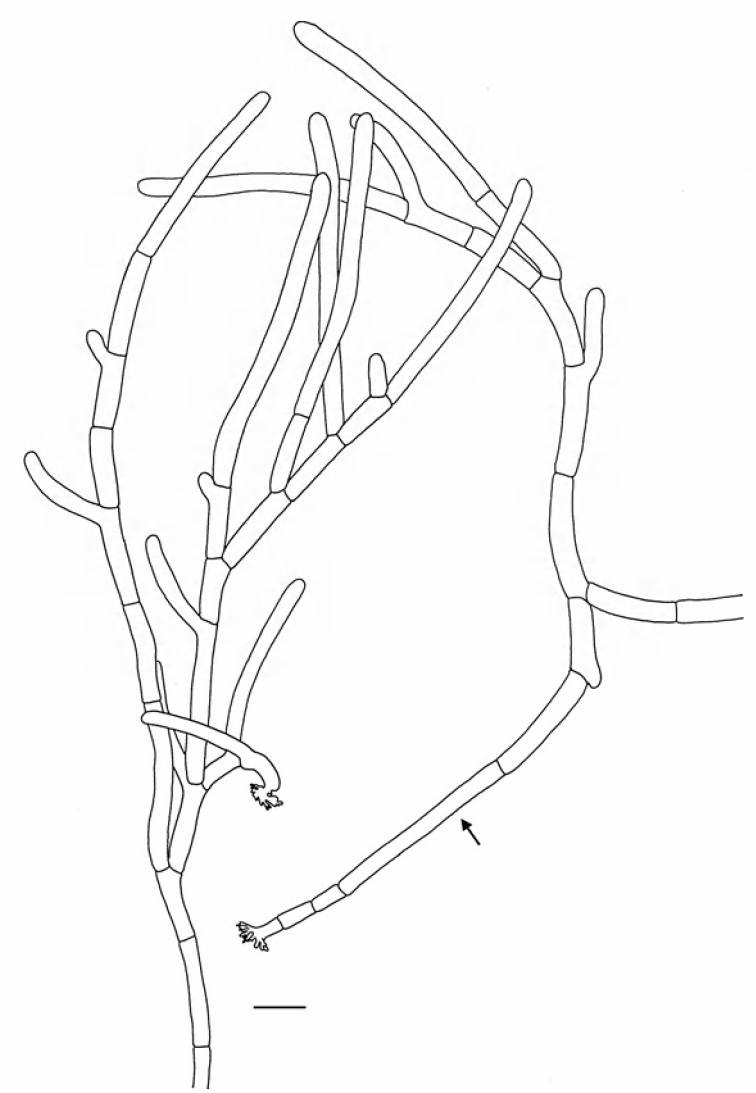


Fig. 4. *Cladophora catenata* (KZN 454). Branching filaments with decumbent filament with inversion of polarity (arrow). Scale bar = 1000 µm.

Section *Aegagropila* (Kützing) Hansgirg

3. ***Cladophora catenata*** (Linnaeus) Kützing, 1843: 271 Fig. 4

Conferva catenata Linnaeus, 1753: 1166-1167

Type locality: Bahamas [van den Hoek (1963: 19, 123) has designated the material of *Conferva ramosa, geniculis longioribus cateniformibus* Dillenius, present in Dillenius's herbarium (OXF) as the type of *C. catenata*].

Description:
Thallus dark green, forming compact cushions, 3-14 cm in diameter, up to 2 cm high, composed of entangled, stiff, often incurved axes. Growth by division of conspicuous apical cells and by intercalary cell division lower down; cells in basipetal direction becoming barely longer and broader. Branch system unilateral or irregular; maximum one (occasionally two) lateral(s) per cell; newly formed laterals often without cross walls at their base; older branches inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification 20°-70°. Some axes decumbent and attached to the substratum by terminal hapteroid structures on the

apical, rhizoid-like cells (inversion of polarity). Apical cells cylindrical or gradually tapering, with rounded tip, often curved, 300-360 µm in diameter, l/w ratio 7-25, up to 8000 µm long; cells of the main axes cylindrical, 240-470 µm in diameter, l/w ratio 2-12. Decumbent axes composed of 4-8 cells, 150-300 µm in diameter; diameter gradually decreasing towards the distal ends. Cell walls 4-12 µm thick in apical cells, up to 40 µm in the main filaments.

Ecology: Epilithic in intertidal pools and in the infralittoral fringe, forming dark green mats.

Specimens examined: Mabibi: KZN 398 (09/08/1999), KZN 454 (11/08/1999); Rabbit Rock, Bhanga Nek: KZN 547 (18/08/1999); Kosi Bay: KZN 767 (16/08/1999).

Geographic distribution: *C. catenata* possibly has a very disjunct distribution in tropical seas; it has been recorded (often as *C. fuliginosa* Kützing) in the Caribbean Sea (Littler & Littler 2000: 320), southern Japan and Taiwan (van den Hoek & Chihara 2000: 45), China (Tseng 1984: 260); Philippines (Silva *et al.* 1987: 97), the Caroline Islands and Queensland, Australia (Phillips 1997: 12). The Mediterranean records of *C. catenata* are possibly misidentifications of *C. lehmanniana* (Lindenberg) Kützing (van den Hoek 1963: 123, note). Recently we collected *C. catenata* in Mozambique, which was the first Indian Ocean record (Coppejans *et al.* 2002). This is the first record for South Africa.

Note: The dimensions and other morphological characters are in good agreement with the amended description of the species by van den Hoek (1982a: 59-60, figs 41-68) and the drawings of Kützing (1854: 14, Tab. 65, fig. 1, as *C. fuliginosa* Kützing). For nomenclatural notes see van den Hoek (1963: 123; 1969: 134; 1982a: 59). The species may be confused with some *Cladophoropsis* species, due to the similarities in growth form, the thick, stiff filaments, terminal hapteroid structures on the apical cells and the delayed cross wall formation in young laterals. Distinction between *Cladophora* and *Cladophoropsis* is primarily based on the relative presence or absence of cross walls in laterals. This character, however, shows considerable variation within the genus *Cladophora* where cross wall formation may be postponed in some branches, but not as distinctly as in *Cladophoropsis*.

References: Littler & Littler (2000: 320, fig. on p. 321); Tseng (1984: 260, fig. 1 as *C. fuliginosa*); van den Hoek (1963: 123, note, pl. 55, fig. 722; 1969: 134-136, fig. 1; 1982a: 59-60, figs 41-68); van den Hoek & Chihara (2000: 45-49, fig. 18).

Section *Boodleoides* van den Hoek

4. ***Cladophora liebetruthii*** Grunow *in* Piccone, 1884b: 53 Fig. 5

Type locality: Gran Canaria, Islas Canarias according to Silva *et al.* (1996: 777). van den Hoek (1963) selected a specimen from the Ionian sea, collected by Liebetruth, in L (937.264, 51) as iso(lecto)type. Prud'homme van Reine *et al.* (1994) proposed a new lectotype from Gran Canaria (in W).

Description:
Thallus dark green, forming three-dimensional netlike cushions, composed of entangled, short-celled filaments. Thallus loosely attached to the substratum by rhizoids developing from the basal or apical poles of cells in the basal region but even in the distal parts of the thallus. Growth mainly by intercalary cell division, giving rise to unbranched filaments of up to 25 cells. Branching irregular, wide-angled (40°-80°); mostly one, sometimes two laterals per cell. Laterals at first laterally inserted at the apical pole of the parent cell; the basal cells of the laterals soon become fused, at their basal poles, with the adjacent cell of the axis. Apical cells often terminating in hapteroidal discs or rhizoid-like structures by means of which they attach to

other filaments. Apical cells cylindrical with rounded tip, 60-80 µm in diameter, l/w ratio 2-5; cells of the main axes cylindrical, 70-95 µm in diameter, l/w ratio 1.5-4. Cell walls 2-5 µm thick in the apical cells, up to 8 µm in the branches.

Ecology: Collected on a single occasion, epilithic in intertidal rock pools.

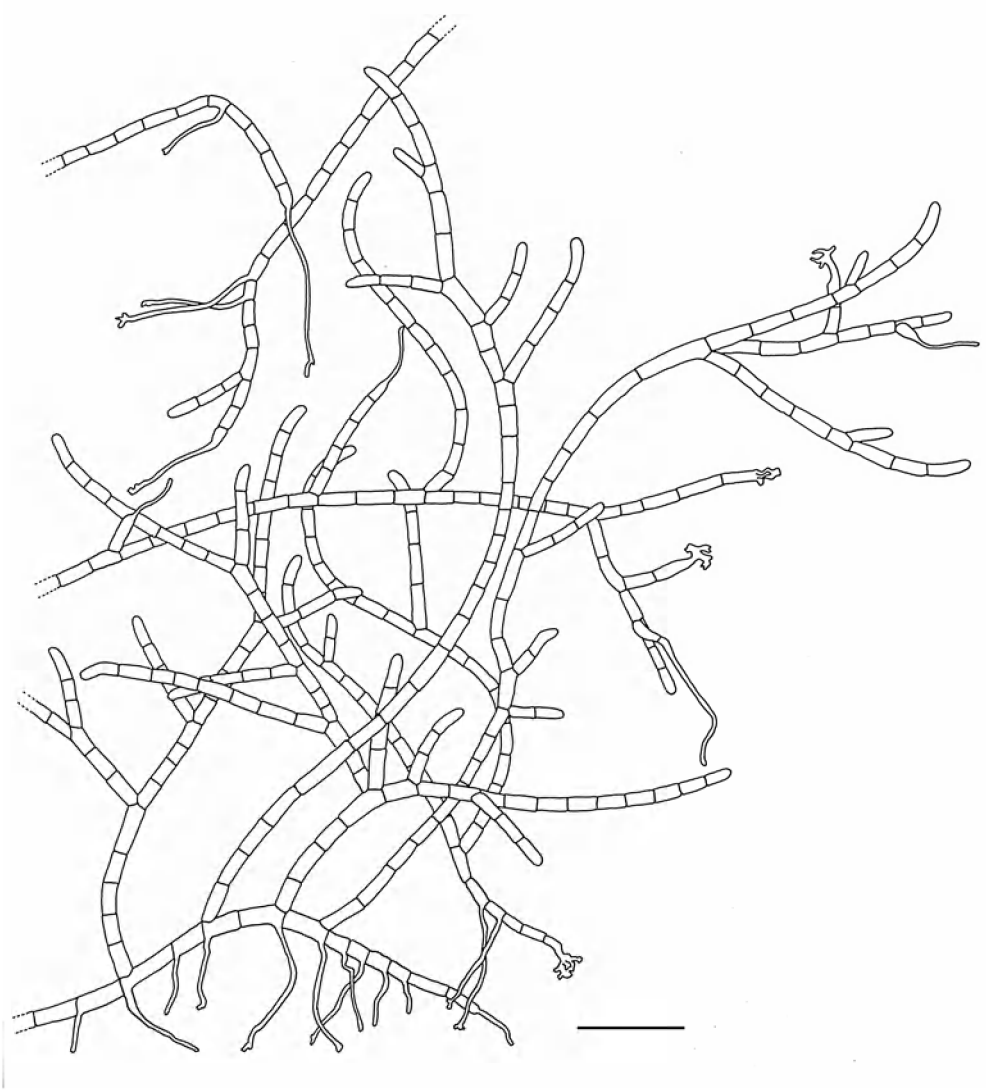


Fig. 5. *Cladophora liebetruthii* (KZN 802). Entangled, short-celled, branched filaments forming the netlike thallus. Scale bar = 500 µm.

Specimen examined: Palm Beach: KZN 802 (19/08/1999).

Geographic distribution: *C. liebetruthii* has a wide distribution in the tropical to warm-temperate Atlantic Ocean (van den Hoek 1963: 59, 1982a: 70-72, map 6). In the Pacific Ocean the species has been recorded from the Philippines (Fortes & Trono 1980: 55, fig. 4), the Great Barrier Reef (Cribb 1984) and Lord Howe Island (Kraft 2000: 564, fig. 22). In the Indian Ocean *C. liebetruthii* has so far only been recorded from India and the Laccadive Islands (as *C. frascatii* Collins & Hervey) (Raghukumar 1986: 290, 293, figs 8-15; Silva *et al.* 1996). The species is listed in Seagrief's (1984: 17) catalogue but no reference for a South African record could be retrieved.

Note: *C. liebetruthii* is the type and was until recently the only species in the section *Boodleoides*. The section is characterized by irregularly branched short-celled filaments which anastomose with one another, forming two- or three-dimensional netlike thalli, resembling *Microdictyon* or *Boodlea* species in habit. Recently two other species have been described in the section: *C. vandenhoekii* Norris & Olsen, a deep-water species from the Bahamas and *C. pachyliebetruthii* van den Hoek & Chihara, an intertidal species from Japan. Kraft (2000: 565) discusses the rather arbitrary nature of the separation of *Cladophora* section *Boodleoides* and the genus *Microdictyon*. Van den Hoek (1982a: 31-33, text figure 4) already formulated a hypothesis for the close relationship between both taxa. This hypothesis was confirmed by a phylogeny of the Cladophorophyceae (18S rRNA) showing that *C. liebetruthii* is indeed closely related with *Microdictyon*, but also clusters with *C. catenata*, *C. coelothrix*, *C. socialis* and *C. prolifera* (Bakker *et al.* 1994).

References: van den Hoek (1963: 59, pl. 12, figs 128, 129; 1982a: 69-72, figs 84-95), Kraft (2000: 564, fig. 22).

Section *Rugulosae* Sakai

5. ***Cladophora prolifera*** (Roth) Kützing, 1843: 271 Figs 6A-C, 7

Conferva prolifera Roth, 1797: 182-183, pl. III: fig. 2

Type locality: "in mare Corsicam" [type lost; neotype designated by van den Hoek (1963: 208): leg. Hauck, locality: Miramare, Italy, L 937/264/23].

Description:
Thallus dark green (blackish when dried), coarse, 2-4 cm high, growing as stiff tufts composed of densely branched, fastigiate filaments. Old cells in the basal and middle part of the thallus each giving off one rhizoid with annular constrictions at their basal poles; these rhizoids grow down along the cell or cells below, where they entangle and form a conspicuous stipe that attaches to the substratum. Growth by apical cell division and subsequent cell enlargement. Branching originally acropetally organised, becoming irregular in older parts of the thallus because of intercalary growth. Each subapical cell forms a lateral, often immediately after being cut off from the apical cell; lower down a cell may form a 2nd or sometimes a 3rd lateral. Apical cells cylindrical with rounded tip, 90-130 µm in diameter, l/w ratio 2.5-5.5; cells of the terminal branch systems cylindrical, 150-200 µm in diameter, l/w ratio 2.5-8, increasing towards base of the thallus. Cells of the main axes and basal cells elongated and club-shaped, up to 200 µm in diameter, l/w ratio 7-10, basal parts often with annular constrictions. Rhizoids 40-100 µm in diameter.

Ecology: epilithic, low intertidal, *Cladophora horii* sometimes grows as an epiphyte on this species.

Specimen examined from South Africa: Rabbit Rock, Kosi Bay: KZN 533 (13/08/1999).

Other specimens examined: Finike, Turkey: HEC 1790 (10/1973); Cap Le Dramont, France: HEC 2707 (07/08/1976); Point Lonsdale, Victoria, Australia: ODC 519 (07/07/1996).

Geographic distribution: *C. prolifera* is widely distributed in tropical and warm-temperate seas (van den Hoek & Chihara, 2000: 54). Along the East African coast *C. prolifera* has been collected in Mozambique (Isaac & Chamberlain (1958: 124); Tanzania (Jaasund 1976: 7, fig. 13, as *C. saviniana* (misapplied name); Jaasund 1977 as *C. rugulosa*), and Kenya (Isaac 1967: 76). The species has been recorded several times from South Africa (Krauss 1846: 215;

Areschoug 1851: 12; Eyre & Stephenson 1938: 33; Stephenson 1939: 533; 1944: 300) but possibly this species was confused with *C. rugulosa* (see below).

References: Isaac & Chamberlain (1958: 124, fig. 1); Littler & Littler (2000: 322, fig. on p. 323); Schneider & Searles (1991: 70-71, figs 55, 56); van den Hoek (1963: 208-212, pl. 51, figs 677-682, pl. 52; 1982a: 166-170, figs 318-327); van den Hoek & Womersley (1984: 193-194, figs 62A, 63A,B); van den Hoek & Chihara (2000: 52-55, fig. 21). As *C. rugulosa* (misapplied name): Egerod (1975: 45, figs 5-7, 12); Tseng (1984: 260, fig. 4).

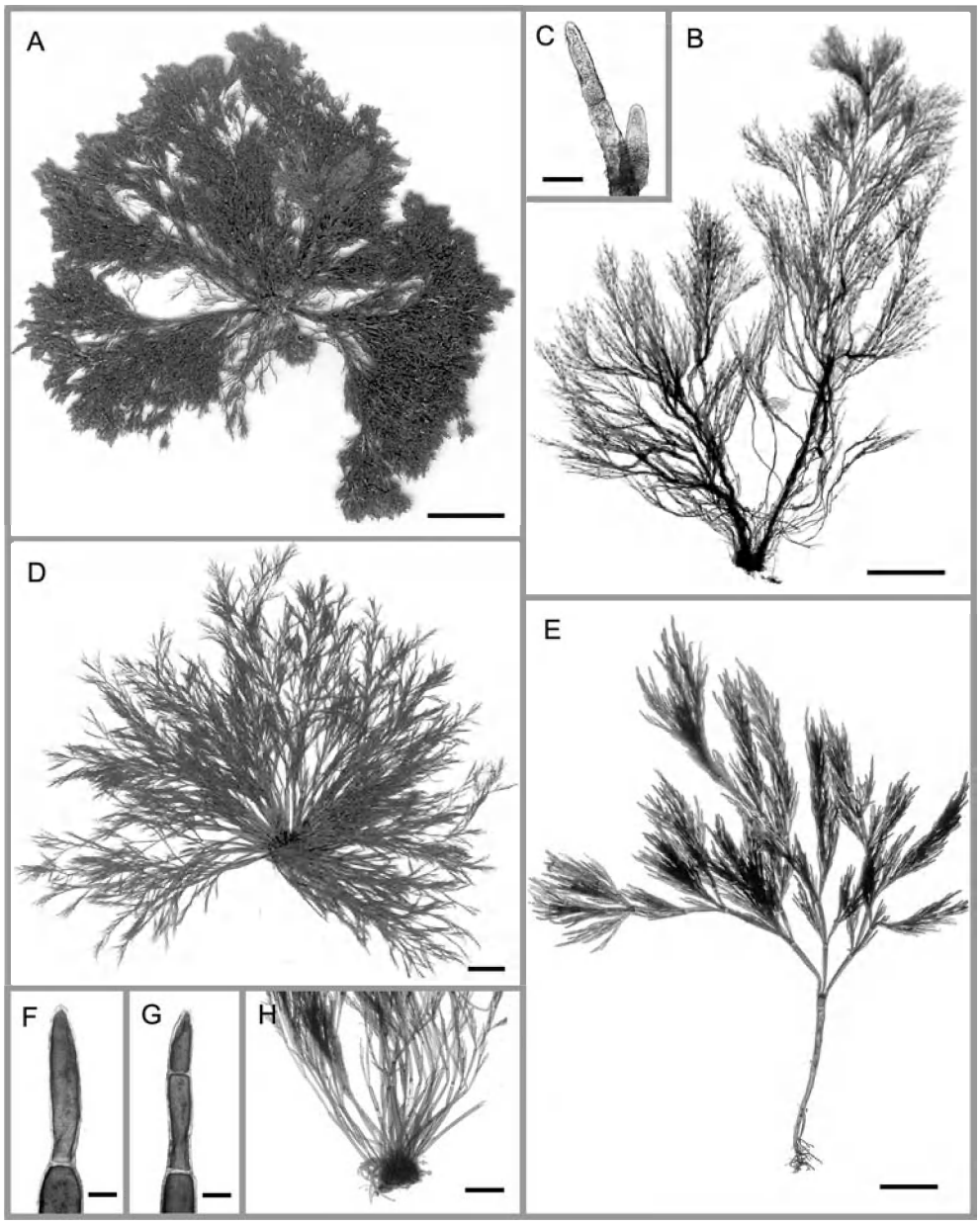


Fig. 6. A-C. *Cladophora prolifera* (KZN 533). A. Tuft composed of densely branched, fastigiate filaments, scale bar = 1 cm; B. Tuft with basal rhizoids forming a conspicuous stipe, scale bar = 5 mm; C. Apical cell, scale bar = 200 µm. D-H. *Cladophora rugulosa* (HEC 11015). D. Broom-like tuft, composed of clustered stipes, giving rise to branched filaments, scale bar = 1 cm; E. Single stipe cell giving rise to densely branched filaments, scale bar = 5 mm; F, G. Apical cells, scale bars = 200 µm; H. Densely clustered stipes, scale bar = 5 mm.

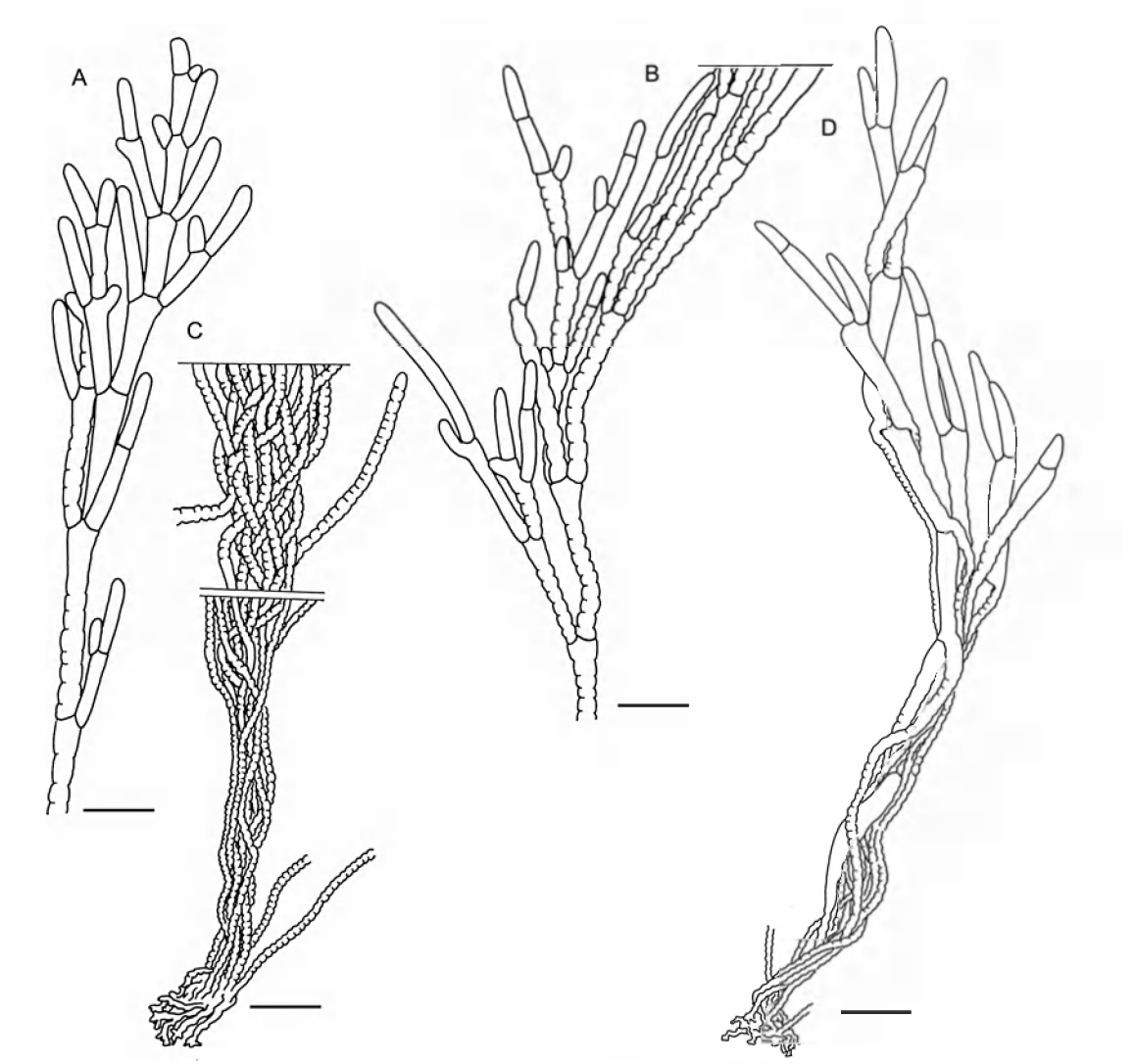


Fig. 7. *Cladophora prolifera* (KZN 533). A. Terminal branch system; B. Main branches in the middle of the thallus; C. Basal rhizoids entangling and forming a stipe; D. Young thallus. Scale bars = 500 µm.

6. ***Cladophora rugulosa*** G. Martens, 1868: 112, pl. II: fig. 3 Figs 6D-H, 8

Lectotype locality: Port Natal [Durban], South Africa according to Papenfuss (1943: 80).

Apjohnia rugulosa (G. Martens) G. Murray, 1891: 209

Description:
Thallus dark green (dark brown when dried), 3-13 cm high, forming stiff, broom-like tufts, composed of densely clustered stipes giving rise to pseudodichotomous or oppositely branching main filaments and densely branched, often fasciculate terminal branch systems. Thallus attached to the substratum by branched, clumped rhizoids developing from the basal part of the stipe. Stipe composed of a single clavate cell with basal annular constrictions. Growth by apical cell division and subsequent cell enlargement. Terminal branch systems acropetally organized. Each new cell, after having been cut off from the apical cell, produces a lateral at its apical pole, either immediately when it has become the subapical cell or when it has become the 2nd cell below the apical cell. Subsequently (when the cell has become the 2nd-3rd cell below the apical cell) a second lateral is formed, resulting in a typical opposite branching pattern in the terminal,

fasciculate branch systems. At increasing distance from the apex a 3rd, 4th and 5th lateral may be produced. Young laterals are inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification 10°-35°. Cells in basipetal direction becoming longer, increasingly club-shaped, with distinct annular constrictions at the base. The basal poles of the old cells often have distinct protuberances (short rhizoid-like processes) that attach to the parent cell below (fig. 8B, E). Apical cells tapering, with rounded tips, (105-) 130-260 (-285) µm in diameter, l/w ratio 2-8; cells of the terminal branches 220-415 µm in diameter, l/w ratio 2,5-12; cells of basal branches and main axes 380-550 µm in diameter at their distal end, 230-325 µm at the base, l/w ratio 5-25 (-50), up to 18 mm in length. Stipe cell 600-700 µm in diameter at the distal end, 230-350 µm at the base, 12-18 mm in length. Cell walls 12-50 µm thick in apical cells and terminal branches, up to 130 µm thick in the main axes, basal cells and stipe.

Ecology: Epilithic in the shallow intertidal or infralittoral fringe; often on wave-exposed rocks. *C. rugulosa* is by far the most common *Cladophora* species along the South African East Coast. In the lower intertidal this species often covers entire rock surfaces.

Specimens examined: Haga-Haga Mouth: KM 18 (26/10/1999); Cape Morgan: KM 182 (24/10/1999), KZN 1345 (24/10/1999), KZN 1302 (25/10/1999); Double Mouth: KM 107 (25/10/1999); Ntlonyana, S of The Haven: KZN 1026.2 (16/02/1999), KZN 1206 (16/02/1999); Port Edward: KZN 1383 (24/12/1999); Palm Beach: FL 258 (22/03/1997), KZN 819 (19/08/1999), KZN 1550 (21/12/1999), KZN 2039 (7/02/2001); Port O'Call, Trafalgar: FL 225 (20/03/1997), KZN 928 (20/08/1999); Crayfish Point, Mapelane: KZN 1836 (20/08/2000); Mission Rocks: HEC 11015 (23/11/1995), KZN 1049 (8/07/1998), HB81-S62R (8/07/1998).

Geographic distribution: *C. rugulosa* is only known from the South African South and East Coast (see note below). Most records from outside South Africa are misapplied names for *C. prolifera*: Australia (Womersley 1956: 359), Thailand (Egerod 1975: 45, figs 5-7, 12), China (Tseng 1984: 260, pl. 129, fig. 4), Japan (Okamura 1910: 103, pl. 80, figs 1-7; Sakai 1964: 67-70; Segawa 1965: 10; Yoshida 1998: 67), Vietnam (Pham-Hoàng Hô 1969: 431, fig. 4.36), Philippines (Marcos-Agngarayngay 1983: 75, fig. 10), and Tanzania (Jaasund 1977: 510). Some other records could not be verified because no description or illustration was provided: Taiwan (Lewis & Norris 1987: 8), Malaysia (Phang & Wee 1991: 57).

Note: Van den Hoek (1982a: 169) proposed to synonymise *C. rugulosa* with *C. prolifera*, based on descriptions and illustrations of *C. rugulosa* by Papenfuss (1943), Jaasund (1976), Egerod (1975), Womersley & Bailey (1970), Sakai (1964) and Taylor (1945). Other authors had differentiated the two species. Papenfuss (1943: 80) distinguished *C. rugulosa* on the basis of longer cells, more prominent main axes, and more pronounced annular constrictions in the cells. Papenfuss & Chihara (1975: 313) argued that small rhizoid-like processes at the proximal end of the basal cells are only present in *C. rugulosa*. Van den Hoek (l.c.) rejects the above arguments because rhizoid-like processes are also occasionally present in some *C. prolifera* plants and cell dimensions are too variable in *C. prolifera* to split off the coarser *C. rugulosa*. We compared the South African specimens with *C. prolifera* from Europe, Kenya and Australia. Based on our observations two species, *C. prolifera* and *C. rugulosa*, both occurring in South Africa, are not identical owing to completely different modes of attachment. *C. prolifera* is characterized by the presence of rhizoids with annular constrictions developing from the lower part of the basal cells, growing down along the cells below where they entangle with one another to form a conspicuous 'stipe' (figs 6B, 7C, D). In *C. rugulosa* this kind of rhizoids is absent (Martens 1868: Pl. 2, fig. 3); here the plants are attached by basal branching rhizoids developing from the base of a conspicuous stipe cell with annular constrictions. The rhizoids form a basal clump giving off numerous, densely clustered stipe cells (fig. 6H). The South African *C. prolifera* also differs from *C. rugulosa* by its smaller cell diameters, but since the cell diameter of *C. prolifera* is shown to be very variable, this character is less useful in distinguishing both species (Table 2).

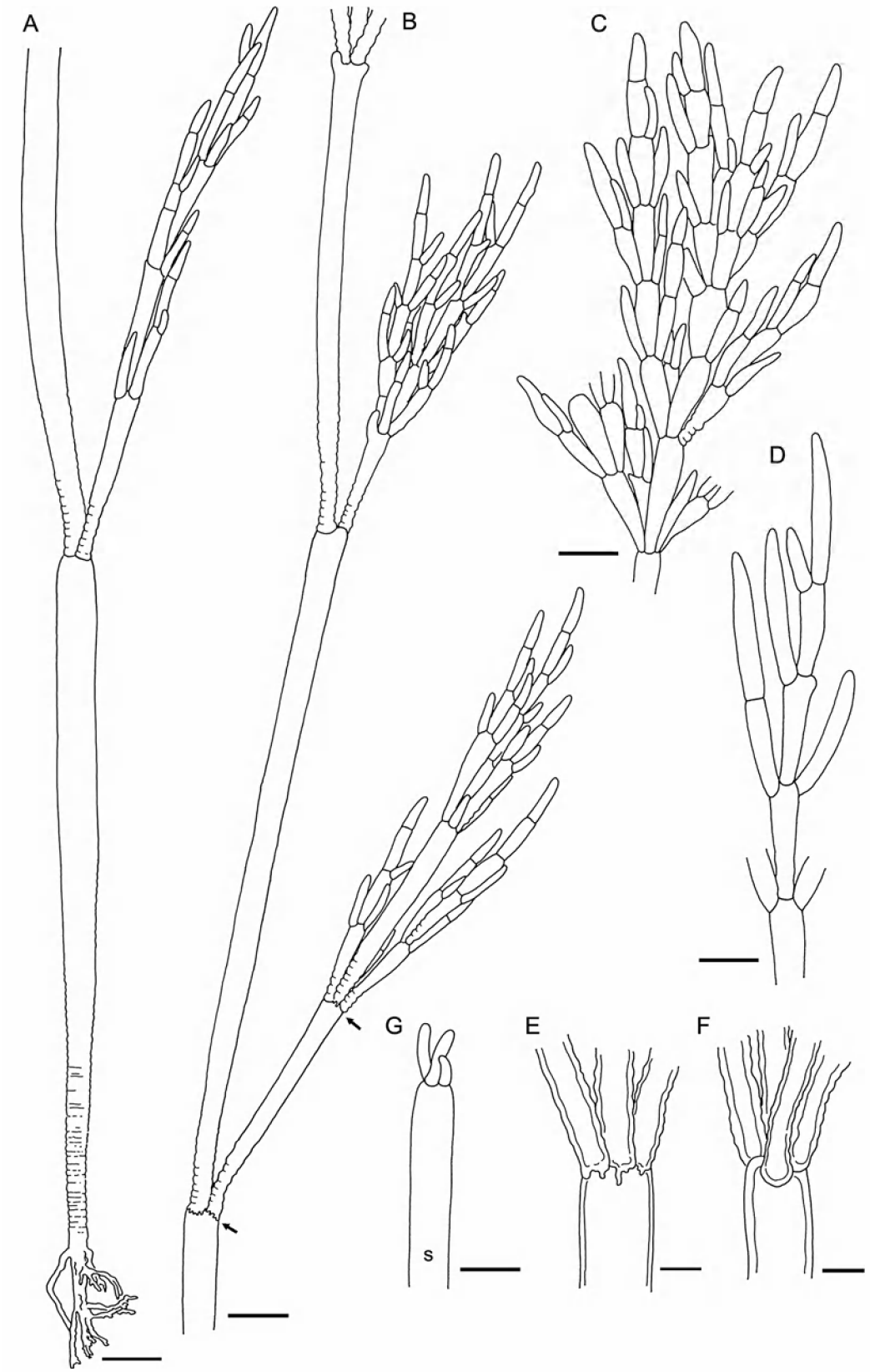


Fig. 8. *Cladophora rugulosa*. A-F (KZN 2039). A. Stipe cell with basal branches and fasciculate terminal branch system, scale bar = 1000 µm; B. Main filaments with fasciculate terminal branch system; basal poles of the older cells with rhizoid-like processes (arrowheads), scale bar = 1000 µm; C, D. Terminal branch systems, scale bars = 500 µm; E. Protuberances at the basal poles of the old cells, scale bar = 300 µm; F. Basal poles of old branches with annular constrictions, scale bar = 300 µm; G. Apical part of a young thallus (s = stipe cell) (KZN 819) scale bar = 1000 µm.

References: Bolton & Stegenga (1987: 168); Farrell *et al.* (1993: 149); Papenfuss (1943: 79-80); Papenfuss & Chihara (1975: 313, figs 12, 13); Seagrief (1967: 22, pl. 5; 1980: 21, fig. on pl. 1; 1988: 37, 40, fig. 5:2); Simons (1969: 246, fig. *s.n.*; 1977: 17, fig. 23).

Table 2. Variation in cell diameter in *C. prolifera* and *C. rugulosa*.

	Geographical region and reference	apical cell diam. (µm)	basal cell max. diam. (µm)
C. prolifera	Europe (van den Hoek 1963)	120-200	330-650
	Australia (van den Hoek & Womersley 1984)	(70-) 100-220	420
	Atlantic (van den Hoek 1982a)	95-240	345
	Japan (van den Hoek & Chihara 2000)	120-220	300
	Thailand (Egerod 1975)	77-118	300
	South Africa (this paper)	90-130	200
C. rugulosa	South Africa (this paper)	(105-) 130-260 (-285)	550 (700)

7. ***Cladophora horii*** van den Hoek & Chihara, 2000: 67-68, fig. 28 Figs 9A-C, 10

Type locality: Okinawa, Sesoko Island, Japan (leg. S. Kamura, C. van den Hoek & T. Hori; van den Hoek no. 90/8.a.4, TNS-AL-46793).

Description:
Thallus dark green, forming stiff, 2-5 cm high, broom-like tufts of densely branched fasciculate filaments; attached to the substratum by branching rhizoids developing from proximal parts of the basal cells. Growth by apical cell division in the terminal branch systems, and by intercalary cell division lower down; cells in basipetal direction becoming slightly longer and broader. Branching more or less acropetally organized. Each new cell after having been cut off from the apical cell produces a lateral at its apical pole, when it has become the 1st or 2nd cell below the apical cell; later a second lateral is often formed, resulting in an opposite branching pattern. Laterals inserted with a steeply inclined cross wall cutting it off from the parent cell. Angle of ramification acute: 5°-25°. Cells in the middle and basal parts of the thallus producing rhizoids that grow along and into the cell walls of the cells below; consequently the stem-like basal branches become completely covered by and the cell walls fused with these rhizoids. Apical cells cylindrical with rounded tip, 60-90 µm in diameter, l/w ratio 1.4-5.5; cells of the terminal branches cylindrical to slightly club-shaped, 70-120 µm in diameter, l/w ratio 3.5-5; basal cells club-shaped, up to 160 µm in diameter, l/w ratio 3-4. Cell walls 2-5 µm thick in apical cells, up to 14 µm thick in basal branches.

Ecology: Epilithic in low intertidal pools or in shallow subtidal (to 1 m deep), or epiphytic on *Cladophora prolifera* in the low intertidal.

Specimens examined: The Bluff, Durban: HEC 10983 (22/11/1995), KZN 101 (03/08/1999), KZN 158 (04/08/1999); Mission Rocks, St. Lucia: KZN 1048 (08/07/1998); Mabibi: KZN 356 (09/08/1999), KZN 1676 (13/08/2000); Rabbit Rock, Bhanga Nek: KZN 533 (epiphytic on *C. prolifera*) (13/08/1999).

Geographic distribution: This is the first record of *C. horii* outside its type locality.

Note: This recently described species from Japan resembles young specimens of *C. prolifera* in general habit. *C. horii* can be distinguished by the lack of annular constrictions in the stipe cell and rhizoids. The rhizoids in *C. prolifera* do not fuse with the cell walls of the cells below, like

in *C. horii*, but remain loose and entangle with one another to form a distinct stipe. Although *C. horii* is placed in the section *Rugulosae*, its systematic position remains somewhat doubtful, primarily because of its polypyramidal pyrenoids (van den Hoek & Chihara 2000: 67, fig. 28D), differing from the bilenticular pyrenoids in the rest of the genus.

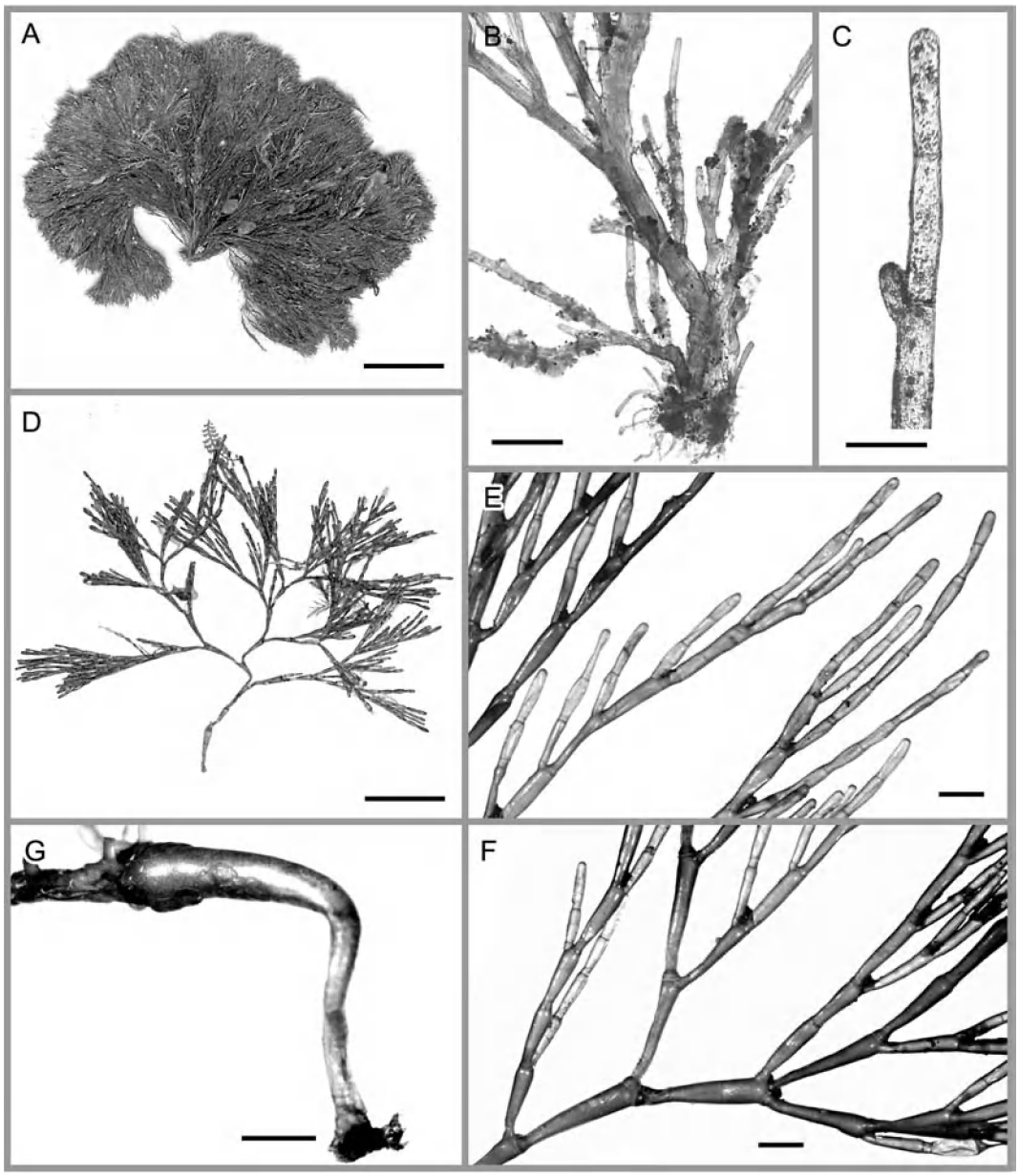


Fig. 9. A-C. *Cladophora horii*. A. Broom-like tuft, composed of densely branched, fasciculate filaments (HEC 10983), scale bar = 1 cm; B. Stem-like basal branches, completely covered by rhizoids (HEC 10983), scale bar = 5 mm; C. Apical cell (KZN 356), scale bar = 200 µm; D-G. *Cladophora dotyana* (FL 343). D. Tuft composed of a one-celled stipe, pseudodichotomously branching main axes and densely branched terminal branch systems, scale bar = 1 cm ; E. Terminal branch systems, scale bar = 1 mm; F. main axes, scale bar = 1 mm; G. Clavate, curved stipe cell, scale bar = 1 mm.

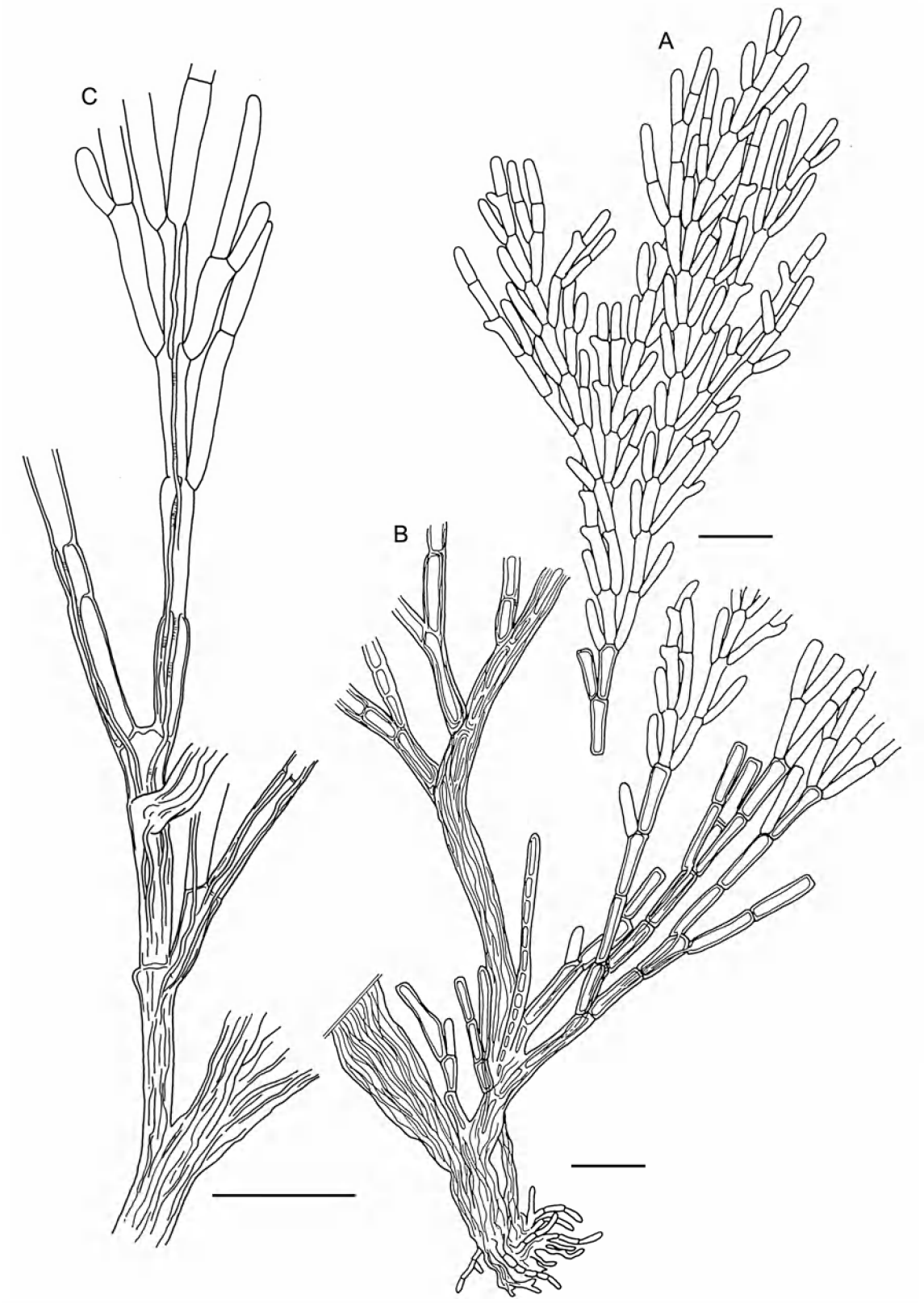


Fig. 10. *Cladophora horii* (KZN 356). A. Terminal branch systems; B. Base of thallus with stem-like branches; C. Cells in basal part of the thallus producing rhizoids at their basal poles growing along and into the cell walls of the cells below. Scale bars = 500 μm.

Section *Longi-articulatae* Hamel

8. ***Cladophora dotyana*** Gilbert, 1965: 486-489, fig. 3 Figs 9D-G, 11

Type locality: Hokipa Park, East Maui, Hawaiian Islands (leg. Gilbert 9214, MICH!).

Description:
Thalli dark green, forming erect, coarse, stiff tufts, up to 4 cm high, composed of a one- or two-celled stipe, pseudodichotomously branching main axes and densely branched terminal branch systems; attached to the substratum by basal branching rhizoids developing from the basal stipe-cell. Growth mainly by apical cell division, and few intercalary divisions lower down; cells in basipetal direction becoming longer, broader and increasingly club-shaped. Terminal branch systems organized more or less acropetally to irregularly. Each new apically formed cell giving off one lateral when arriving at the position of the 2nd to 8th cell below the apical cell; lower down a cell may occasionally produce a 2nd branch. Young laterals are apically inserted with a feebly inclined cross wall cutting it off from the parent cell; with age these walls become almost horizontal. The basal cells of the older laterals become fused at their basal poles with the basis of the cells of the main axes. Angle of ramification ranging from 20°-30° in the terminal branch systems to ca. 45° in the basal branches. Apical cells cylindrical with rounded tip, 250-290 µm in diameter, l/w ratio 3-6. Cells of the terminal branch systems cylindrical to slightly clavate, 280-480 µm in diameter, l/w ratio 2-6. Cells of basal branches clavate with a distinct basal bulge, diameter of cell apices 520-840 µm, diameter of the basal bulge 480-600 µm, diameter just above basal bulge 320-480, cell length 2.8-4 mm. Stipe cells clavate, often curved, diameter at cell apex 940-990 µm, diameter at lower end 380-440 µm, length 4.5-6.2 mm. Cell walls in apical cells ca. 10 µm thick, in basal filaments up to 140 µm thick.

Ecology: Epilithic, subtidal (at -19 m).

Specimens examined: Port Edward: FL 343 (24/03/1997); Salmon Banks, Shelly Beach: KZN 2003 (06/02/2001).
Additional specimen examined: Hawaiian Islands, Hokipa Park, East Maui, on the under surface of a rocky overhang in tide pool (leg. Gilbert 9214, 24.iii.1959, MICH: holotype).

Geographic distribution: Up to now *C. dotyana* was only known from Hawaii (type locality), Japan (van den Hoek & Chihara 2000) and Lord Howe Island (Kraft 2000). This is the first record of the species for the Indian Ocean.

Discussion: *C. dotyana* is characterized by thick, stiff filaments and distinct cylindrical to clavate, often curved basal cells. The South African material is in general agreement with the original description of *C. dotyana* from the Hawaiian Islands (Gilbert l.c.) and the description of the Japanese plants by van den Hoek & Chihara (2000: 88-91, figs 38, 39). A comparison of *C. dotyana* from Hawaii, Japan and South Africa is given in Table 3.

Table 3. Comparison of *C. dotyana* from Hawaii (Gilbert 1965), Japan (van den Hoek & Chihara 2000) and South Africa (this paper).

	Hawaii	Japan	South Africa
Basal cell diameter	up to 600 µm	400-700 µm	480-600(-960) µm
Cell diameter of terminal branch systems	210-300 µm	180-340 µm	280-480 µm
Diameter of apical cells	ca. 220 µm (derived from fig. 3)	160-340 µm	250-290 µm
Maximum number of laterals per cell	3 (rarely 5)	3	2
Cell shape of basal branches	cylindrical to clavate[1]	cylindrical to slightly clavate	distinctly clavate

[1] Although it is stated in the original description "cells cylindrical throughout the thallus", the illustrations and the holotype demonstrate that most basal cells are slighlty to distinctly clavate.

Reference: Kraft (2000: 554, fig. 18A-C), van den Hoek & Chihara (2000: 88-91, figs 38-39).

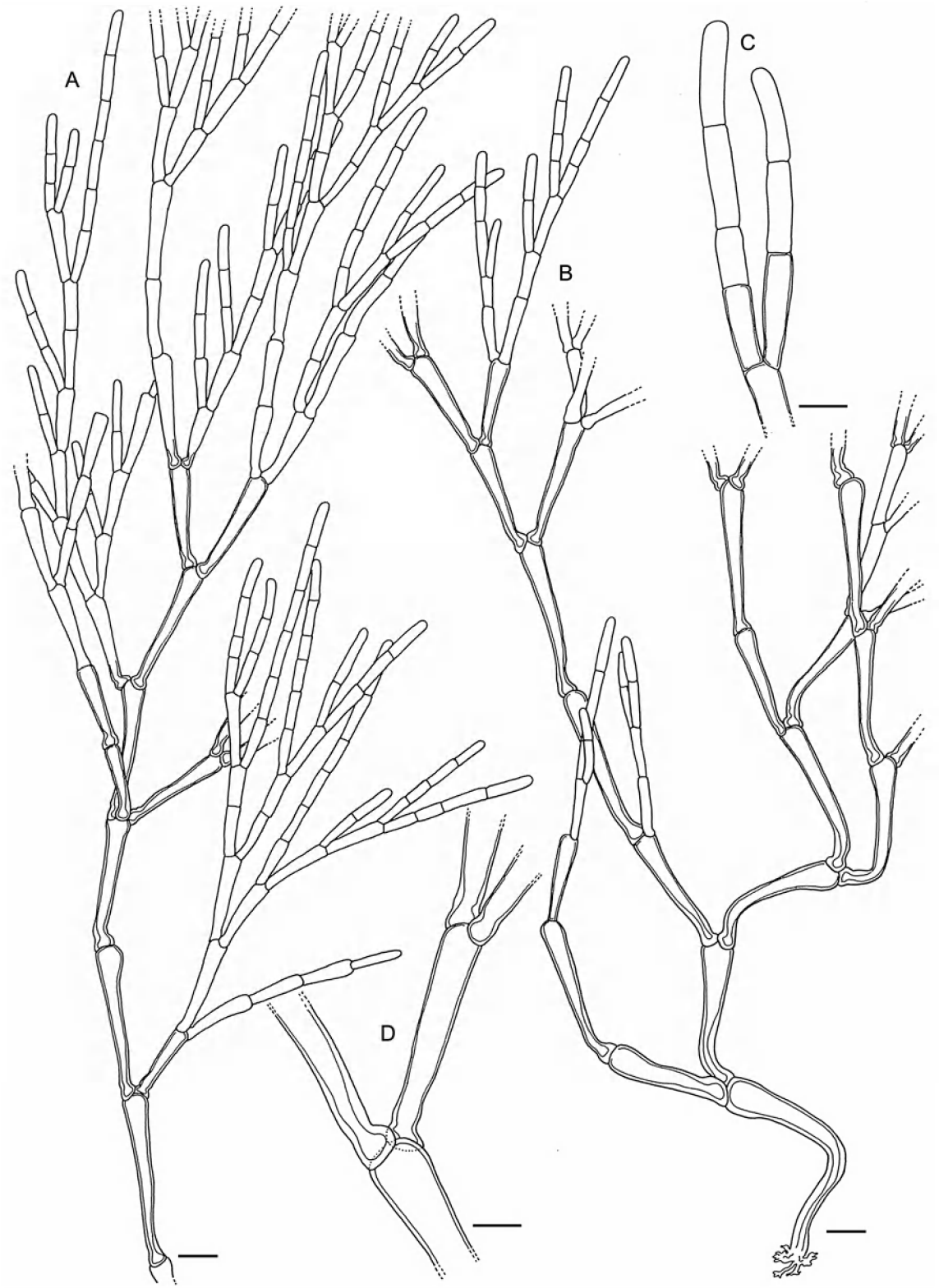


Fig. 11. *Cladophora dotyana* (KZN 2003). A. Main filaments and terminal branch systems, scale bar = 1000 µm; B. Stipe cell and basal branches, scale bar = 1000 µm; C. Apical cells, scale bar = 500 µm; D. Clavate cells of the main filaments with basal bulges, scale bar = 500 µm.

9. ***Cladophora* sp.** Fig. 12

Description:
Thallus light green, forming 1.5 cm high, penicillate, densely branched tufts. Branching system organized acropetally. Growth mainly by apical cell division, each 4th or 5th cell below the apical cell giving off one lateral at its apical pole; at increasing distance from the apex a cell may give off a second and sometimes a third branch. Branches inserted at the apical cell pole with an almost horizontal cross wall, cutting it off from the parent cell. Angle of ramification ranging from 20°-40° in the basal branches to 5°-30° in the terminal branch system. Apical cells tapering, with obtuse tip, diameter 80-95 (-125) µm, l/w ratio 10-16. Cells of the terminal branch systems 75-110 µm in diameter, l/w ratio 9-15. Cells of the basal branches 100-300 µm in diameter, l/w ratio 5-10. The basal cell has been detached when collected.

Ecology: Epilithic, subtidal (at -12 m).

Specimen examined: 2-Mile Reef, Sodwana: KZN 2098 (10/02/2001).

Note: Only a fragment of the plant was present in our collections, lacking the basal branch system and stipe. Therefore a certain identification cannot be made. Important missing characters are the dimensions of the basal stipe cells, the number of cells composing the basal stipe, and clustering of the basal stipe cells. Based on branching pattern, insertion mode of branches and the cell dimensions of the cells in the apical parts of the thallus this specimen can possibly belong to *C. pellucidoidea* van den Hoek, *C. feredayi* Harvey, *C. japonica* Yamada var. *kajimurae* van den Hoek & Chihara or *C. sakaii* Abbott (van den Hoek *pers. comm.*). Table 4 gives an overview of character states of these four taxa.

Table 4. Comparison of 4 species in the section *Longi-articulatae* and the unidentified South African specimen.

	C. pellucidoidea	*C. feredayi*	*C. japonica* var. *kajimurae*	*C. sakaii*	*C. sp.* KZN
References	van den Hoek (1982a); Schneider & Searles (1991)	van den Hoek (1963); van den Hoek & Womersley (1984)	van den Hoek & Chihara (2000)	Abbott (1972); Abbott & Hollenberg (1976); van den Hoek & Chihara (2000)	this paper
Number of laterals per cell	up to 2 (rarely 3)	up to 5	up to 4 (rarely 5)	up to 4	up to 2, sometimes 3
Diam. apical cells (µm)	50-95	(35-) 40-120 (-135)	70-150 (170)	(50-) 60-150	80-95 (-125)
Diam. stipe cells (µm)	?	350-600 (-800)	350-800	170-250 (-300)	?
Number of cells composing the stipe	1-4	?	1-3	1-3 (rarely 4)	?
Stipes	single?	single or clustered	clustered	clustered	?
Ecology	deep-water	shallow subtidal, 1-10 m deep	shallow to deep subtidal, 1-40 m deep	deep-water	subtidal, 12 m deep
Type locality	North Carolina	Tasmania	Japan	Japan	/
Geographic distribution	North Carolina, Georgia, Curacao	Australia, Tasmania, New Zealand, Mediterranean, Canary and Salvage Islands	Japan	Japan, Korea, California	/

Fig. 12. *Cladophora* sp. (KZN 2098). A. Main filaments and terminal branch systems, scale bar = 1000 µm; B. Main filaments with young laterals, scale bar = 500 µm.

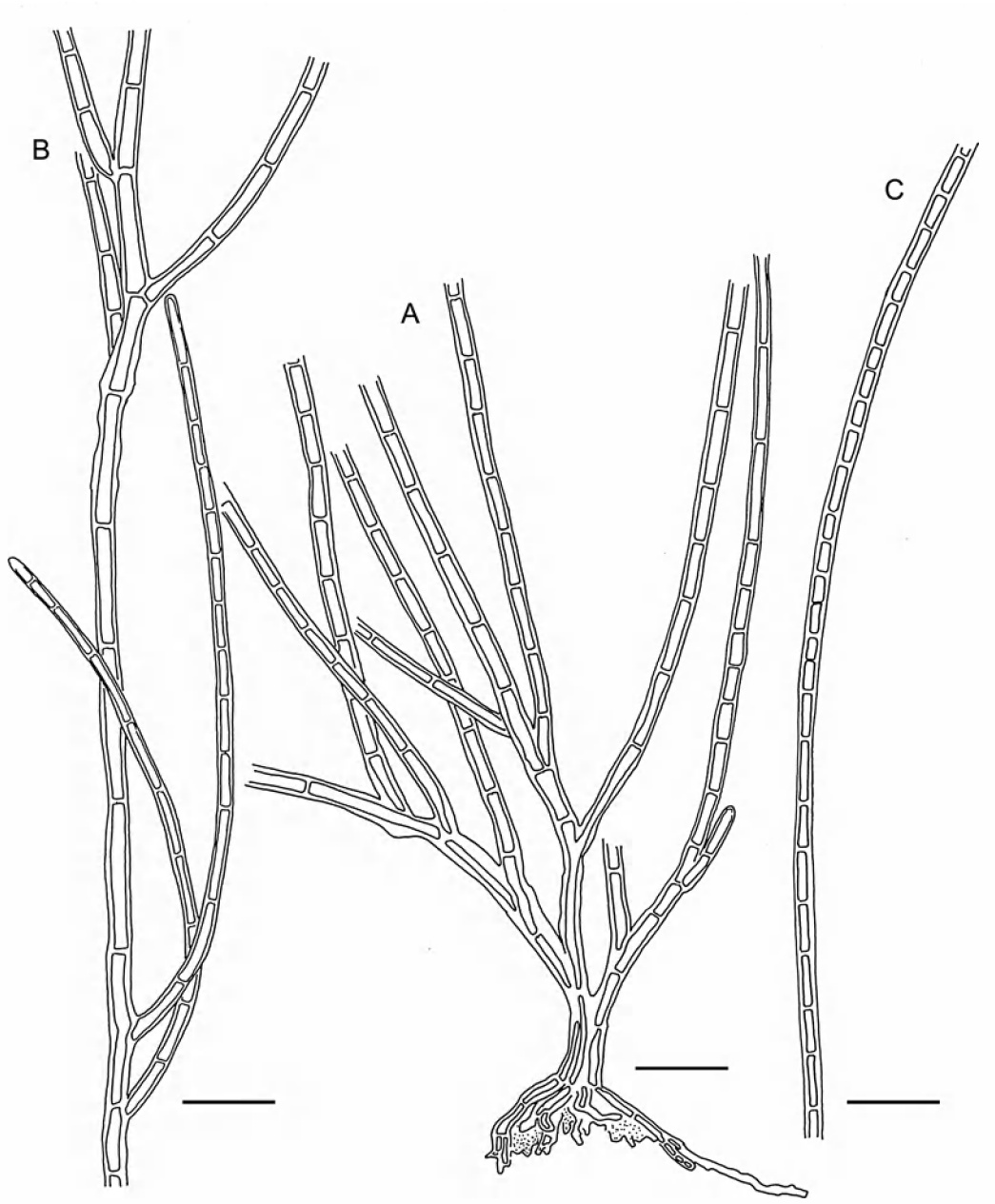


Fig. 13. *Cladophora flagelliformis* (KZN 68). A. Lower branches and rhizoidal holdfast; B. Basal branches; C. Unbranched terminal filament. Scale bars = 500 µm.

Table 5. Comparison of *C. flagelliformis* from the South African West and East Coast.

	Diam. basal cells	Diam. cells of main axis	Diam. apical cells of actively growing branches	Diam. fertile cells
West coast (Stegenga *et al.* 1997)	?	100-150 µm	50-70 µm	up to 400 µm
specimens Cape Peninsula	90-220 µm	100-260 µm	50-100 µm	150-270 µm
specimens East Coast	85-125 µm	60-205 µm	52-80 µm	150-240 µm

Section *Glomeratae* Kützing

10. ***Cladophora flagelliformis*** (Suhr) Kützing, 1849: 388 Fig. 13

Conferva flagelliformis Suhr, 1840: 294

Type locality: Cape of Good Hope, South Africa [Material of *Conferva flagelliformis* Suhr collected at "Caput bonae spei" (nos 7963-7964) is present in the Agardh herbarium (LD). It is not certain that these specimens are part of the original material since the collector, Drége, mentioned in the original description is not mentioned on the herbarium specimens].

Taxonomic synonym: *Cladophora virgata* Kützing, 1843: 271 (type locality: Cape of Good Hope, South Africa).

Description:
Thallus dark green, forming dense tufts of erect filaments, up to 8 cm tall; attached basally by branched, septate rhizoids developing from the proximal part of the basal cells. Growth in the main filaments mainly by intercalary cell divisions, in the young laterals also by apical cell division. Branching irregularly organized, maximum one lateral per cell, inserted by an oblique wall cutting it off from the parent cell. Branches restricted to the basal parts of the thallus, the distal part of the thallus unbranched and flagelliform. Apical cells of actively growing branches cylindrical, with rounded tip, 52-80 µm in diameter, l/w ratio 1.5-5.5; cells of branchlets 67-105 µm in diameter, l/w ratio 1.4-3.5; cells of the main filaments 60-115 µm in diameter in the basal part of the thallus, generally increasing towards the distal part up to 205 µm in diameter, l/w ratio 3-4.8 decreasing towards the distal part to about 1.5-2.5; basal cells 85-125 µm in diameter, l/w ratio 5-34. Cell walls relatively thick throughout the thallus; ca. 5-25 µm thick in apical cells and young laterals, 12-50 µm in main filaments, up to 58 µm thick in basal cells. Fertile cells developing in long, unbranched apical parts of the thallus, 150-240 µm in diameter.

Ecology: epilithic, subtidal (at -18 m)

Specimens examined: Cape Morgan: KZN 1350 (24/10/1999); The Bluff, Durban: KZN 68 (3/08/1999).

Geographic distribution: *C. flagelliformis* occurs along the South African West Coast (from Brandfontein to Namibia) in the lower intertidal to subtidal (to –8 m) (Stegenga *et al.* 1997; Leliaert *et al.* 2000; pers. obs.). Farrell *et al.* (1993: 149) recorded this species for Isipingo Beach as *C. virgata* Kützing (see Silva *et al.* 1996: 773 for nomenclatural note). *C. flagelliformis* has been recorded from Tristan da Cunha (Baardseth 1941: 11, fig. 2A) but the description and illustration remind one of *C. rupestris* (Linnaeus) Kützing. The Tanzanian record of *C. flagelliformis* (Gerloff 1957: 759) remains uncertain since no illustration and only a poor description are given.

Note: Our specimens are in general agreement with the description of Stegenga *et al.* (1997: 109) except for the maximum number of laterals per cell (4 in the West Coast plants, 1 in the East Coast plants). We compared the East Coast specimens with *C. flagelliformis* from the Cape Peninsula (voucher specimens of Leliaert *et al.* 2000). In these specimens the maximum number of laterals per cell varies from 2 to 4. The cell dimensions of the East Coast specimens fall within the limits of these of the West Coast plants (table 5).

References: Kützing [1853: 23, Tab. 77, fig. I (as *C. virgata*), fig. II (*C. flagelliformis*)]; Seagrief [1980: 21, fig. on pl. 1 (as *C. virgata*)]; Stegenga *et al.* (1997: 109, Pl. 20: 2; Colour Plate 26).

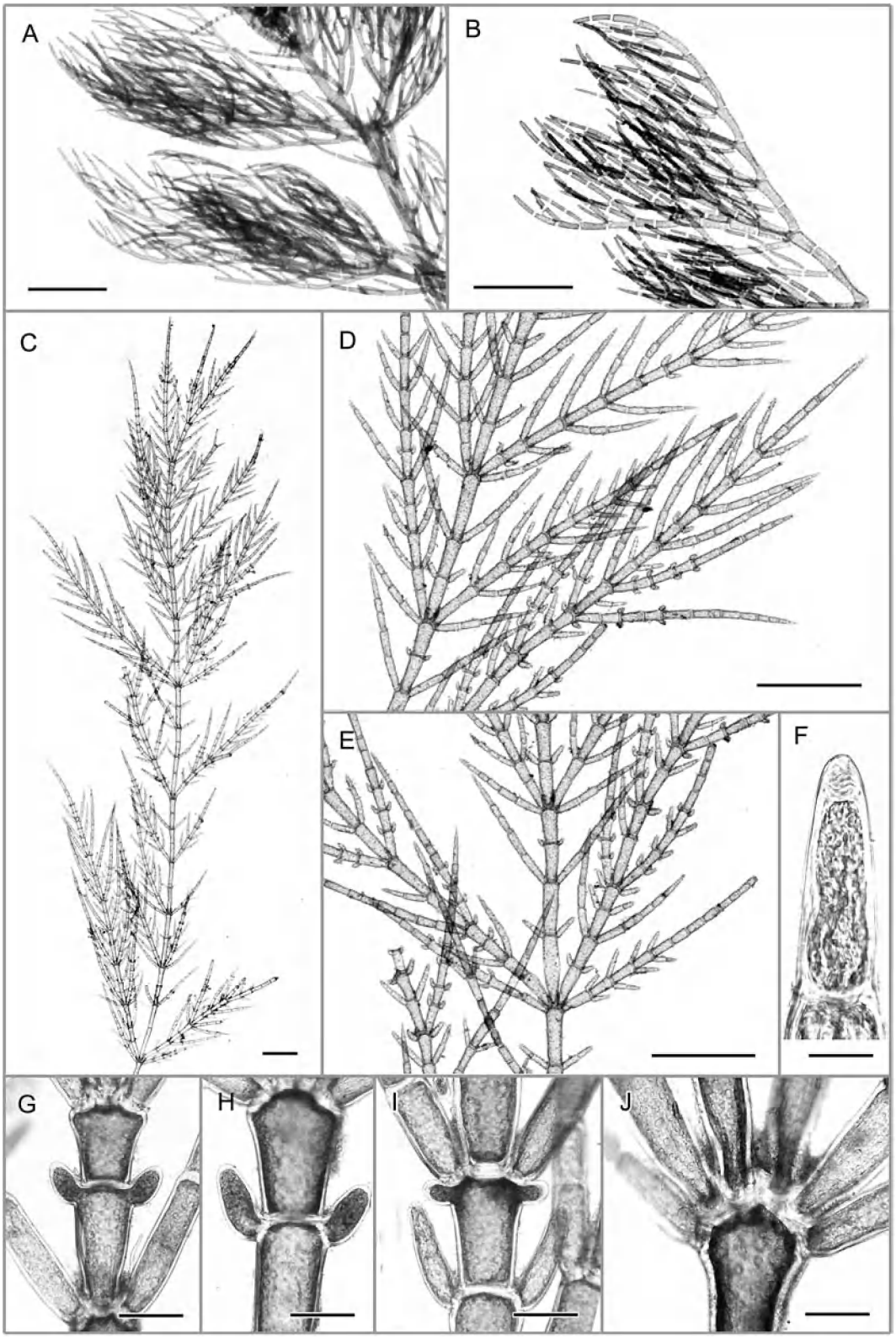


Fig. 14. A, B. *Cladophora vagabunda* (KZN 2152). A, B. Densely branched fasciculate terminal branch systems, scale bars = 1 mm; C-J. *Cladophora ordinata*. C-D. Main axes and terminal branch systems with opposite to flabellate branches (KZN 1927), scale bars = 1 mm; F. Apical cell (KZN 452), scale bar = 25 µm; G-J. Intercalary cell division and formation of flabellate branches (KZN 452), scale bars = 100 µm.

11. ***Cladophora vagabunda*** (Linnaeus) van den Hoek, 1963: 144 Figs 14A-B, 15

Conferva vagabunda Linnaeus, 1753: 1167

Lectotype locality: Selsey, Sussex, England [van den Hoek (1963: 19, 144) has indicated the material of *Conferva marina trichodes, lanae instar expansa* Dillenius, present in Dillenius's herbarium (OXF) as the type of *C. vagabunda*].

Description:
Thallus light green, forming lax tufts, 0.5 to 3 cm tall, composed of pseudodichotomously branching main axes ending in densely branched fasciculate terminal branch systems; attached to the substratum by basal branching rhizoids developing from the basal cells. Rhizoids also growing down from the proximal ends of the basal branches with which they partly coalesce. Growth in the terminal branch system by apical cell division; intercalary cell divisions starting at some distance from the apex; cells in basipetal direction becoming markedly longer and broader. Terminal branch systems distinctly acropetally organized, (refracto-) falcate. Each new cell, after being cut off from the apical cell and when arriving at the position of the 3rd cell under the apex, giving off one branch at its distal pole; at increasing distance from the apex a cell may give off a 2nd, 3rd and sometimes a 4th branch. Branches inserted at the apical cell pole by an oblique wall cutting it off from the parent cell; the position of the wall becoming nearly horizontal in older branches, resulting in pseudodichtotomously branching main axes. Angle of ramification ranging from 50°-90° (-140°) in the main axes to 25°-55° in the terminal branch systems. Apical cells cylindrical, with rounded tips or slightly tapering, diameter (35-) 45-55 µm, l/w ratio 3.5-8.5. Cells of terminal branch systems cylindrical, 50-160 µm in diameter, l/w ratio 2.5-5.5. Cells of the main axes cylindrical, 180-210 µm in diameter, l/w ratio 4-10.

Ecology: Epilithic, intertidal to subtidal (to 6 m deep).

Specimens examined: ¼ Mile Reef, Sodwana: KZN 2109 (10/02/2001), KZN 2152 (11/02/2001); Bhanga Nek: KZN 680 (15/08/1999).

Geographic distribution: *C. vagabunda* is a wide-spread and ubiquitous species in tropical to warm-temperate seas; along the East African coast it has been recorded from Somalia (Sartoni, l.c.), Kenya [Isaac 1968: 1 as *C. fascicularis* (Mertens ex C. Agardh) Kützing)], Tanzania (Jaasund 1976: 7, fig. 15, pl. 1 as *C. fascicularis*), and Mozambique (Coppejans *et al.* 2002). This is the first record for South Africa.

Note: Molecular analyses (DNA-DNA hybridisation and nuclear rDNA ITS sequences) have demonstrated that the morphological species *C. vagabunda*, occupying one huge continuous geographic area, represents at least four divergent lineages (Bot *et al.* 1990; Bakker *et al.* 1995b; van den Hoek & Chihara 2000). Depending on the interpretation of these molecular data, *C. vagabunda* can be seen as a single species or a cryptic species complex (multiple species). No African representatives were included in the molecular analyses.

References: Børgesen [1935: 24-27, fig. 12, pl. 4 (as *C. monumentalis* Børgesen); 1940: 34-35, fig. 10 (as *C. fascicularis* (Mertens ex C. Agardh) Kützing); 1946: 21-24, figs 8a,b, 9, 10 (as *C. fascicularis*)]; Jaasund [1976: 7, fig. 16 (as *C. mauritiana* Kützing); 7, fig. 15 (as *C. fascicularis*)]; Littler & Littler (2000: 324, fig. on p. 325); Schneider & Searles (1991: 74-76, figs 63-65); Sartoni (1992: 304, figs 6C, D, E); van den Hoek (1963: 144-148, pls 33, 36, 37, 39; 1982a: 137-138, figs 264-294), van den Hoek & Womersley (1984: 202-203, figs 64E, 65G); van den Hoek & Chihara (2000: 180-194, figs 76-79).

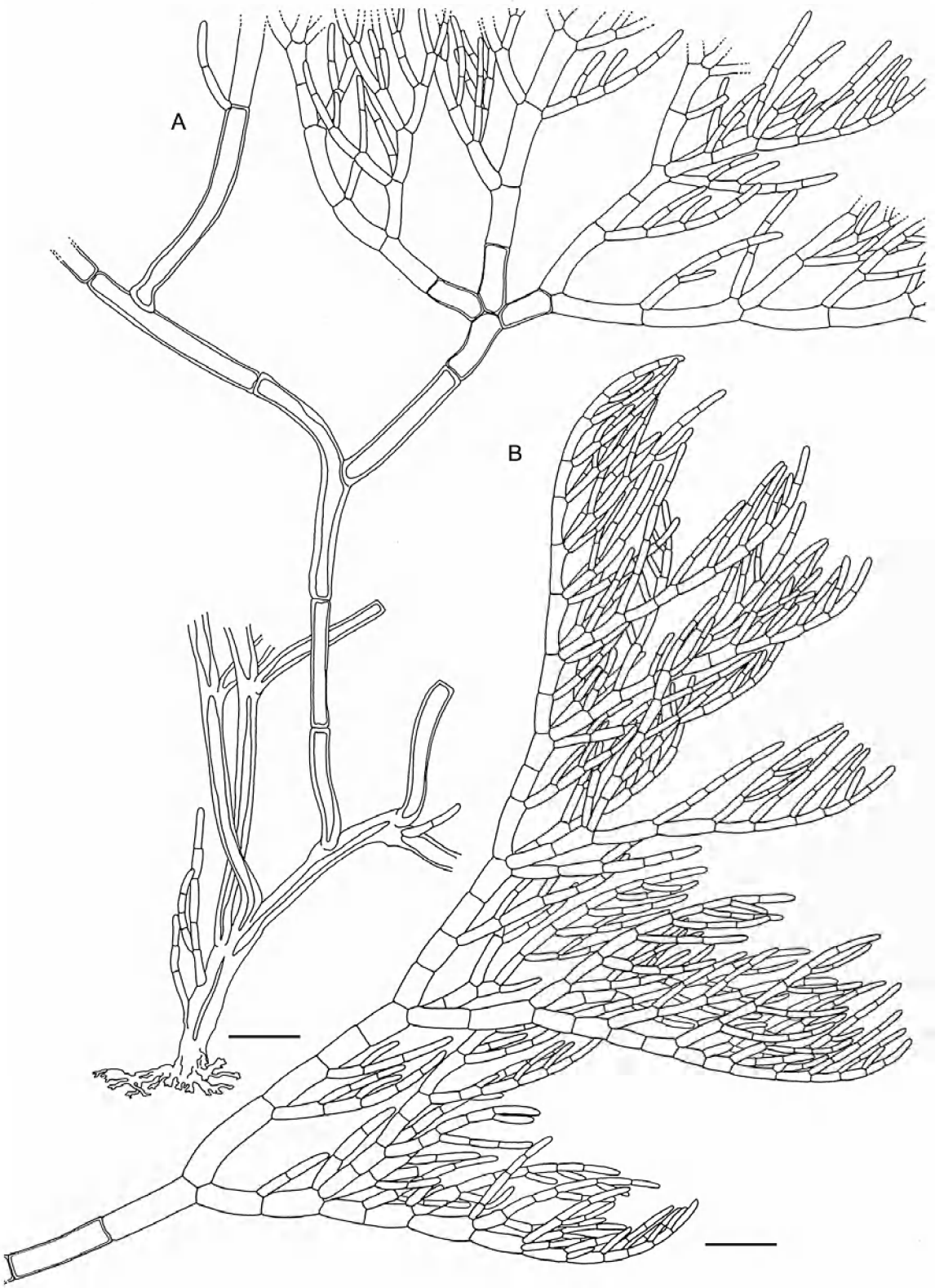


Fig. 15. *Cladophora vagabunda* (KZN 2152). A. Basal branches and rhizoidal holdfast; B. Terminal branch system. Scale bars = 500 µm.

Section *Willeella* (Børgesen) van den Hoek

12. ***Cladophora ordinata*** (Børgesen) van den Hoek, 1982a: 123-125, pl. 22: figs 235-237

Figs 14C-J, 16

Willeella ordinata Børgesen, 1930: 155-158, figs 3, 4a,b, pl. I: fig. 1

Type locality: Dwarka, Okha Port, India (leg. Børgesen, nr 5563, type in C).

Description:
Thallus dark to medium green, forming 4-8 cm high, bushy, fan-like tufts with distinct main axes; attached to the substratum by branching basal rhizoids developing from the proximal part of the basal cells. Growth by division of apical and intercalary cells; diameter and length of cells basipetally increasing (cells becoming extremely elongated and slightly decreasing in diameter in the basal parts of the thallus). Branch systems mainly acropetally organized; each new apically formed cell giving off a pair of opposite laterals, when arrived at the position of the 3rd to 8th cell from the apex. At increasing distance from the apex a cell may give off a second, and sometimes a third pair of opposite laterals in the same plane, resulting in flabellate branches. All branches typically lie in one plane; sometimes this plane is slightly spirally twisted. Angle of ramification (i.e. angle between the lateral and the main axis) ranging between 35°-45° in the opposite branches, 20°-65° in flabellate branches. Apical cells conical with a small obtuse tip and an apical thickening of the cell wall (27-) 30-45 µm in diam., l/w ratio 2-3.5; cell of the terminal branch systems cylindrical, 45-120 µm in diam., l/w ratio 1-3; main axes (70-) 110-175 µm in diam., l/w ratio 2-10; basal cells cylindrical to somewhat clavate, 75-120 µm in diam., l/w ratio 15-20. Cell walls in apical cells and ultimate filaments ca. 2-5 µm thick, increasing to 7-20 µm in main filaments, and up to 45 µm thick in basal cells.

Ecology: epilithic, intertidal rock pools to subtidal (to 37 m deep).

Specimens examined: Port Edward: FL 341, FL 342, FL 344: (24/03/1997); Palm Beach: KZN 816, KZN 869: (19/08/1999); Broken Reef, Trafalgar: KZN 959 (21/08/1999); Protea Banks, Shelly Beach: KZN 1927 (4/02/2001); Boboyi Reef, Shelly Beach: KZN 1973 (5/02/2001); Uvongo Reef, Shelly Beach: KZN 2002 (6/02/2001); Mabibi: KZN 452 (11/08/1999).

Geographic distribution: *C. ordinata* has a disjunct distribution pattern in the tropical to warm temperate Atlantic and Indo-Pacific Oceans. The species has been collected from India (type locality), South Africa (Papenfuss & Egerod 1957: 82-83), Ghana (Lawson & John 1987: 82, pl. 6, fig. 1), Venezuela (van den Hoek & Rios 1972), and Japan (van den Hoek & Chihara 2000: 219-224, figs 93, 94). The Somalian record (based on Sartoni 1992: 300-302, figs 5C-F) is most probably a misapplied name for *C. montagneana* Kützing.

Note: Van den Hoek (1982a) reduced Børgesen's genus *Willeella*, in which *C. ordinata* was first described, to a section of *Cladophora*. Other authors (Silva *et al.* 1996: 787) prefer to retain the name *Willeella* and await a new classification of the Cladophorales based on molecular data. Two other species have been described for *Willeella*: *W japonica* Yamada & Segawa and *W mexicana* Dawson. Van den Hoek (1982a) and van den Hoek & Chihara (2000) reduced the first species to a synonym of *C. ordinata*. *W mexicana* was reduced to a synonym of *Pseudostruvea robusta* (Setchell & Gardner) Egerod [= *Struveopsis robusta* (Setchell & Gardner) Rhyne & H. Robinson] by Egerod (1975: 47). The holotype of *P. robusta*, however, does not correspond with its original illustration, and is instead referable to *Valoniopsis pachynema* (G. Martens) Børgesen (see discussion of *Cladophoropsis mexicana* in chapter 5).

References: Børgesen [1934: 17, fig. 3 (as *Willeella ordinata*)]; Lawson & John (1987: 82, pl. 6, fig. 1); Sartoni (1992: 300-302, figs 5C-F); Segawa [1938: 133-135, fig. 2, pl. 33,1 (as *Willeella japonica* Yamada & Segawa)]; van den Hoek (1982a: 123-125, figs 231-237); van den Hoek & Chihara 2000: 219-224, figs 93, 94.

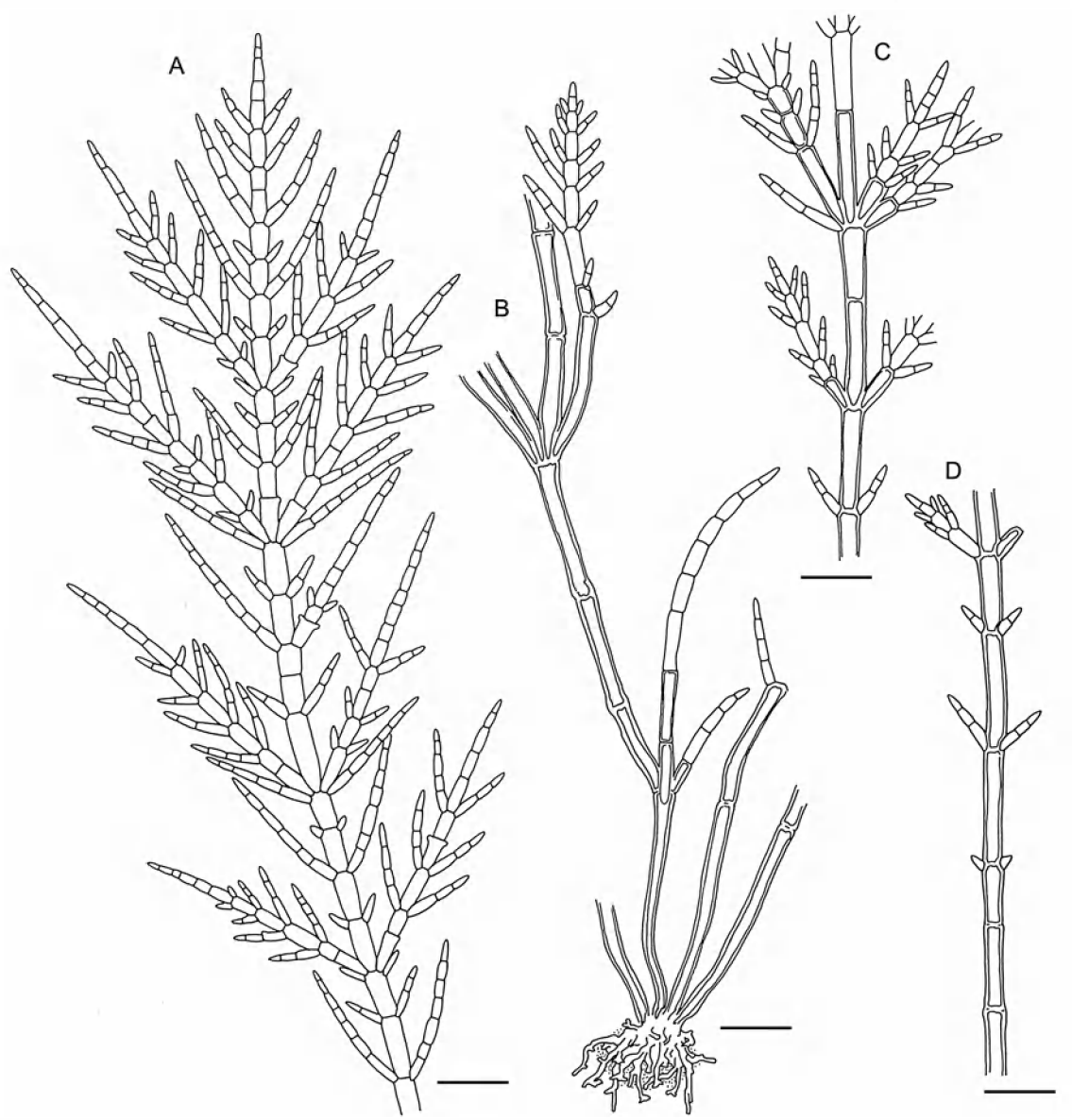


Fig. 16. *Cladophora ordinata* (KZN 2002). A. Terminal branch system; B. Basal filaments and rhizoidal holdfast; C, D. Main filaments with flabellate branching young laterals. Scale bars = 500 µm.

Key to the species of *Cladophora* from the South African East Coast

1.a. Thallus forming cushion-like mats, composed of interwoven filaments; attached to the substratum at several places 2
1.b. Thallus forming erect tufts, attached to the substratum at a single point 5

2.a. Filaments short-celled (l/w ratio of the apical cells 2-5), anastomosing with one another to form compact, three-dimensional netlike cushions ..... *C. liebetruthii*
2.b. Filaments long-celled (l/w ratio of the apical cells 5-40), loosely entangled with one another (infrequently anastomosing) 3

3.a. Thallus attached to the substratum by terminal hapteroid structures on the apical cells of decumbent axes; apical cell diameter larger than 250 µm ..... *C. catenata*
3.b. Thallus attached to the substratum by rhizoids developing from the proximal poles of the stolon-like filaments; apical cell diameter smaller than 100 µm 4

4.a. Apical cell diameter 57-75 µm ..... *C. coelothrix*
4.b. Apical cell diameter 25-50 µm ..... *C. socialis*

5.a. Thallus attached to the substratum by a conspicuous basal stipe, composed of one or two cells which are much longer than the apical cells (stipe-cells generally longer than 3 mm) 6
5.b. Thallus lacking a conspicuous stipe, or if present composed of entangling rhizoids 8

6.a. Stipe cell and cells of the main axes with conspicuous annular constrictions at their proximal parts ..... *C. rugulosa*
6.b. Stipe cell and cells of the main axes lacking annular constrictions 7

7.a. Cells of the main axes clavate, often curved, with a distinct basal bulge; apical cell diameter 250-290 µm ..... *C. dotyana*
7.b. Cells of the main axes subcylindrical, straight; apical cell diameter 80-125 µm ..... *C.* sp.

8.a. Cells in the basal part of the thallus each giving off one rhizoid at their proximal pole 9
8.b. Rhizoids only developing from the proximal end of the basal cell 10

9.a. Rhizoids with annular constrictions, growing down and entangling along the cells below, forming a conspicuous stipe that attaches to the substratum ..... *C. prolifera*
9.b. Rhizoids lacking annular constictions, growing along and into the cell walls of the cells below; basal branches becoming completely covered by and the cell walls fused with these rhizoids ..... *C. horii*

10.a. Branches restricted to the basal part of the thallus, the distal part of the thallus unbranched and flagelliform ..... *C. flagelliformis*
10.b. Terminal branch systems densely branched 11

11.a. Thallus with pseudodichotomous main axes, ending in acropetal, often falcate terminal branch systems ..... *C. vagabunda*
11.b. Erect thalli fan-like, composed of opposite to flabellate branches, developing in one plane ..... *C. ordinata*

Discussion

The Cladophorophyceae are believed to be an originally tropical group with members (including a large number of *Cladophora* species) that succesfully invaded the warm-temperate and even cold-temperate regions (Bakker *et al.* 1994; van den Hoek & Chihara 2000). However the tropical representatives of *Cladophora* remain largely unstudied. In the tropical Western Indian Ocean limited studies of the genus *Cladophora* are restricted to the publications of Sartoni (1986, 1992; Somalia), Jaasund (1976; Tanzania) and Børgesen (1940, 1946, 1948; Mauritius).

Seven distribution groups of the genus *Cladophora* have been distinguished, based on the species' northern and southern boundaries in combination with winter and summer isotherms of the sea surface (van den Hoek 1979, 1982a; van den Hoek & Chihara 2000). The 11 species identified along the South African East Coast fall into three biogeographical categories: two species belong to the strictly tropical distribution group and have their southernmost boundary in northern KwaZulu-Natal (*C. catenata* and *C. horii*), eight species belong to the tropical to warm temperate distribution group, and *C. rugulosa* that was previously regarded as a synonym of *C. prolifera*, seems to be restricted to the South and East Coast of South Africa. Two species are reported for the first time in the Indian Ocean (*C. dotyana* and *C. horii*) and three others are recorded for the first time in South Africa (*C. catenata*, *C. liebetruthii* and *C. vagabunda*).

The genus *Cladophora* is a heterogeneous assemblage of species. Based on morphological characters, van den Hoek (1982a) demonstrated that the genus does not conform to the requirement that the species contained in the genus are mutually more related than with species in other genera. Some species of *Cladophora* share typical characters with other genera within the Cladophorophyceae and, as a consequence, can easily be confused with them. *C. coelothrix*, *C. socialis* and *C. catenata* are characterized by delayed cross wall formation and the presence

of rhizoidal or hapteroidal structures, characters that typify the genus *Cladophoropsis*. *C. liebetruthii* shares common characters with the genus *Microdictyon*: anastomosis of filaments to form net-like thalli, rhizoids developing from the basal poles of the cells (van den Hoek 1982a, Kraft 2000). Molecular data based on SSU rRNA (Bakker *et al.* 1994; Hanyuda *et al.* 2002) and partial LSU rRNA (chapter 3) confirm the close relationship of some *Cladophora* species with other genera in the Cladophorophyceae.

Acknowledgements

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Chapter 3

Phylogeny of the Cladophorophyceae inferred from partial LSU rRNA gene sequences: is the recognition of a separate order Siphonocladales justified?

Adapted from: Frederik Leliaert, Florence Rousseau, Bruno de Reviers* & Eric Coppejans. 2003. Phylogeny of the Cladophorophyceae (Chlorophyta) inferred from partial LSU rRNA gene sequences: is the recognition of a separate order Siphonocladales justified? European Journal of Phycology 38: 233-246.*

Abstract – Phylogenetic relationships within the green algal class Cladophorophyceae were investigated. For 37 species, representing 18 genera, the sequences of the 5'-end of the large subunit rRNA were aligned and analysed. *Ulva fasciata* and *Acrosiphonia spinescens* (Ulvophyceae) were used as outgroup taxa. The final alignment consisted of 644 positions containing 208 parsimony-informative sites. The analysis showed three lineages within the Cladophorophyceae: *Cladophora horii* diverged first, followed by two main lineages. The first lineage includes some *Cladophora* species and genera with a reduced thallus architecture. The second lineage comprises siphonocladalean taxa (excluding part of *Cladophoropsis* and including some *Cladophora* species). From this perspective the Siphonocladales form a monophyletic group, the Cladophorales remaining paraphyletic.

Introduction

The Cladophorophyceae nom. nud. (van den Hoek *et al.*, 1995), including about 32 genera, comprise a mainly marine class of siphonocladous Chlorophyta with a tropical to cold-water distribution. Thallus organization in the class ranges from branched or unbranched uniseriate filaments to more complex architectural types such as (pseudo)parenchymatic thalli, thalli composed of inflated cells, stipitate plants, blade-like thalli, and reticulate plants composed of anastomosing filaments. Anastomosis of neighboring cells is accomplished by four types of tenacular cells (Olsen-Stojkovich, 1986): (1) unspecialized cells with crenulate or annulate apices; (2) minute hapteroid cells formed laterally between adjacent vesicular cells; (3) minute hapteroid cells formed at the the distal ends of branches and anastomosing to neighboring filaments; (4) minute hapteroid cells formed intracellularly between septa. In some *Cladophora* species neighboring cells occasionally adhere by means of rhizoids sprouting from the basal poles of the cells. Cells in the Cladophorophyceae devide by four modes of cell division (Olsen-Stojkovich, 1986): (1) centripetal invagination (CI): new cross walls formed by centripetal invagination of a primordial septum (Enomoto & Hirose 1971); (2) lenticular cell type (LC): a convex septal disk formed along the cell-wall followed by elongation of a new lateral; (3) segregative cell division sensu stricto (SDSS): multinucleate aggregates of cytoplasm spontaneously form walled spheres that remain in the parent cell, expand and rupture old parental cell-walls; (4) modified segregative cell division (SDM): cytoplasmic spheres are released from the parent cell and grow into new thalli.

The classification of the Cladophorophyceae has been a matter of much confusion and disagreement. The genera presently included have traditionally been placed either in the single order Siphonocladales or in two separate orders, Siphonocladales and Cladophorales. The earliest circumscriptions of the two orders were very vague. The Siphonocladales (type:

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Siphonocladus Schmitz) were created by Oltmanns (1904) to accommodate a rather heterogeneous assemblage of green algae with multinucleate cells. The order was later redefined by Børgesen (1913, 1925), Feldmann (1938*a*, 1938*b*), Egerod (1952) and Jónsson (1962, 1965). The Cladophorales (type: *Cladophora* Kützing) was described by Haeckel (1894) to include green algae with multinucleate cells, lacking oogonia, and its circumscription modified by West (1904), Fritsch (1935, 1947) and Papenfuss (1955). The rationale for placing all genera in a single order, Siphonocladales *sensu lato* (Børgesen, 1913, 1925; Feldmann, 1938*b*; Jónsson, 1962, 1965) was the apparent homogeneity of thallus organization, chloroplast morphology and cell wall structure in the group. The separation of the group into the Siphonocladales and the Cladophorales (Børgesen, 1948; Egerod, 1952; Papenfuss, 1955; Womersley, 1984; Bold & Wynne, 1985; Sartoni, 1992) was primarily based on differences in thallus complexity: the Cladophorales s.s. comprised taxa with a relatively simple thallus architecture and included *Cladophora* (branched uniseriate filaments), *Chaetomorpha* and *Rhizoclonium* (unbranched uniseriate filaments); the Siphonocladales s.s. contained taxa with a more complex morphology. Some authors (Børgesen, 1913; Egerod, 1952) considered segregative cell division to be a principal ordinal character, although they realized that this character does not occur in all genera of the Siphonocladales. We refer to Egerod (1952), Jónsson (1962) and Olsen-Stojkovich (1986) for a more detailed taxonomic history of this complex.

Four families (Anadyomenaceae, Cladophoraceae, Siphonocladaceae and Valoniaceae) are traditionally recognized within the Cladophorophyceae, based on thallus architecture and mode of cell division. Børgesen (1925) recognized a fifth family, Boodleaceae. The boundaries of the families are rather vague and the included genera have changed frequently in the course of time. We refer to Feldmann (1938*b*), Egerod (1952) and Olsen-Stojkovich (1986) for the circumscriptions and taxonomic history of the families.

Within *Cladophora*, the largest genus of the class, 11 different architectural types can be distinguished, representing the sections of *Cladophora* as conceived by van den Hoek (1963, 1982a) and van den Hoek & Chihara (2000). Based on comparison of morphology, van den Hoek (1981, 1982a, 1984) hypothesized that numerous reduction and specialization events have occured independently several times in *Cladophora* sections, resulting in the various reduced (cladophoralean) and specialized (siphonocladalean) morphologies. These reductions and specializations were circumscribed in eight morphological tendencies (1) planification of thallus (formation of blades), (2) interweaving of filaments by tenacular cells to strengthen thallus, (3) lateral coalescence of cells to strengthen blades, (4) replacement of successive initiation of laterals by simultaneous lateral formation, (5) increase of number of laterals per cell, (6) inflation of cells, (7) differentiation between axis and laterals, and (8) reduction of branching. Van den Hoek (l.c.) considered therefore that it would be incorrect to range the simpler genera (*Cladophora*, *Rhizoclonium*, *Chaetomorpha*) in one order, Cladophorales, and genera with a more complicated architecture in an other order, Siphonocladales. The first molecular evidence supporting van den Hoek's hypothesis was based on immunological distances (Olsen-Stojkovich, 1986) and single-copy DNA-DNA hybridization studies (Bot, 1992). Later, Bakker *et al.* (1994) demonstrated, on the basis of 18S rRNA sequences of 20 species, that neither the Cladophorales nor the Siphonocladales forms a monophyletic group and that there is no basis for the independent recognition of both orders. The 18S rRNA phylogeny supports two lineages, one containing predominantly tropical members including almost all siphonocladalean taxa, the other consisting of mostly warm- to cold-temperate species of *Cladophora*. Hanyuda *et al.* (2002) extended Bakker's phylogeny with 18S rRNA sequences of 21 additional species, including some freshwater representatives of the class. This analysis reveals a new sister clade of the two main lineages (termed the "*Aegagropila*-clade"), which comprises a mixture of marine and freshwater genera with a simple, *Cladophora*-type architecture. The general

consensus today is the recognition of a single order Cladophorales (the choice of name being based on priority) in the class Cladophorophyceae (van den Hoek *et al.*, 1995; van den Hoek & Chihara, 2000).

This study extends the phylogenies of Bakker *et al.* (1994) and Hanyuda *et al.* (2002), mainly with representatives of species traditionally ascribed to the Siphonocladales s.s. including 37 species in 18 genera. The genus *Cladophora* is represented by 10 species, belonging to six sections. The goals of this study are (1) to compare partial LSU rRNA sequences with the previously published SSU rRNA phylogenies [the LSU is known to be more variable than the SSU (Hassouna *et al.*, 1984; Michot *et al.*, 1984; Rousseau *et al.*, 1997, 2001) and its phylogenetic potential at different taxonomic levels in plants has been demonstrated by Kuzoff *et al.* (1998)]; (2) to test van den Hoek's (1984) hypothesis that different genera with complex and simplified thallus architectures represent further specializations of the basic architectural types of *Cladophora*, and that these specialization and reduction events happened several times independently; (3) examine whether the recognition of a single order Cladophorales is justified and (4) test the taxonomic significance of morphological characters that were considered to be important in the delineation of the two orders and the different families in the group.

Material and methods

The specimens used in this study are listed in Table 1. The collected samples were desiccated in silica gel according to Chase & Hills (1991); parts of the same thallus were processed as herbarium specimens and deposited in GENT; for some species, only dried herbarium specimens were available. Although *Boodlea siamensis* is generally regarded as a taxonomic synonym of *B. composita* (Børgesen, 1946: 16), it is treated as a separate entity in this study, based on differences in branching pattern. Morphological characters and their states were collected from specimens also included in the molecular study to permit direct comparison.

DNA was extracted using the DNeasy Plant Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. PCR amplifications were performed in a Biomed thermocycler with an initial denaturation step of 94°C for 3 min followed by 35 cycles of 30 s at 94°C, 30 s at 53°C, and 30 s at 72°C, with a final extension step of 3 min at 72°C. The reaction volume was 50 µl and comprised about 0.3 µg genomic DNA, 2 nmol of each dNTP, 30 pM of each primer, 31 µl H_2O, 5 µl of 10x reaction buffer, 5 mM $MgCl_2$, 10 µg BSA, 5 µl dimethylsulphoxide (DMSO), and three units of TAQ polymerase (Goldstar). The approximately 550-nucleotide fragment was amplified using the universal primers C'1 and D2 at positions 25 and 1126 of the complete *Mus musculus* 28S rDNA (Hassouna *et al.*, 1984). For some specimens an additional universal primer C'2B at position 383 of the complete mouse 28S rDNA had to be used. Nucleotide sequences of the primers are

C'1	forward	(5'-ACCCGCTGAATTTAAGCATAT-3')
D2	reverse	(5'-TCCGTGTTTCAAGACGG-3')
C'2B	forward	(5'-GAGTCGGGTYGYTTGGGAATGCA-3').

The amplified fragment includes the conserved zones C1 (partial) and C2 and the variable zones D1 and D2 (Michot *et al.*, 1984), and comprises about 550 bp. Amplifications were checked for correct length, purity and yield on 1.5% agarose gels and stained with EtBr. Excess primers and nucleotides were removed from PCR products using MnElute (Qiagen) according to the manufacturer's instructions. About 100 fm of PCR product was used for the sequencing reaction. Both strands of the PCR products were directly sequenced with the PCR primers using the CEQ Cycle Sequencing Kit (Beckman) in the CEQ-2000 DNA Analysis System (Beckman).

The final consensus sequences was constructed by means of Sequencher 4.0.5 software (Gene Codes Corporation, Ann Arbor, USA).

Alignment of rRNA sequences taking into account the secondary structure are available on the web site http://oberon.rug.ac.be:8080/rRNA/ for LSU sequences (Wuyts *et al.*, 2001). The chlorophycean sequences provided in this database were used as a model for building our alignment. Alignment of the highly variable D2 region was aided by constructing the secondary structure of each sample by using the MFOLD software available at http://www.bioinfo.math.rpi.edu (Zuker *et al.*, 1999; Mathews *et al.*, 1999). The different optimal and suboptimal secondary structures for each species were compared. Compensatory mutations were examined in order to confirm the homologous stem and loop regions, and the sequences were aligned accordingly using the software DCSE v 2.60 (Dedicated Comparative Sequence Editor) (De Rijk & De Wachter, 1993) (Figs 1, 2). The underlying principles of using secondary structure models for aligning rRNA sequences have been discussed by Kjer (1995).

The distribution of phylogenetic signal in the data set was explored by comparing the pairwise sequence divergence (minimum, maximum and average), the number of parsimony-informative sites in the four regions C1, D1, C2 and D2 (Table 2), and by plotting inferred character changes for each alignment position (Fig. 3). All calculations were done after exclusion of sites with ambiguous alignment. Measure of skewness (g_1-vallue calculated by using 10,000 randomly selected trees in PAUP*) was compared with the empirical threshold values in Hillis & Huelsenbeck (1992) to verify for nonrandom structuring of the data.

All phylogenetic analyses were performed using PAUP 4.0* beta test version 10 (Swofford, 2002). *Ulva fasciata* and *Acrosiphonia spinescens* were used as outgroup taxa. Gaps were taken into account as missing characters in all analyses. Maximum parsimony (MP) analyses were carried out using a general heuristic search, with 100 random sequence additions, TBR swapping and MULTREES options; branches were collapsed if it was possible for them to have zero length.

Substitution rates were compared through relative rate tests using the program RRTree (Robinson-Rechavi & Huchon, 2000) (Table 3). The choice of taxa was based on the MP strict consensus phylogram which showed considerable variation in branch lenght within certain clades (Fig. 4). A first test was performed using all taxa within clade A4 (between *Cladophora rupestris*, the *Chaetomorpha spiralis*-clade and the *Cladophora vagabunda*-clade), using clade A3 as outgroup. A second test compared all taxa of the clades B4, B5 and B6, using clade B3 as outgroup. The program MODELTEST version 3.04 (Posada & Crandall, 1998) was used to find the model of sequence evolution that best fits the data set by a hierarchical likelihood ratio test (LRT) ($\alpha = 0.05$) or the Akaike Information Criterion (minimum theoretical information criterion, AIC). Models were estimated for complete and partial datasets (Table 4). Various preliminary ML analyses indicated that trees were strongly affected by the model chosen. For example ML trees generated by using the more complex models selected by MODELTEST for the complete dataset (TrNef+G, TIMef+I+G and GTR+I+G) differed from the MP trees by failing to recover lineage A. Given that various models were calculated for the different partial datasets (e.g. different models for lineages A and B) (Table 4) and since there were changes in the subsitution rates between lineages (Table 3), it would have been unlikely that the model estimated for the complete dataset would be correct for all sequences in this datatset. Therefore the ML analysis was carried out using the simplest model, a Jukes-Cantor model, as recommended by Takahashi & Nei (2000) and McIvor *et al.* (2002).

Bootstrapping (Felsenstein, 1985) was performed in PAUP* using 1000 replicates for MP the analysis, and 250 replicates for the ML analysis. Decay analysis of MP trees was performed with AutoDecay version 4.0 (Eriksson, 1998).

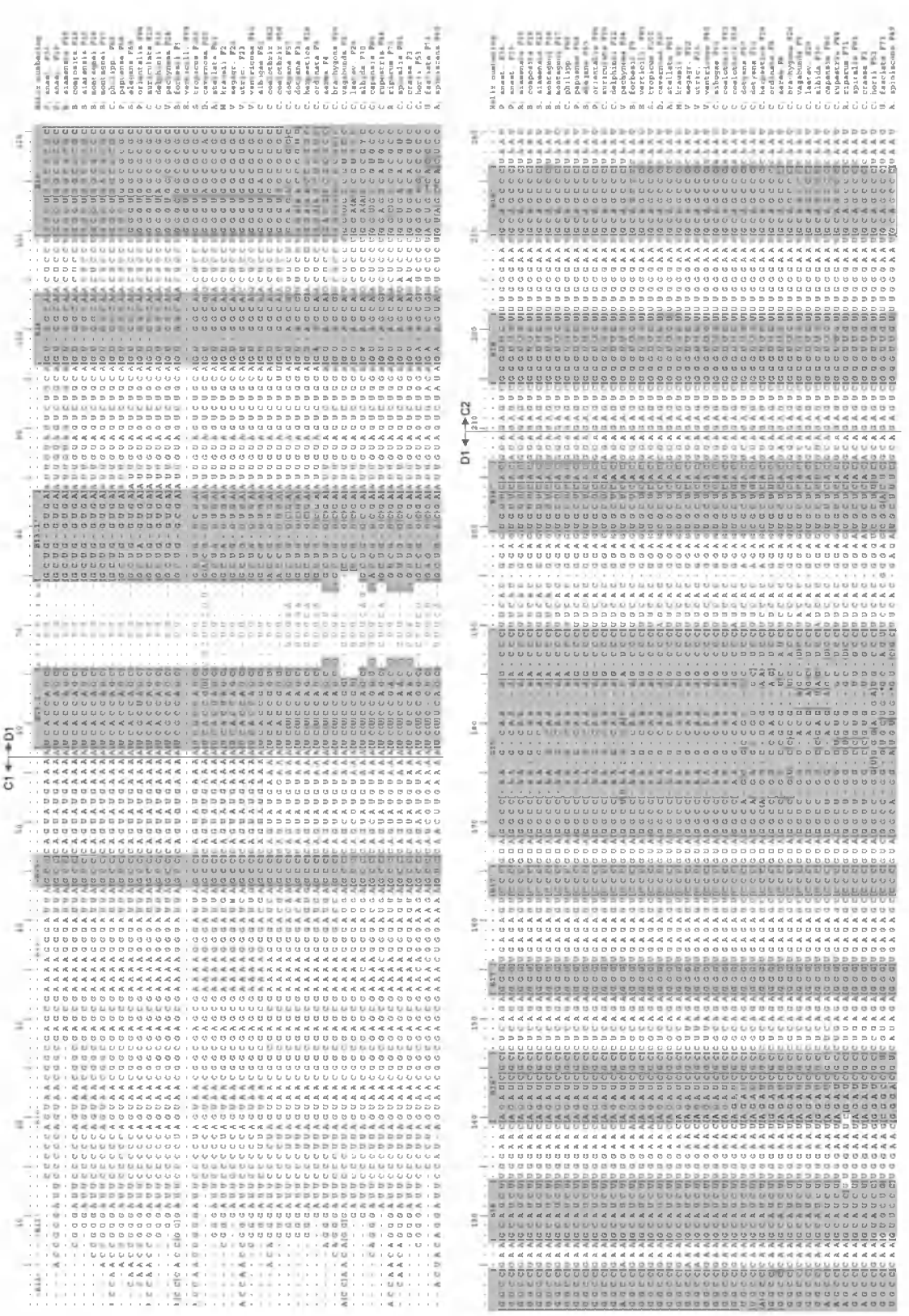
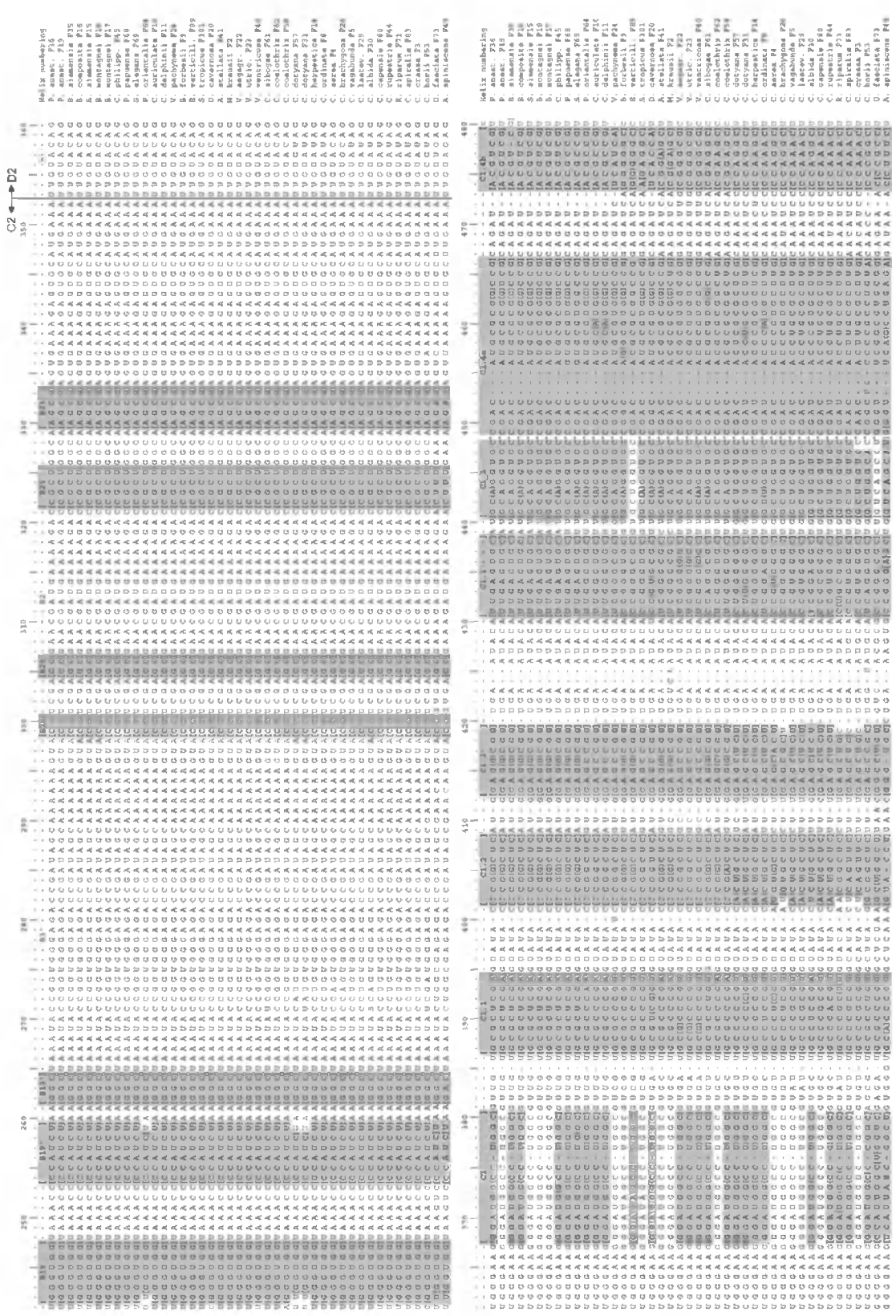


Fig. 1. Partial LSU rRNA gene sequence alignment of the Cladophorophyceae taxa with *Ulva fasciata* and *Acrosiphonia spiniscens*. Numbering of the alignment positions is indicated on top of the alignment blocks. Conserved stem regions are indicated in grey background; helix numbering according to De Rijk *et al*. (1998) and Wuyts *et al*. (2001). Positions with ambivalent alignment, omitted from the analysis, are in grey symbols. Indication of the conserved zones (C1, C2) and variable zones (D1, D2) according to Michot *et al*. (1984). Note that "C1" is both the first conserved zone of the LSU (Michot *et al*. 1984) and a conserved stem region in the D2 zone (De Rijk *et al*. 1998). See also Fig. 2.



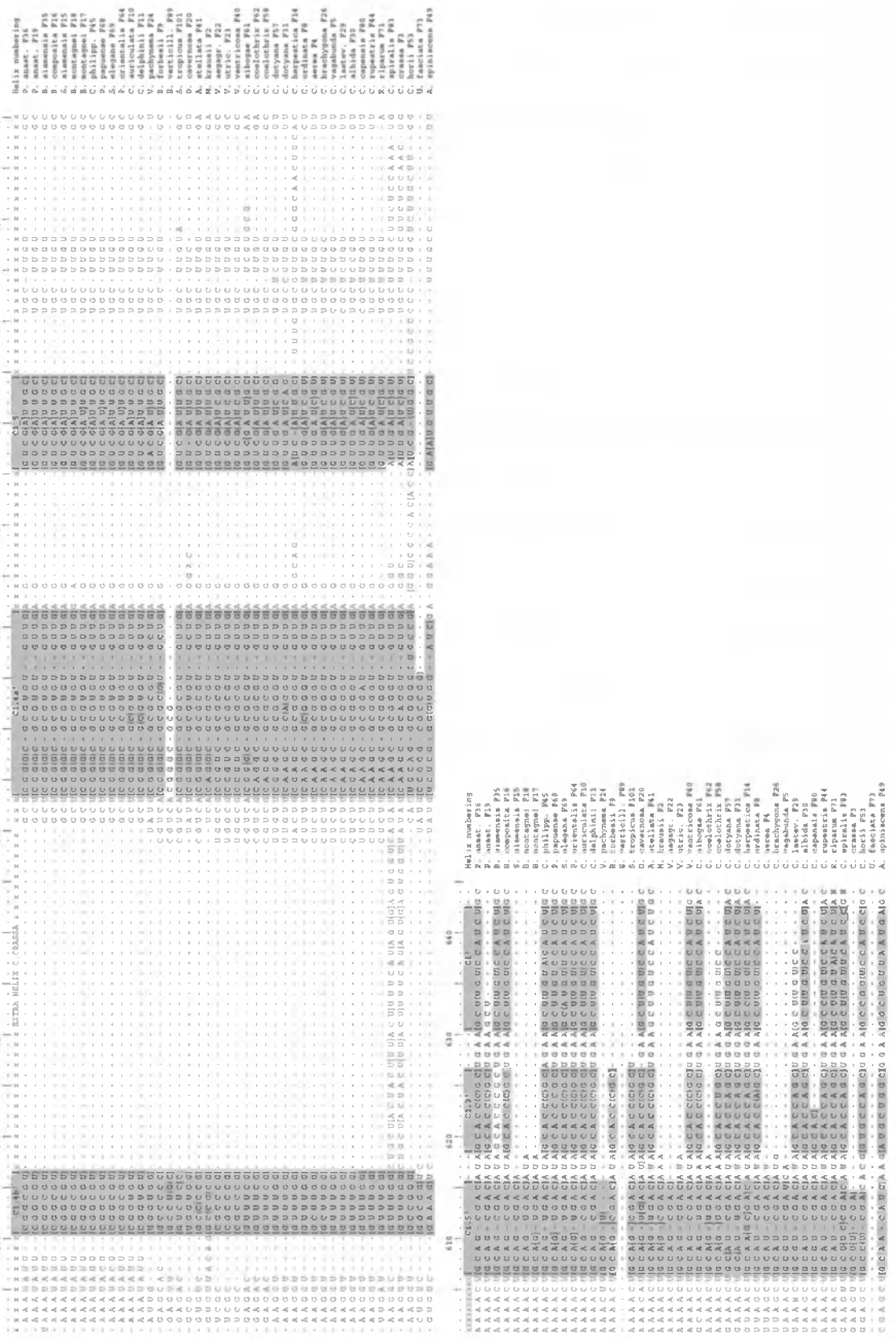


Fig. 1. (continued).

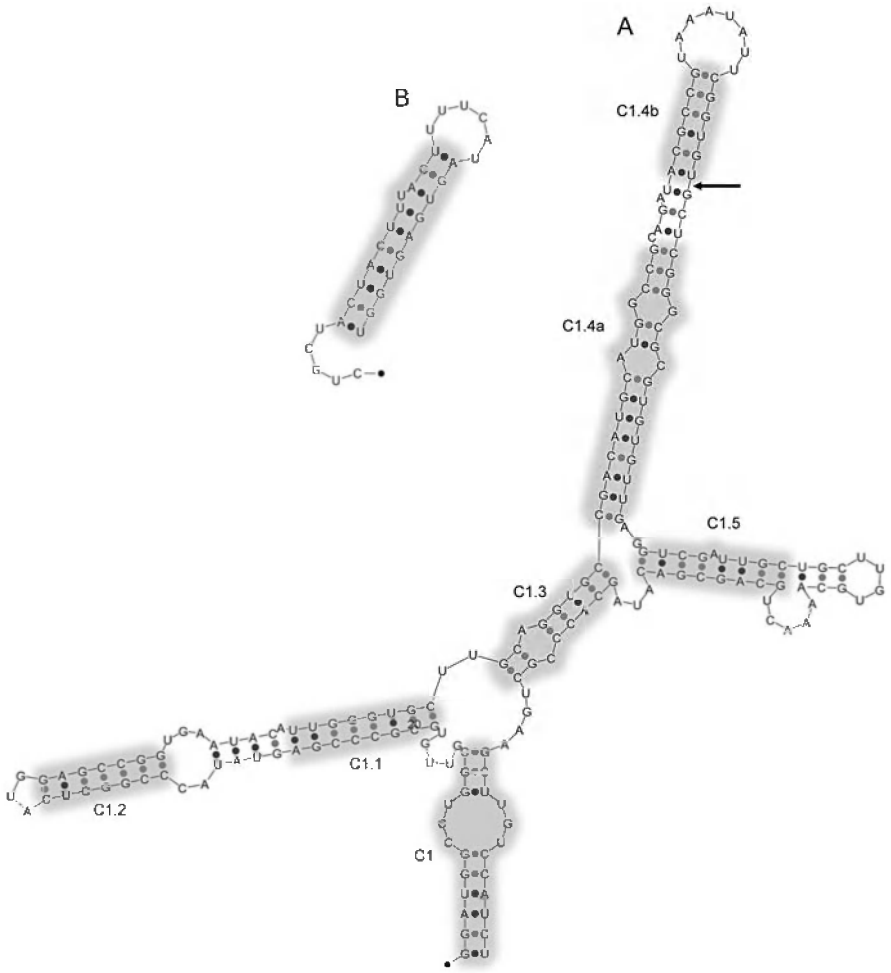


Fig. 2. A. Secondary structure model of the D2 region of *Chamaedoris auriculata* (F10) presented in a two-dimensional format (dG= –86.73 kcal/mole), constructed with MFOLD (Zuker *et al.*, 1999). Indication of conserved helix regions for all ingroup taxa in grey shadows with corresponding numbering according to Wuyts *et al.* (2001). Arrow indicating insert of extra helix found in *Chaetomorpha crassa* (F3) and *C. spiralis* (F83): illustrated in **B**.

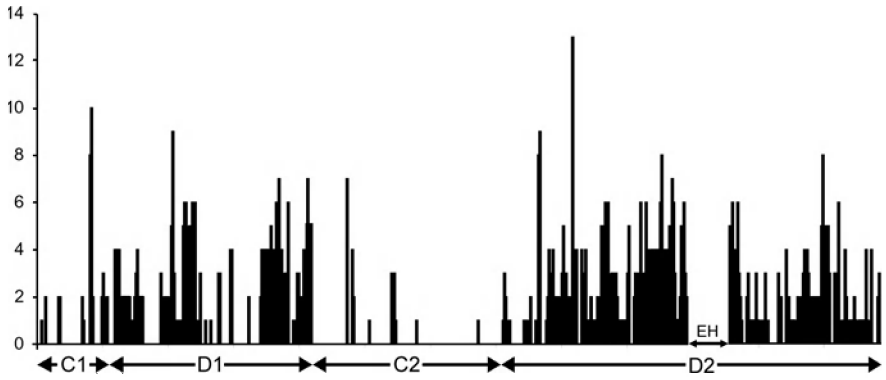


Fig. 3. Histogram showing inferred character changes for each alignment position (analysis with ingroup taxa only). Indication of conserved (C1, C2) and divergent (D1, D2) zones according to Michot *et al.* (1984). EH = extra helix found in *Chaetomorpha crassa* and *C. spiralis*.

Table 1. Specimens used in the phylogenetic analysis with their collecting sites, herbarium number (Voucher), number used in this study (No.), location and EMBL accession numbers.

Species	Voucher	No.	Location	EMBL acc. no.
Anadyomene stellata (Wulfen) C. Agardh	PH 209	F41	Cebu, Philippines	AJ544746
Boergesenia forbesii (Harvey) J. Feldmann	FL 1009	F09	Zanzibar, Tanzania	AJ544742
Boodlea composita (Harvey) Brand	FL 950	F16	Zanzibar, Tanzania	AJ544731
Boodlea montagnei (Harvey ex J. Gray) Egerod	PH 646	F17	Mactan Island, Philippines	AJ544734
Boodlea montagnei (Harvey ex J. Gray) Egerod	FL 958	F18	Zanzibar, Tanzania	AJ544733
Boodlea siamensis Reinbold	FL 999	F35	Zanzibar, Tanzania	AJ544730
Chaetomorpha aerea (Dillwyn) Kützing	FL 998	F04	Zanzibar, Tanzania	AJ544758
Chaetomorpha brachygona Harvey	FL 982	F26	Zanzibar, Tanzania	AJ544759
Chaetomorpha crassa (C. Agardh) Kützing	FL 908	F03	Zanzibar, Tanzania	AJ544767
Chaetomorpha spiralis Okamura	HEC 11621	F83	Weligama, S-coast of Sri Lanka	AJ544766
Chamaedoris auriculata Børgesen	SOC 395	F10	Bidhola, S-coast of Socotra	AJ544739
Chamaedoris delphinii (Hariot) Feldmann & Børgesen	KZN 2110	F11	KwaZulu-Natal, South Africa	AJ544740
Cladophora capensis (C. Agardh) De Toni	HEC 10900	F80	Cape Peninsula, South Africa	AJ544763
Cladophora coelothrix Kützing	HEC 9394	F58	Mombasa, Kenya	AJ544754
Cladophora coelothrix Kützing	HEC 7418	F62	Malindi, Kenya	AJ544753
Cladophora dotyana Gilbert	HEC 12336	F57	Bulusan, Philippines	AJ544755
Cladophora dotyana Gilbert	KZN 2003	F31	KwaZulu-Natal, South Africa	AJ544756
Cladophora horii van den Hoek & Chihara	HEC 10983	F53	KwaZulu-Natal, South Africa	AJ544728
Cladophora laetevirens (Dillwyn) Kützing	FL 997	F29	Zanzibar, Tanzania	AJ544761
Cladophora montagneana Kützing	FL 900	F30	Zanzibar, Tanzania	AJ544762
Cladophora ordinata (Børgesen) van den Hoek	KZN 2002	F08	KwaZulu-Natal, South Africa	AJ544757
Cladophora rupestris (Linnaeus) Kützing	WIM 01	F44	Boulonais, France	AJ544764
Cladophora sibogae Reinbold	ODC 352	F61	Zanzibar, Tanzania	AJ544752
Cladophora vagabunda (Linnaeus) van den Hoek	FL 1001	F05	Zanzibar, Tanzania	AJ544760
Cladophoropsis herpestica (Montagne) Howe	FL 909	F14	Zanzibar, Tanzania	AJ544751
Cladophoropsis philippinensis Taylor	PH 567	F45	Cebu, Philippines	AJ544735
Dictyosphaeria cavernosa (Forsskål) Børgesen	FL 913	F20	Zanzibar, Tanzania	AJ544745
Ernodesmis verticillata (Kützing) Børgesen	WF 23-3-99	F89	Limon, Costa Rica	AJ544743
Microdictyon kraussii J. Gray	KZN 0272	F02	KwaZulu-Natal, South Africa	AJ544747
Phyllodictyon anastomosans (Harvey) Kraft & Wynne	FL 959	F19	Zanzibar, Tanzania	AJ544729
Phyllodictyon anastomosans (Harvey) Kraft & Wynne	FL 961	F36	Zanzibar, Tanzania	AJ544725
Phyllodictyon orientale (A. Gepp & E. Gepp) Kraft & Wynne	HEC 6173	F64	Bi Ya Doo Island, Maldives	AJ544738
Phyllodictyon papuense nom. prov.	HEC 4548	F68	Madang Prov., Papua New Guinea	AJ544736
Rhizoclonium riparium var *implexum* (Dillwyn) Rosenvinge	HEC 9623	F71	Bretange, France	AJ544765
Siphonocladus tropicus (P. Crouan & H. Crouan) J. Agardh	Dargent s.n.	F101	Dominican Republic	AJ544744
Struvea elegans Børgesen	HEC 10437	F69	Port Moresby, Papua New Guinea	AJ544737
Struveopsis siamensis (Egerod) P. Silva	FL 916	F15	Zanzibar, Tanzania	AJ544732
Valonia aegagropila C. Agardh	FL 960	F22	Zanzibar, Tanzania	AJ544748
Valonia utricularis (Roth) C. Agardh	FL 922	F23	Zanzibar, Tanzania	AJ544749
Valoniopsis pachynema (G. Martens) Børgesen	FL 1006	F24	Zanzibar, Tanzania	AJ544741
Ventricaria ventricosa (J. Agardh) Olsen & J. West	FL 952	F40	Zanzibar, Tanzania	AJ544750
Outgroup taxa				
Ulva fasciata Delile	KZN 813	F73	KwaZulu-Natal, South Africa	AJ544726
Acrosiphonia spinescens (Kützing) Kjellmann	HEC 9608	F49	Bretagne, France	AJ544727

Results and discussion

Sequence analyses and phylogeny

The aligned partial rRNA sequences were 644 sites in total. Average base composition was A 0.24; U 0.19; C 0.23; G 0.33. The two conserved regions (C1 and C2) were easily aligned but in the divergent domains D1 and D2 numerous gaps had to be introduced, mainly in the loop regions. Site variability (calculated on the basis of pairwise sequence divergence, and the number of inferred character changes for each alignment position) was greatest in the divergent domain D2 (Table 2, Fig. 3). The alignment of this region had been made possible by its common secondary structure in all ingroup taxa: a basal stem, two central loops connected by a central stem, and three periferal helices with terminal loops of variable size (Fig. 2A). *Chaetomorpha crassa* and *C. spiralis* possessed an extra helix of 32 nucleotides (positions 497-528) (Fig. 2B).

Table 2. Comparison of the domains C1 (partial), D1, C2, D2. Length and position of the regions; number of sites removed prior to phylogenetic analysis; pairwise sequence divergence between ingroup taxa (minimum, maximum and average); number and percentage of parsimony informative sites with and without outgroup taxa.

Domain name	Length and position of the region	Number of sites removed	Pairwise sequence divergence[1]: min.-max. (aver.)	Number and percentage of parsimony informative sites[1]	
				In- and outgroup taxa	Ingroup taxa only
C1 (partial)	56 bp (1-56)	0	0 - 0.190 (0.074)	12 (6%)	10 (7%)
D1	153 bp (57-209)	9	0 - 0.326 (0.151)	65 (31%)	55 (36%)
C2	143 bp (210-352)	0	0 - 0.063 (0.013)	23 (11%)	6 (4%)
D2	292 bp (353-644)	94	0 - 0.415 (0.203)	108 (52%)	84 (54%)
total	644 bp	103	0 - 0.232 (0.120)	208	155

[1] Calculations with ambiguous sites excluded and gaps treated as missing

71 positions with ambivalent alignment (all situated in the loop regions of the divergent domains) and the 32 sites in the extra helix of *Chaetomorpha crassa* and *C. spiralis* were removed prior to phylogenetic analysis. Of the 541 included nucleotide positions, 278 were variable and 208 parsimony-informative. The D2 domain contained the highest number of parsimony-informative sites (Table 2). The skewness value [g_1 = - 0.50; threshold value g_1 = - 0.12 (P = 0.01) for 25 taxa and 100 characters] indicated that the partial LSU rRNA sequences contained significant non-random structure that likely reflected phylogenetic signal. The average transition/transversion (ti/tv) ratio for the 541 nt alignment was 1.35 for the ingroup taxa alone.

Phylogenetic trees constructed with MP and ML methods gave similar topologies. Trees generated by MP analyses with the D2 region excluded also gave comparable topologies, except for the terminal clades being unresolved. The MP strict consensus tree will be discussed below as will the minor differences in the ML tree. MP analysis of the 43 taxa yielded 24 most parsimonious trees of 795 steps (CI = 0.57, RI = 0.78). The MP strict consensus phylogram with indication of bootstrap and decay index values is shown in Fig. 4. Within the Cladophorophyceae, *Cladophora horii* is placed as the sister-taxon of the rest of the group with high bootstrap support. The two main ingroup lineages have long basal branches and are

supported by high bootstrap and decay index values. The first lineage (A) consists of four clades with high bootstrap support, and includes the majority of *Cladophora* species, with *Chaetomorpha* and *Rhizoclonium* (three genera traditionally placed in the Cladophorales), and one *Cladophoropsis* species. The second lineage (B) consists of six clades with moderate to high bootstrap support, and contains genera traditionally placed in the Siphonocladales and two *Cladophora* species. The basal branches in both lineages remain largely unresolved. Clade B6 consists of a mixture of species belonging to six genera but the sequences are too conserved to resolve the ultimate polytomies in this clade. The ML differs from the MP consensus tree in some minor aspects: clade A2 forms a sister group to clades A3 and A4 with low bootstrap support, and in lineage B, clade B1 branches off first, followed by clades B3 and B2 which group together, all with low bootstrap support.

Table 3. Relative rate tests of sequences within clade A4, and between clades B4, B5 and B6.

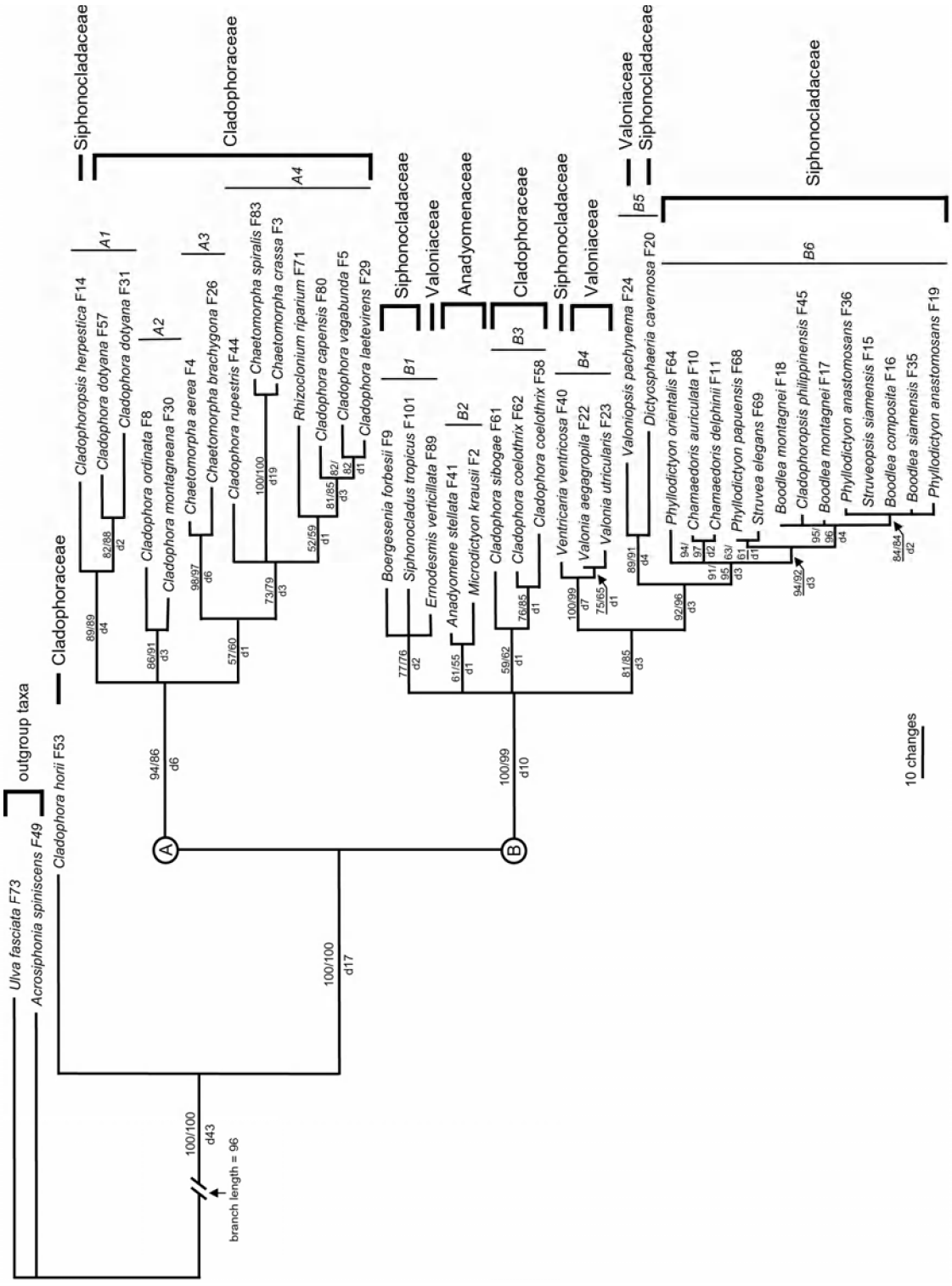
	probability[1]
within clade A4	
rupestris vs *spiralis*	p = 0.003
rupestris vs *vagabunda*	p = 0.368
spiralis vs *vagabunda*	p = 0.019
between B4, B5 and B6	
B4 vs B5	p = 0.012
B4 vs B6	p = 0.572
B5 vs B6	p = 0.025

[1] p-levels < 0.05 indicate that two clades evolve at significantly different rates

The MP strict consensus phylogram shows considerable variation in branch lenght within certain clades. For example, within clade A4 the branches leading to *Chaetomorpha spiralis* and *C. crassa* are much longer than the branches leading to other taxa. In lineage B, the branches leading to the species in clade B5 are much longer than the branches in clades B4 and B6. Relative rate tests carried out on all taxa within clade A4 demonstrate that *Chaetomorpha spiralis* and *C. crassa* evolve at a significant faster rate than *Cladophora rupestris* and the species of the *Cladophora vagabunda*-clade. The same tests carried out on all taxa of clades B4, B5 and B6 shows that there are significant differences in the substitution rates for species in clade B5 when compared with clades B4 and B6 (Table 3).

Table 4. Models of DNA substitution estimated for different datasets (ambiguous alignments excluded from the analyses).

region		all taxa	ingroup taxa	lineage A&B	lineage A	lineage B
complete alignment	hLRT	TrNef+G	TIMef+I+G	TIMef+I+G	TrNef+G	TrN+I+G
	AIC	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	TIM+I+G
D1 region	hLRT	K80+G	K80+G	K80+G	K81+G	K80+G
	AIC	TVM+G	TVM+I+G	TVM+I+G	TVMef+G	K81uf+I
C2 region	hLRT	F81+G	JC+I+G	JC+I+G	JC	JC+I
	AIC	TIM+G	GTR+I	GTR+I	TrN	TrN+I
D2 region	hLRT	TrN+G	TrN+G	TIMef+I+G	K80+G	TIM+G
	AIC	GTR+G	GTR+I+G	GTR+I+G	TVM+G	TIM+G


Ulva fasciata F73
Acrosiphonia spiniscens F49
outgroup taxa
Cladophora horii F53
Cladophoraceae
Cladophoropsis herpestica F14
Cladophora dotyana F57
Cladophora dotyana F31
Cladophora ordinata F8
Cladophora montagneana F30
Chaetomorpha aerea F4
Chaetomorpha brachygona F26
Cladophora rupestris F44
Chaetomorpha spiralis F83
Chaetomorpha crassa F3
Rhizoclonium riparium F71
Cladophora capensis F80
Cladophora vagabunda F5
Cladophora laetevirens F29
Siphonocladaceae
Boergesenia forbesii F9
Siphonocladus tropicus F101
Ernodesmis verticillata F89
Valoniaceae
Anadyomenaceae
Anadyomene stellata F41
Microdictyon krausii F2
Cladophoraceae
Cladophora sibogae F61
Cladophora coelothrix F62
Cladophora coelothrix F58
Siphonocladaceae
Ventricaria ventricosa F40
Valonia aegagropila F22
Valonia utricularis F23
Valoniaceae
Valoniopsis pachynema F24
Dictyosphaeria cavernosa F20
Valoniaceae
Siphonocladaceae
Phyllodictyon orientalis F64
Chamaedoris auriculata F10
Chamaedoris delphinii F11
Phyllodictyon papuensis F68
Struvea elegans F69
Boodlea montagnei F18
Cladophoropsis philippinensis F45
Boodlea montagnei F17
Phyllodictyon anastomosans F36
Struveopsis siamensis F15
Boodlea composita F16
Boodlea siamensis F35
Phyllodictyon anastomosans F19
Siphonocladaceae
A1
A2
A3
A4
B1
B2
B3
B4
B5
B6
A
B
branch length = 96
10 changes

The phylogeny in this study is in general agreement with the 18S rRNA phylogenies of Bakker *et al.* (1994) and Hanyuda *et al.* (2002) but differs in sample strategy. The two previous studies included mainly *Cladophora* species while the present study focuses on Siphonocladales (s.s.). It remains uncertain if *Cladophora horii* in this study would fit in the *Aegagropila*-clade found by Hanyuda *et al.* (2002) (see footnote on p. 71).

Phylogeny and morphology

The morphological tendencies generating the morphological variety in the class, as hypothesized by van den Hoek (1984), are mapped on the strict consensus MP tree in Figs 5A-G. Planification of the thallus (1) has evolved at least three times independently in the Cladophorophyceae (Fig. 5A): in *Phyllodictyon*, *Struvea* and *Boodlea montagnei* (clade B6), *Anadyomene* and *Microdictyon* (clade B2), and *Cladophora ordinata* (clade A2). Tenacular cells (2) are found only in taxa of lineage B (Fig. 5B). Tenacular cells of the first type (Olsen-Stojkovich, 1986) occur in *Anadyomene* and *Microdictyon* (clade B2); this type is considered here to be equivalent with van den Hoek's (l.c.) third morphological tendeny, "lateral coalition of cells". In *Microdictyon* cell-coalition occurs solely at the tips of the apical cells; in *Anadyomene* cells grow closely to one another resulting in lateral coalition. The similarity in mode of cell-coalition in the two genera is evident in immature thalli of *Anadyomene* where the thallus has an open reticulate structure, and anastomosis occurs at the cell apices, as in *Microdictyon* (Littler & Littler, 1991; unpublished pers. obs.). Tenacular cells of the first type also sporadically occur in *Cladophora coelothrix* (clade B3) (van den Hoek & Chihara, 2000). Tenacular cells (type 2) are found in *Valonia* (clade B4) and *Dictyosphaeria* (clade B5), and most likely evolved twice independently. Tenacular cells (type 3) characterize all taxa in clade B6 (except *Struveopsis*) and may have evolved once in the common ancestor of the clade. The fourth type of tenacular cells were only found in *Phyllodictyon orientalis* (clade B6). Simultaneous lateral formation (4) characterizes the genera *Boodlea*, *Phyllodictyon*, *Struvea* and *Struveopsis* (clade B6), and is also present to some extent in *Valoniopsis* (clade B5) (Fig. 5C). High numbers of laterals per cell (5) characterize *Cladophora ordinata* (clade A2), *C. rupestris* (clade A4), *Ernodesmis* (clade B1), *Anadyomene* and *Microdictyon* (clade B2), *Valonia* (clade B4), *Valoniopsis* (clade B5), *Chamaedoris* and *Phyllodictyon orientale* (clade B6) (Fig. 5D). This feature may have evolved once in the common ancestor of lineages A and B, or alternatively evolved several times independently. Inflated cells (6) occur in *Boergesenia*, *Ernodesmis* (clade B1), *Valonia*, *Ventricaria* (clade B4), *Valoniopsis* and *Dictyosphaeria* (clade B5) (Fig. 5E). Inflation of cells may have evolved once in the common ancestor of lineage B, or alternatively been gained several times independently. Differentiation between axis and laterals (7) is prominent in *Cladophora ordinata* (clade A2), *Cladophora dotyana* (clade A1), *Anadyomene* (clade B2), *Chamaedoris* and *Struvea* (clade B6) (Fig. 5F). Unbranched thalli (8) originated several times independently in *Chaetomorpha* (clades A3 and A4) and in *Rhizoclonium* (clade A4); the thallus of *Ventricaria ventricosa* (clade B4), consisting of a single cell, can be regarded as an extreme example of branch reduction (Fig. 5G).

← **Fig. 4.** Strict consensus phylogram of the 24 most parsimonious trees inferred from partial large subunit rRNA sequence data (gaps treated as missing). Tree length = 795 steps, CI = 0.57, RI = 0.78. Bootstrap percentages (MP/ML) are indicated above branches; decay index values are given below branches.

The four modes of cell division as defined by Olsen-Stojkovich (1986) are mapped on the strict consensus MP tree in Figs 5H-I. CI occurs in *Cladophora horii*, in all taxa of lineage A, and in the clades B1 (only in the rhizoids of *Boergesenia*, *Ernodesmis* and *Siphonocladus*), B2, B3, B5 (only in rhizoids of *Valoniopsis*) and B6 (in *Struvea elegans* CI only occurs in the rhizoids) (Fig. 5H). LC occurs in the clades B1 (only *Ernodesmis*), B4 (only *Valonia*) and B5 (only *Valoniopsis*). Okuda *et al.* (1997) demonstrates that in LC division of *Valonia*, protoplasm divides into a lenticular cell by a septum wall which is produced inwardly from the cell wall. This type of cell division can be seen as a modification of CI in taxa with inflated cells, where it is impossible to bridge the large diameter of the cells by invagination of cell walls. The occurrence of LC has co-evolved with the inflation of cells, which in their turn evolved several times independently in lineage B. SDSS and SDM only occur in taxa of lineage B. SDSS occurs in *Siphonocladus* (clade B1), *Dictyosphaeria* (clade B5) and *Struvea* (clade B6); the cells of *Boergesenia*, *Ernodesmis* (clade B1) and *Ventricaria* (clade B4) divide by SDM. In some species of clade B6 (*Phyllodictyon* spp., *Boodlea* spp., *Cladophoropsis philippinensis* and *Chamaedoris* spp.) SDSS occurs only occasionally, for example in association with wounding

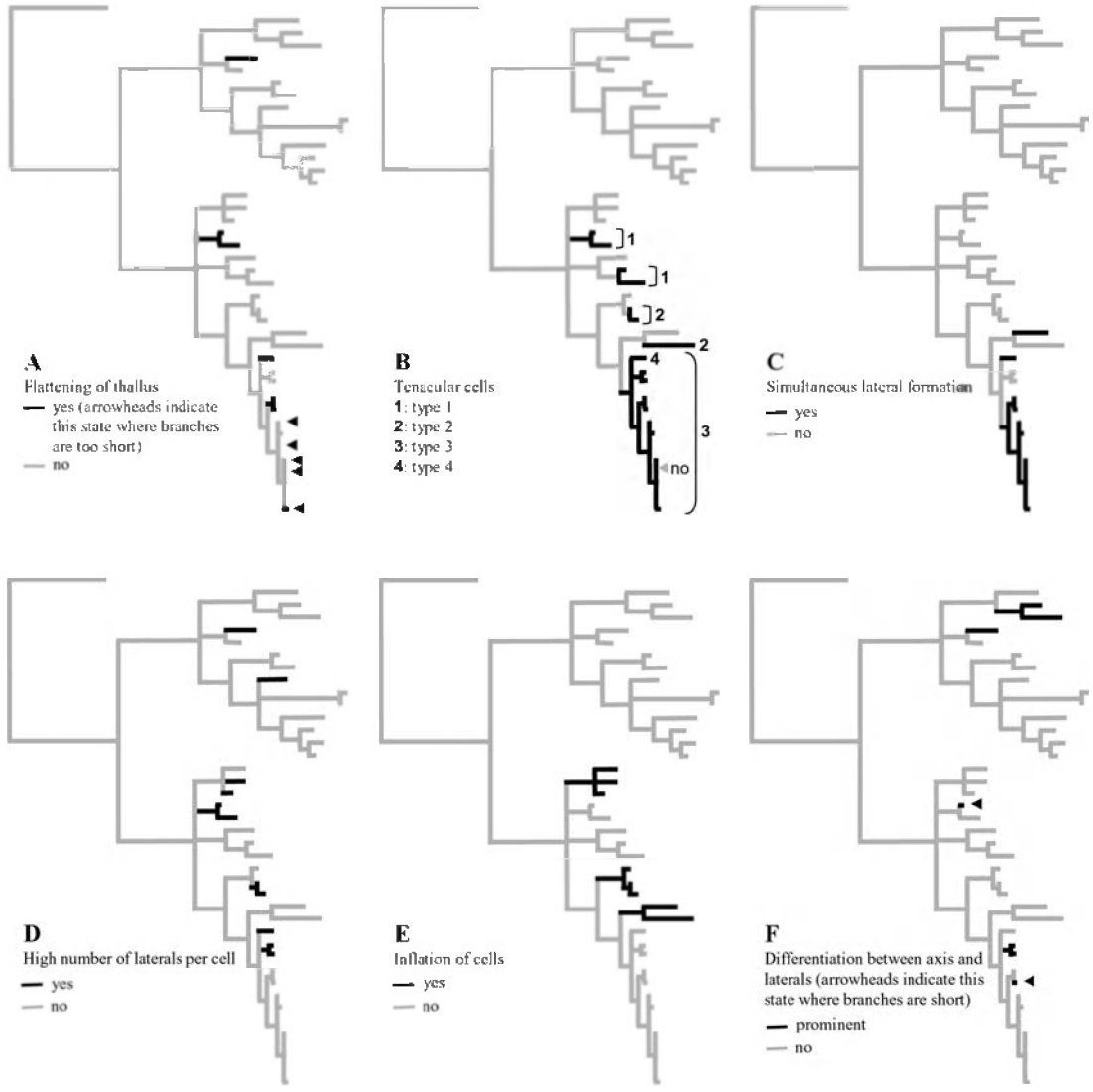


Fig. 5. Character mapping on the strict consensus MP tree.

response (La Claire, 1982; van den Hoek & Chihara, 2000; unpublished pers. obs.). Apparently the mode of cell division is not a clear cut character in the Cladophorophyceae. Four types are recognized but many species exhibit a mixture of two or three of these types. Moreover, mode of cell division cannot be used to typify the monophyletic clades in the present phylogeny (Fig. 5I).

The evolution from *Cladophora*-type architecture (branched filaments with cross walls at the base of newly formed laterals) to a *Cladophoropsis*-like morphology (mostly unilaterally branched filaments with delay of cross wall formation) has happened at least twice independently in the Cladophorophyceae (Fig. 5J). Delay of cross wall formation is prominent in *Cladophoropsis* and *Chamaedoris* but also occurs to some extent in *Cladophora coelothrix* (clade B3) and in all other species of clade B6.

Calcium oxalate crystals have been observed in certain species of the Cladophorophyceae (see chapter 4) (Fig. 5K). Three morphological types have been classified: (1) needle-shaped to hexagonal, (2) clustered rod-shaped and (3) octahedral crystals. Species situated in

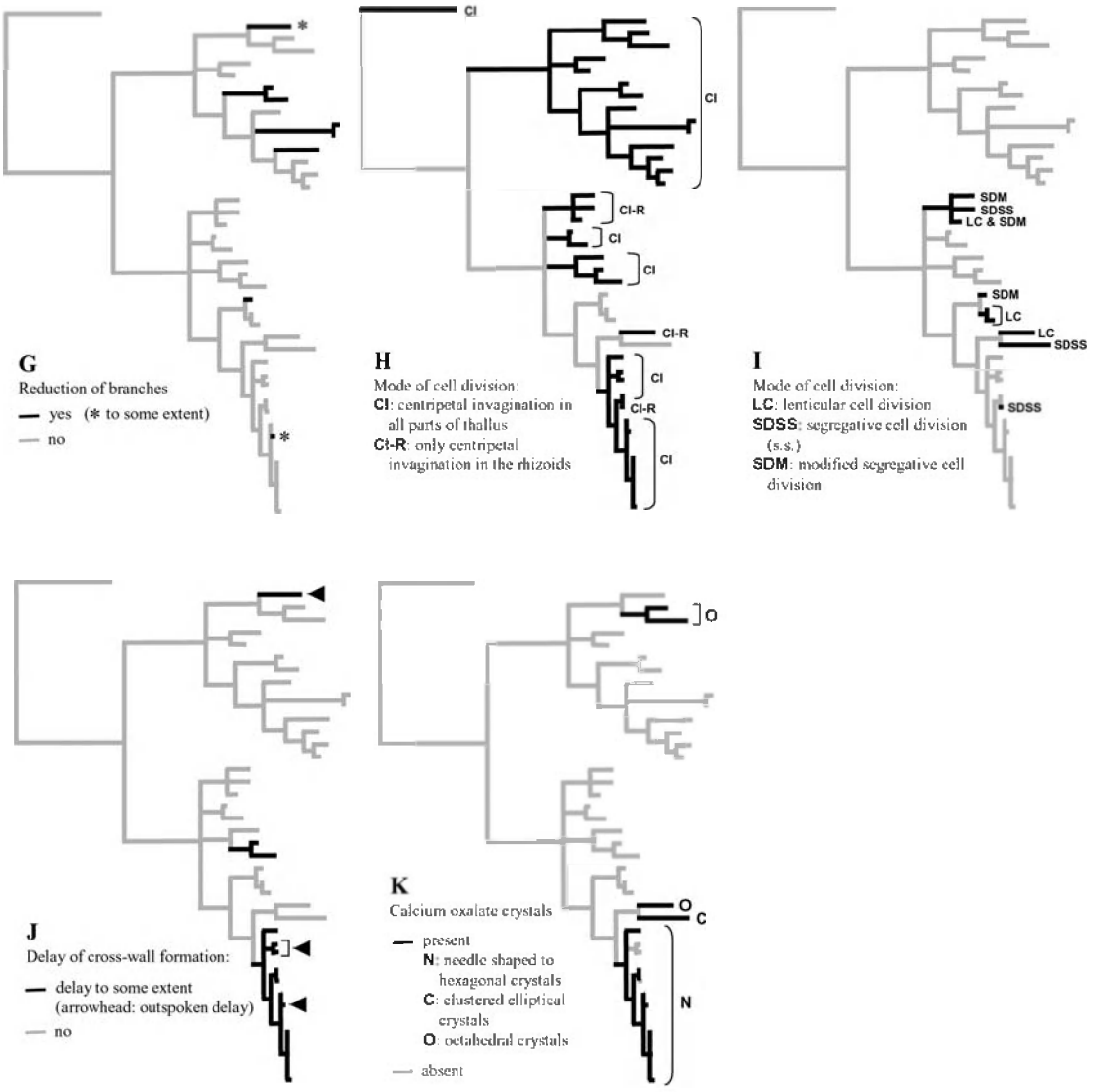


Fig. 5. (continued).

clade B6 (except *Struvea elegans* and *Chamaedoris*) possess crystals of the first type. Clustered rod-shaped crystals are present in the cells of *Dictyosphaeria* (clade B5). Octahedral crystals have been found in *Valoniopsis pachynema* (clade B5) and *Cladophora dotyana* (clade A1). Calcium oxalate crystals have evolved at least twice independently, although the crystalline inclusions of the first type may have evolved only once in clade B6.

Phylogeny and taxonomy

The molecular phylogeny of the Cladophorophyceae differs considerably from the traditional classification based on thallus architecture and mode of cell division. Homoplasy caused by convergence, parallel evolution and secondary reduction seems to be an important factor in clouding the evolutionary relationships within the Cladophorophyceae based on a morphology. Of the four or five recognized families, only the morphogically well characterized Anadyomenaceae (including *Anadyomene* and *Microdictyon*) appears to form a monophyletic group. The other families are polyphyletic. The species of some genera (e.g. *Valonia*, including *Ventricaria*) seem to form natural groups but other genera are clearly polyphyletic (*Cladophora* and *Chaetomorpha*) or belong to a genus complex (e.g. clade B6).

The genus ***Cladophora*** as presently conceived is polyphyletic, corresponding with the results of Hanyuda *et al.* (2002). Ten species of *Cladophora* are included in the study, representing six sections: *Rugulosae*, *Glomeratae*, *Longi-articulatae*, *Repentes*, *Rupestres* and *Willeella*. The species of the first section are placed in lineage B while all other *Cladophora*'s fall within the sister lineage (*C. horii*) or lineage A.

The section ***Repentes*** is characterized by cushion-like growth forms and the development of rhizoids sprouting from the basal poles of cells in any part of the thallus. The two species included in this study, *C. coelothrix* and *C. sibogae* are sister taxa in clade B3. Based on morphological characters, van den Hoek (1984) suggested possible relationships between the *Cladophora* section *Boodleoides* and the genus *Microdictyon*, and between the sections *Boodleoides*, *Aegagropila* and *Repentes*. There is no support for this hypothesis in the present study but the 18S rRNA phylogeny of Bakker *et al.* (1994) confirmed the affinity between *Microdictyon boergesenii*, *Cladophora liebetruthii* (section *Boodleoides*) and *Cladophora catenata* (section *Aegagropila*), and indicated a possible relationship of the species above with two *Cladophora* species of the section *Repentes* (*C. coelothrix*, *C. socialis*) and *C. prolifera* (section *Rugulosae*).

Thallus architecture in the section ***Glomeratae*** s.l. (van den Hoek & Chihara, 2000) is relatively heterogeneous and varies from strictly acropetal to irregular; thallus growth takes place by apical or intercalary cell division. Based on the four species included in this study this section is polyphyletic: three species (*C. capensis*, *C. laetevirens* and *C. vagabunda*) are grouped in clade A4 with *Rhizoclonium riparium* var. *implexum*; the fourth species, *C. montagneana*, is located in clade A2 together with *C. ordinata* (section *Willeella*, see below). The section ***Longi-articulatae***, characterized by acropetally organized branch systems, growth by apical cell division and thalli with a conspicuous basal stipe, is represented here by a single species, *C. dotyana*. *Cladophora dotyana* from the Philippines and South Africa always clade together, with *Cladophoropsis herpestica* forming a sister taxon (clade A1). The grouping of *C. herpestica* with *C. dotyana* is unexpected from a morphological viewpoint, as these taxa have very few characters in common. The section ***Rugulosae*** is characterized by dark green, broom-like thalli composed of acropetally organized branch systems, growth mainly by apical cell division, attached by numerous stipes producing descending rhizoids. The section is represented

in this study by a single newly described species, *C. horii* (van den Hoek & Chihara, 2000), which forms a sister lineage to the two main Cladophorophyceae lineages A and B. In the 18S rRNA phylogeny of Bakker *et al.* (1994), *C. prolifera*, another representative of the section *Rugulosae* (not included in this study), grouped with *C. coelothrix* and *C. socialis* in a clade corresponding to clade B3 in the present study. The section ***Rupestres*** (s.s.) (van den Hoek & Chihara, 2000) is also characterized by dark green, broom-like thalli, but they are composed of dense, irregular branch systems with distinct main axes bearing several short laterals. *C. rupestris*, the only species of the section, groups together in clade A4 with the species of the section *Glomeratae*, *Rhizoclonium* and two *Chaetomorpha* species. According to van den Hoek & Chihara (2000), *C. rupestris* fits perfectly in the section *Glomeratae* from a morphological viewpoint, but is placed in a different section because of its position in the 18S rRNA phylogenetic tree of Bakker *et al.* (1994).

The section ***Willeella*** is characterized by fan-like thalli composed of regular, oppositely branched laterals in a single plane. The section is represented by a single species, *C. ordinata*, the type and only species of *Willeella* (Børgesen (1930). Its distinct morphology has led to this taxonomic view-point being still widely accepted today (van den Hoek & de Rios, 1972; Silva *et al.*, 1996). *C. ordinata* groups together with *C. montagneana* (section *Glomeratae*) in clade A2. The two species have a number of characters in common: similar general architecture; apical cells with an obtuse tip and an apical thickening of the cell wall; and opposite and equal laterals (less frequent in *C. montagneana*). van den Hoek (1982a: 124) suggested a close relationship between *C. ordinata* and *C. rupestris* based on similarities in branch-pattern, but in our phylogeny these species do not group together. Based on the present results the genus *Willeella* could either be reduced to a section of *Cladophora* (*s.l.*, comprising all taxa of lineage A), or alternatively the genus *Willeella* could be maintained and *C. montagneana* should then be transferred to this genus.

The genus ***Chaetomorpha*** is characterized by unbranched filaments growing exclusively by intercalary cell division. Species are distinguished by only a few characters such as cell shape and diameter, thallus morphology, and mode of attachment (thalli are either basally attached and erect, or unattached and form entangled, free floating masses). Four *Chaetomorpha* species are included in this study, two attached and two unattached species. *Chaetomorpha aerea* (attached) and *C. brachygona* (unattached) always group together in clade A3. The other *Chaetomorpha* species (the attached *C. spiralis* and unattached *C. crassa*) are located in clade A4, together with some *Cladophora* species and *Rhizoclonium*. As already suggested by van den Hoek (1984), *Chaetomorpha* can be regarded as a reduced form of *Cladophora* and not the primitive sister genus of *Cladophora*. The genus is polyphyletic and evolved at least twice independently within lineage A. Bakker *et al.* (1994) already showed that *Chaetomorpha* falls within a *Cladophora* clade on the basis of one (unidentified) *Chaetomorpha* species. Hanyuda *et al.* (2002) found *Chaetomorpha okamurae* in the *Aegagropila*-clade, but this species may belong to *Cladophora* (van den Hoek, 1963). Since all *Cladophora* species in this study have attached thalli, it is likely that unattached forms of *Chaetomorpha* are derived from attached forms; this event took place at least twice independently. Moreover juvenile plants of *C. crassa* have been observed attached as epiphytes; older plants soon come loose and are able to grow further as unattached forms (E. Coppejans, unpublished data).

Rhizoclonium also falls within *Cladophora*, and can be regarded as a reduced form in lineage A. Hanyuda *et al.* (2002) have already demonstrated that the evolution from *Cladophora*-type architecture to *Rhizoclonium*-like morphology (unbranched filaments with rhizoidal laterals) has taken place several times independently.

The monotypic genera ***Ernodesmis*** and ***Boergesenia***, and ***Siphonocladus tropicus*** always group together in clade B1. Their systematic positions were the subject of earlier speculation (Papenfuss & Chihara, 1975; Olsen-Stojkovich, 1986). Some authors considered *Ernodesmis* to be a member of the Siphonocladaceae based on the annular constrictions (Børgesen, 1913, 1940), while others (Oltmanns, 1922; Taylor, 1960) allied *Ernodesmis* with *Valonia* and placed it in the Valoniaceae based on lenticular and tenacular cells. *Boergesenia* has been allied with both *Ventricaria ventricosa* and *Siphonocladus*, based on the mode of cell division and presence of basal annular constrictions, respectively (Olsen-Stojkovich, 1986). Olsen-Stojkovich (1986) considered *Siphonocladus* to be related to *Dictyosphaeria* based on immunological and morphological evidence. *Ernodesmis*, *Boergesenia* and *Siphonocladus* are all characterized by inflated, club-shaped cells with basal annular constrictions but differ in their mode of cell division, and consequently in their thallus architecture. *Ernodesmis* forms spherical thalli composed of cells with verticillate, apical clusters of branches formed by LC (SDM occurs only occasionally). The branches in *Siphonocladus tropicus* are formed by SDSS and radiate laterally from the club-shaped main axes. In *Boergesenia* the club-shaped cells remain unbranched and cell division occurs by SDM.

The genera ***Microdictyon*** and ***Anadyomene***, characterized by unistratose, blade like thalli and similar modes of cell-coalition, always group together in clade B2, a relationship proposed by Kützing (1843: 302, 311) who established the family Anadyomenaceae for them. The family has been placed either in the Siphonocladales (s.s.) because of the blade-like thalli (Børgesen, 1942; Egerod, 1952) or in the Cladophorales (s.s.) based on the mode of cell division (Papenfuss, 1955). In the present study the family is positioned among the siphonocladalean taxa.

Valonia has traditionally been allied with *Dictyosphaeria* and placed in the Valoniaceae because thalli lack a central axis and are composed of inflated cells (Feldmann, 1938*b*; Egerod, 1952). Olsen & West (1988) linked *Valonia* to *Ernodesmis* and *Valoniopsis* on the basis of lenticular cell division. They erected *Ventricaria* based on *Valonia ventricosa* on the evidence of immunological data, mode of cell division and reduced habit, and suggested that it had phylogenetic alliances with *Siphonocladus* and *Dictyosphaeria*. *Valonia*, in contrast, seemed to be closely related to *Valoniopsis*, *Chaetomorpha* and *Cladophora vagabunda*. In the present study the *Valonia* species were placed in clade B4, very closely related to *Ventricaria* (divergence of only 0.86 %), questioning wether the recognition of a separate genus is warranted. The three species form a sister group to clades B5 and B6 (see below).

Valoniopsis has been considered to be related either to *Anadyomene*, based on similarities in branching pattern (Børgesen, 1934) or *Valonia* and *Ernodesmis* in the Valoniaceae because of lenticular cell-division and inflated cells (Papenfuss & Egerod, 1957). This study shows neither position to be correct, instead linking *Valoniopsis* with ***Dictyosphaeria***, although the two genera differ in thallus architecture and mode of cell division.

The tight clustering of ***Boodlea***, ***Chamaedoris, Cladophoropsis*** (p.p.), ***Phyllodictyon***, ***Struvea*** and ***Struveopsis*** in clade B6 is not surprising given that only *Chamaedoris* can be easily distinguished (Børgesen, 1913; Egerod, 1952; Kooistra *et al.*, 1993; Leliaert *et al.*, 1998). Based on ITS sequences, Kooistra *et al.* (1993) already suggested the very close affinity between *Boodlea coacta* (a taxonomic synonym of *B. composita*), *Phyllodictyon anastomosans* and *Cladophoropsis membranacea* (not included in this study). Immunological results (Olsen-Stojkovich, 1986) indicated that *Chamaedoris* is closely related to *Cladophoropsis membranacea*, but to a lesser extent to *Boodlea* and *Phyllodictyon*.

The two ***Cladophoropsis*** species included in the present study emerge in the two main lineages: *C. philippinensis* falls within the *Struvea*-complex (clade B6), while *C. herpestica* groups together with *Cladophora* species of the section *Longi-articulatae* in lineage A. Non-monophyly of *Cladophoropsis* has also been demonstrated by Bakker *et al.* (1994), based on 18S rRNA sequences of *C. membranacea* and *C. zollingeri*. Two important characters distinguishing the *Cladophoropsis* species from both lineages are the mode of cell division and calcium oxalate crystals. In the *Cladophoropsis* species of lineage B segregative cell division occasionally occurs, especially in response to wounding (La Claire, 1982) and the cells contain calcium oxalate crystals (unpublished pers. obs.). The *Cladophoropsis* species of lineage A devide by centripetal invagination and lack calcium oxalate crystals. The *Cladophoropsis* species in lineage A can be regarded as reduced forms of a *Cladophora*-type architecture. The *Cladophoropsis* species in clade B6 can either be seen as reduced forms of a *Boodlea*/*Struvea*-type architecture, or the *Cladophoropsis*-type morphology can be considered as an ancestral state from where the *Boodlea*/*Struvea*-type architecture has evolved.

Conclusions

The partial LSU rRNA sequences contain the appropriate amount of variation to resolve the basal divergences within the Cladophorophyceae. The present study in combination with previously published 18S rRNA phylogenies (Bakker *et al.*, 1994 and Hanyuda *et al.*, 2002) reveals three lineages within the Cladophorophyceae: one sister lineage comprising taxa with a *Cladophora*-type architecture, and two main lineages[1]. The first main lineage (A) includes most *Cladophora* species and several taxa with a reduced thallus architecture. The second main lineage (B) comprises taxa with specialized morphologies and a few *Cladophora* species with some unique characters (e.g. rhizoids in the apical regions of the thallus) not found in the species of lineage A. The sister lineage comprising *Cladophora horii* suggests that the siphonocladalean morphologies arose as specialized forms from a *Cladophora*-like ancestor. The present study partially confirms van den Hoek's (1984) hypothesis. Different reduction events have indeed occured several times independently. All taxa with specialized thalli however, are grouped in one lineage, with the first divergences being unresolved. This polytomy may simply reflect the uncertainty about phylogenetic relationship (soft polytomy), or it might indicate a single evolution event of an ancestor with a *Cladophora* type architecture to the siphonocladalean taxa (i.e. a common ancestral population split through cladogenesis into multiple lineages) or a number of independent evolution events (multiple speciation events) which took place in a relative short period of time and therefore cannot be revealed in the present phylogeny (hard polytomies). The grouping of all siphonocladalean taxa (excluding part of *Cladophoropsis* and including some *Cladophora* species) in one lineage, separated by long branches from the cladophoralean lineages, clearly supports the recognition of a separate order Siphonocladales with the Cladophorales (s.s.) remaining paraphyletic. This is in contrast with the viewpoint of Bakker *et al.* (1994) who regarded the order Siphonocladales as polyphyletic and stated that there is no basis for independent recognition of the Cladophorales (s.s.) and Siphonocladales (s.s.).

[1] At the time of publication (August 2003) the relationship of *Cladophora horii* with species in the *Aegagropila*-clade discovered by Hanyuda *et al.* (2002) was still uncertain. In the meantime Hanyuda kindly send us an unpublished SSU nrDNA tree of his PhD thesis where it is demonstrated that a Japanese specimen of *C. horii* groups together with *Cladophora conchosphaeria* in this *Aegagropila*-clade (see Fig. 1 on p. 3 of this thesis).

In order to construct a classification that reflects the evolutionary history of the Cladophorophyceae, drastic taxonomic changes have to be made. The polyphyletic genus *Cladophora* could be split up in different genera as already pointed out by Bakker *et al.* (1994) and van den Hoek & Chihara (2000)[2], or the other genera in the lineage [*Chaetomorpha*, *Cladophoropsis* (p.p.) and *Rhizoclonium*] could be transferred to *Cladophora*. The very close relationship between *Boodlea*, *Chamaedoris*, *Cladophoropsis* (pro parte), *Phyllodictyon*, *Struvea* and *Struveopsis*, in combination with fuzzy morphological boundaries between these genera would favour the recognition of a single genus. Merging other closely related genera (e.g. *Valoniopsis* and *Dictyosphaeria*) would be more problematic from a morphological viewpoint since both genera are characterized by distinct characters. In general, the essential difficulty arising from reforming the cladophorophycean taxonomy is finding apomorphic morphological characters for the monophyletic groups. Before undertaking radical taxonomic and nomenclatural changes, further morphological and molecular research is needed. Ultrastructural and chemical studies might provide useful characters to delimit natural groups in the rest of the Cladophorophyceae (Hanyuda *et al.*, 2002). In future, extended phylogenies, the different genera should be represented by additional species, including their types. This is essential because the simple morphological characters that determine the generic concept in the class can easily have evolved multiple times. The relationship between taxa in the terminal clade B6 requires further investigation using more variable molecular markers.

Acknowledgements

We thank Annie Tillier and Céline Bonillo (Institut de Systematique Moleculaire, Muséum National d'Histoire Naturelle, Paris) for their help with the molecular analyses. We are grateful to Wilson Freshwater (Center for Marine Science Research, University of North Carolina at Wilmington, USA) for providing material of *Ernodesmis verticillata*. We also thank Drs Christine Maggs (Queens University, Belfast, UK) and an anonymous reviewer for helpful suggestions and comments on the manuscript. We thank Takeaki Hanyuda (Institute of Biological Science, University of Tsukuba, Japan) for sharing unpublished information on the phylogenetic position of *Cladophora horii*. Financial support was provided by the FWO Research Project 3G002496.

[2] Since the phylogenetic affinity of the type species of the genus *Cladophora* [*C. oligoclona* (Kützing) Kützing = *C. rivularis* (Linnaeus) van den Hoek] has not yet been studied, it remains uncertain which clade should be named *Cladophora*.

Chapter 4

Crystalline cell inclusions: a new diagnostic character in the Cladophorophyceae

Adapted from: Frederik Leliaert & Eric Coppejans. 2004. Crystalline cell inclusions: a new diagnostic character in the Cladophorophyceae (Chlorophyta). Phycologia 43(2), in press.

Abstract – Crystalline cell inclusions were observed in 45 species of Cladophorophyceae. The crystals can be classified into eight morphological types, including needle-shaped, prismatic, octahedral, tetrahedral, cubical or globular, and they were found to occur in clusters or as single crystals. In addition to the different morphological types, the crystals are characterized by different chemical composition. Chemical tests distinguished the crystals as being composed of calcium oxalate, calcium carbonate or proteins. The diversity of crystal types raises the possibility that these structures have systematic value. The occurrence of crystalline structures is compared with previously published phylogenies of the Cladophorophyceae. Some types of crystals were found to be genus- or species-specific, while other types occurred in distantly related groups. The crystalline cell inclusions can be useful diagnostic characters. For example, *Cladophoropsis sundanensis* and *Cladophora coelothrix* are distantly related but have similar thallus architecture, and they can be distinguished from one another by the presence or absence of crystals.

Introduction

The Cladophorophyceae (van den Hoek *et al.* 1995), encompass a mainly marine class of coenocytic Chlorophyta. Thallus architecture includes branched and unbranched uniseriate filaments, blade-like thalli, (pseudo)parenchymatic thalli, and thalli consisting of inflated cells. Diagnostic morphological characters are scarce and are generally unsuitable for retrieving evolutionary relationships, owing to repeated convergence and parallel evolution (Leliaert *et al.* 2003).

A wide variety of crystalline structures have been observed in vascular plants and macroalgae; however, they have long been neglected in the latter. Vascular plants accumulate crystals of calcium oxalate (CaOx) in a diversity of shapes, sizes, amounts, and spatial locations. These crystals may be important in structural reinforcement, calcium regulation (Volk *et al.* 2002), and in defence against grazers. Both the morphology and distribution of CaOx crystals within plants exhibit species-specific patterns, indicating that their development is genetically controlled. The morphology and distribution of crystals vary widely among genera and often between closely related species; however, they have been shown to be systematically useful in some cases (Franceschi & Horner 1980; Webb 1999). In macro-algae CaOx crystals have been rarely recorded, but the reports that do exist represent a broad sample of algae (Pueschel 2001). In the Chlorophyta, needle-shaped CaOx crystals have been reported in vacuoles of the bryopsidophycean genera *Penicillus* (Friedmann *et al.* 1972; Turner & Friedmann 1974; Böhm *et al.* 1978), *Chlorodesmis* (Ducker 1967: 158, 161, Tab. 27, d; Menzel 1987; Coppejans & Prud`homme van Reine 1989: 127, fig. 12) and *Codium* (Coppejans, unpublished pers. obs.). Cruciate CaOx crystals have been observed in the zygnematophycean genus *Spirogyra* (Klein 1877, Pueschel 2001). Protein crystals have been reported in a wide range of Rhodophyta (Feldmann-Mazoyer 1941; Fritsch 1945, Pueschel 1992) and in the brown alga *Haplogloia kuckuckii* (Pueschel 1994). Few records have been found of crystalline, proteinaceous inclusions in Chlorophyta.

Reports of crystalline cell inclusions in members of the Cladophorophyceae are sparse. Børgesen (1905: fig. 13; 1913: fig. 32, b) casually illustrated needle-shaped crystals in *Cladophoropsis membranacea*. Klein (1882), Chemin (1931), Jónsson (1962) and van den Hoek & Chihara (2000: 96, fig. 44G) briefly described protein crystalloids with various morphologies in several *Cladophora* species, including *C. pellucida* (Hudson) Kützing, *C. prolifera* (Roth) Kützing, *C. rupestris* (Linnaeus) Kützing, *C. sakaii* Abbott and *C. ohkuboana* Holmes.

This study describes the morphological variation of crystalline cell inclusions observed in a survey of numerous taxa of Cladophorophyceae. The chemical nature of the crystals is briefly considered by the use of solubility tests and staining methods. The major aim of this study is to detect any possible systematic value of the various types of crystalline cell inclusions.

Material and methods

The cell contents of 66 species of Cladophorophyceae were examined to detect the presence of crystalline structures. The specimens studied are listed in Appendix 1 (herbarium abbreviations follow Holmgren *et al.* 1990). The specimens were collected during various fieldtrips or requested from different herbaria; 24 type specimens are included in the study. Collected samples were prepared as herbarium specimens or preserved in 4% formalin/seawater. When possible, fresh specimens were studied in the field with a Nikon hand microscope. Preserved specimens were studied on a Leitz-Diaplan light microscope. To improve visualization of the cell-inclusions, cells were dissected and the cell contents examined. Photographs were taken with a Olympus-DP50 mounted on the light microscope.

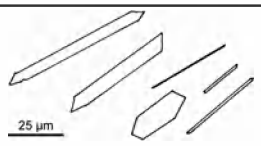
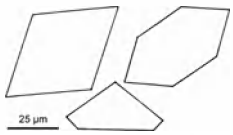
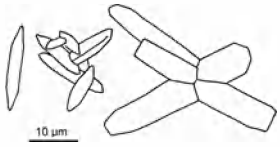
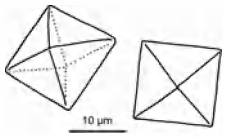
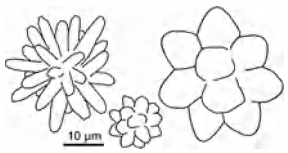
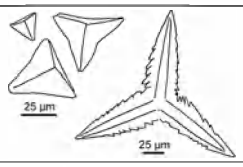
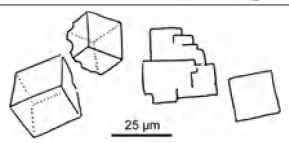
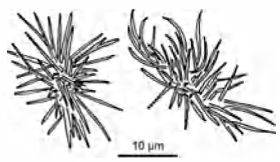
To confirm the presence of crystalline structure, cells were examined under differential interference (Nomarski) contrast for characteristic crystalline birefringence. Chemical solubilities of the inclusions were tested by viewing specimens exposed to 1.0 N hydrochloric acid, 5 % sodium hypochlorite, or 67 % aqueous acetic acid (Yasue 1969; Friedmann *et al.* 1972; Pueschel 2001). The Yasue (1969) method for CaOx staining was performed as follows: filaments were placed in 5% aqueous $AgNO_3$ for 10 min., rinsed in water, and then mounted on a microscope slide in a solution of 70% ethanol saturated with dithiooxamide (Sigma Chemical). After a few minutes, water was added to the edge and the effect monitored (Pueschel 2001). Protein crystalloids were stained with aniline blue and Lugol's Iodine as a general staining method for proteins (Gurr 1965).

Results

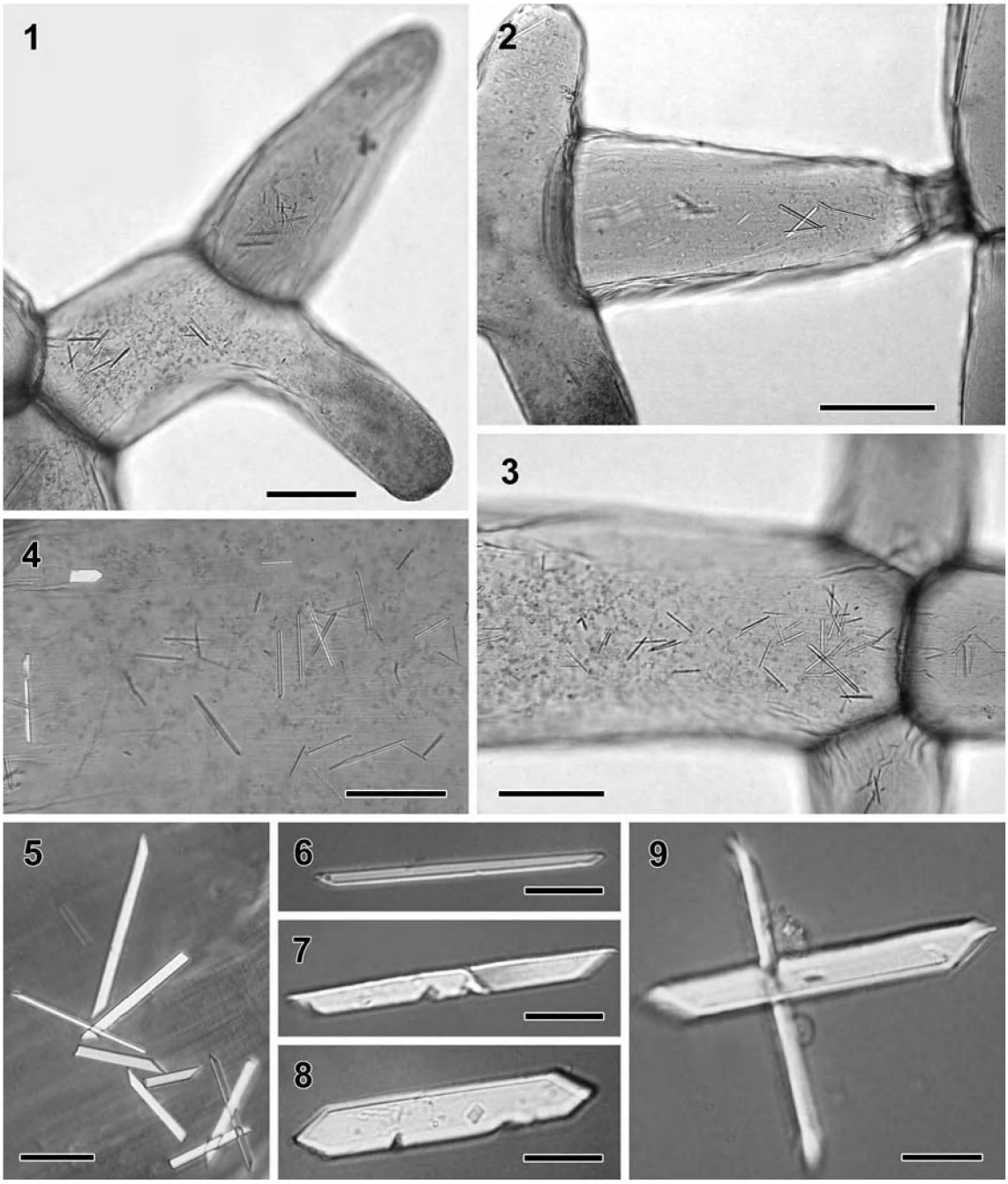
Of the 66 species examined, 45 were found to possess some kind of crystalline cell inclusion (Appendix 1). A large morphological variety of crystals was observed in the different genera: fine needle-shaped or elongated hexagonal rod-shaped crystals, single or grouped in clusters; broad hexagonal, diamond-shaped or triangular structures; tetrahedrons; octahedrons and star-shaped structures. The morphological variation of the cell inclusions can be classified into eight morphological types (Table 1). Cells of some species contain only one crystal type while those of others (e.g. some *Valonia* species) have up to three morphological crystal types. In some taxa crystals are present in all cells of the thallus, while in others crystals are restricted to the older cells or the axial filaments. The number of crystals varies from a few to thousands per cell. The vacuolated nature of the cells in the Cladophorophyceae makes it difficult to preserve the

tonoplast and to determine the subcellular location of the inclusions. This problem was also encountered by Pueschel (1995) who studied CaOx crystals in the cells of *Antithamnion*.

Table 1. Morphological types of crystalline cell inclusions in the Cladophorophyceae; taxa where these types have been observed; chemical solubility, staining and birefringence under polarized light, and probable chemical composition

Morphological type			Taxa	Chemical solubility[1], staining[2], birefringence and probable chemical composition (in bold)
Type-1a	Crystals single, elongated prismatic Figs 1–9		*Boodlea* spp. (except *B. vanbosseae*) *Phyllodictyon anastomosans* *Struveopsis siamensis* *Chamaedoris orientalis* *Cladophoropsis* (pro parte)	HCl: dissolve Acet. acid: intact Sod. hyp.: intact Y: positive L: negative Birefringence **calcium oxalate**
Type-1b	Crystals single, broad prismatic, hexagonal to diamond-shaped or triangular Figs 10–16		*Chamaedoris peniculum* *Cladophoropsis magnus* *Phyllodictyon* spp. (pro parte) *Struvea* spp. (pro parte)	
Type-2	Crystals single, needle-shaped, attenuating to one or both ends, or elongated rod-shaped Figs 17–22		*Apjohnia laetevirens*	
Type-3	Crystalline structures elongated elliptical to irregular rod shaped, single or clustered in cruciate to star-shaped aggregates Figs 23–27		*Dictyosphaeria cavernosa* *Dictyosphaeria versluysii*	
Type-4	Octahedral crystals Figs 28–32		*Valoniopsis pachynema* *Cladophora dotyana* *Siphonocladus tropicus*: rare	
Type-5	Globular aggregates of rod- or cone-shaped crystals Figs 33–35		*Valonia* spp. *Ventricaria ventricosa* (*Cladophora dotyana*: rare)	HCl: dissolve Acet. acid: dissolve Sod. hyp.: intact Y: negative L: negative Birefringence **calcium carbonate**
Type-6	Tetrahedral crystals; in most species **(marked with *)** growing into 4-armed (apparently 3-armed), star-shaped structures Figs 36–44		*Cladophoropsis herpestica* *Chamaedoris auriculata** *Chamaedoris delphinii** *Phyllodictyon papuense* (stipe) *Valonia aegagropila** *Valonia fastigiata** *Valonia utricularis**	HCl: intact Acet. acid: intact Sod. hyp.: dissolve Y: negative L: Dark brown staining No birefringence **Protcins**
Type-7	Cubical cell inclusions, single or fused Figs 45, 46		*Cladophora prolifera* *Cladophora rugulosa* *Cladophora rupestris*	
Type-8	Star-shaped or irregular clusters of fine, needle-shaped crystals Figs 47–49		*Boodlea vanbosseae* *Chaetomorpha* spp. *Chamaedoris* spp. *Cladophora coelothrix* *Microdictyon tenuius* *Siphonocladus tropicus* *Valonia* spp. *Valoniopsis pachynema* *Ventricaria ventricosa*	HCl: intact Acet. acid: intact Sod. hyp.: intact Y: negative L: negative Birefringence **Silica**

[1] HCl: hydrochloric acid; Acet. acid: acetic acid; Sod. hyp.: sodium hypochlorite.
[2] Y: Yasue method for CaOx staining; L: staining with Lugol's iodine.

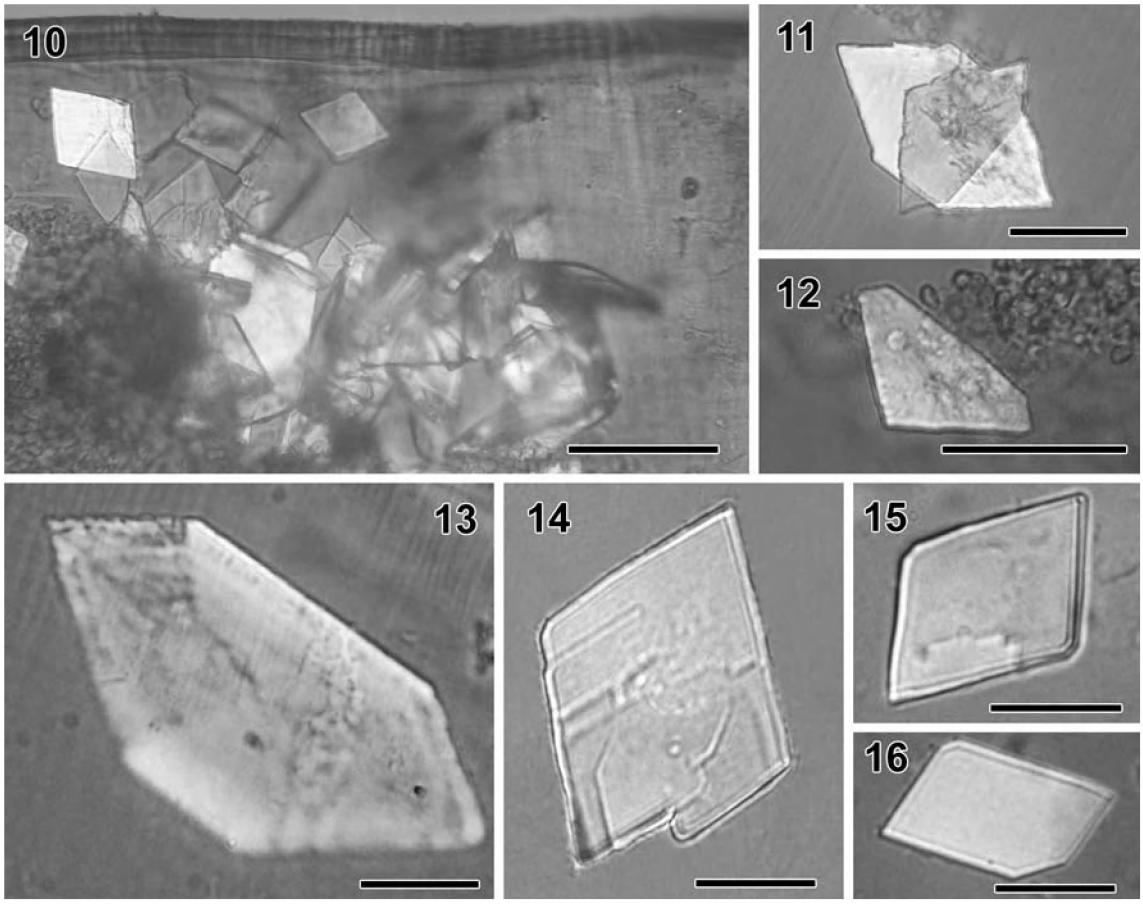


Figs 1-9. Elongate prismatic crystals (Type-1a) in *Phyllodictyon anastomosans*. Figs 1-2. Crystals present in the apical cells and absent in the tenacular cell. Scale bars = 50 µm. Figs 3-4. Crystals abundant in the cells of the main axes. Scale bars = 50 µm. Fig. 5. Aggregate of crystals. Birefringence under polarizing optics demonstrates crystallinity of inclusions. Scale bar = 25 µm. Figs 5-8. Morphological variation of crystals within a single cell. Scale bars = 10 µm. Fig. 9. Fusion of two crystals to form cruciate structures. Scale bar = 10 µm.

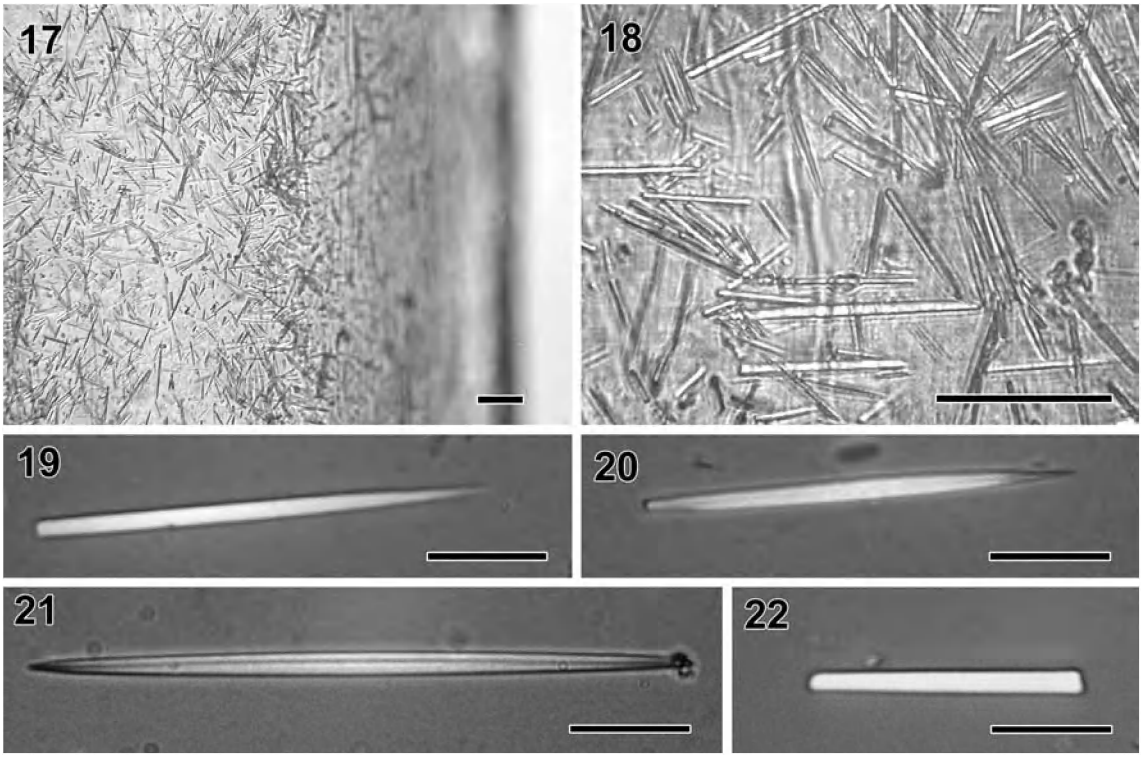
Crystal types 1 to 4 (Table 1) could be detected with brightfield light microscopy but are especially conspicuous when viewed with Nomarski contrast, under which they appear bright due to birefringence; birefringence indicates a crystalline substructure. The crystals stay intact when treated with acetic acid or sodium hypochlorite; this eliminates the possibility that the structures are composed of calcium carbonate or protein, respectively. The crystals dissolve very quickly in hydrochloric acid, eliminating the possibility of silica composition. The Yasue method for CaOx staining resulted in dark staining of the crystals. The chemical solubility tests

and staining method indicate that the chemical composition of these types of crystals is calcium oxalate.

Elongate prismatic crystals (**Type-1a**: Figs 1-9), single or grouped in loose aggregates are present in the cells of *Boodlea* species (except *B. vanbosseae*), *Phyllodictyon anastomosans*, *Struveopsis siamensis*, *Siphonocladus rigidus* and the *Cladophoropsis* species *C. carolinensis*, *C. macromeres*, *C. membranacea*, *C. philippinensis* and *C. vaucheriiformis*. The crystals occur in all cells of the thallus except the tenacular cells (Figs 1-8); the number per cell ranges from 1-30 in the apical cells (Figs 1, 2) to more than 200 in the cells of the main axes (Figs 3, 4). Crystals are 1.5-5 (-8) μm in diameter, 25-70 μm long, with a l/w ratio of 3-14. Infrequently, two crystals fuse and form cruciate structures (Fig. 9). Crystals in *C. sundanensis* are rectangular to elongated rod-shaped, present in most cells, up to 7 crystals per cell, 2-15 μm in diameter, 15-25 μm long, with a l/w ratio of 1-12. In *Siphonocladus rigidus*, crystals are present in a small number of cells, up to 5 per cell, 3-12 μm in diameter, up to 60 μm long. No type-1 crystals were observed in the *Cladophoropsis* species *C. herpestica* and *C. javanica*. In *Chamaedoris orientalis* crystals are abundant in all cells of the capitulum filaments (over 200 per cell) but are absent in the stipe cell; crystals are 0.5-1.5 μm in diameter and up to 30 μm long.



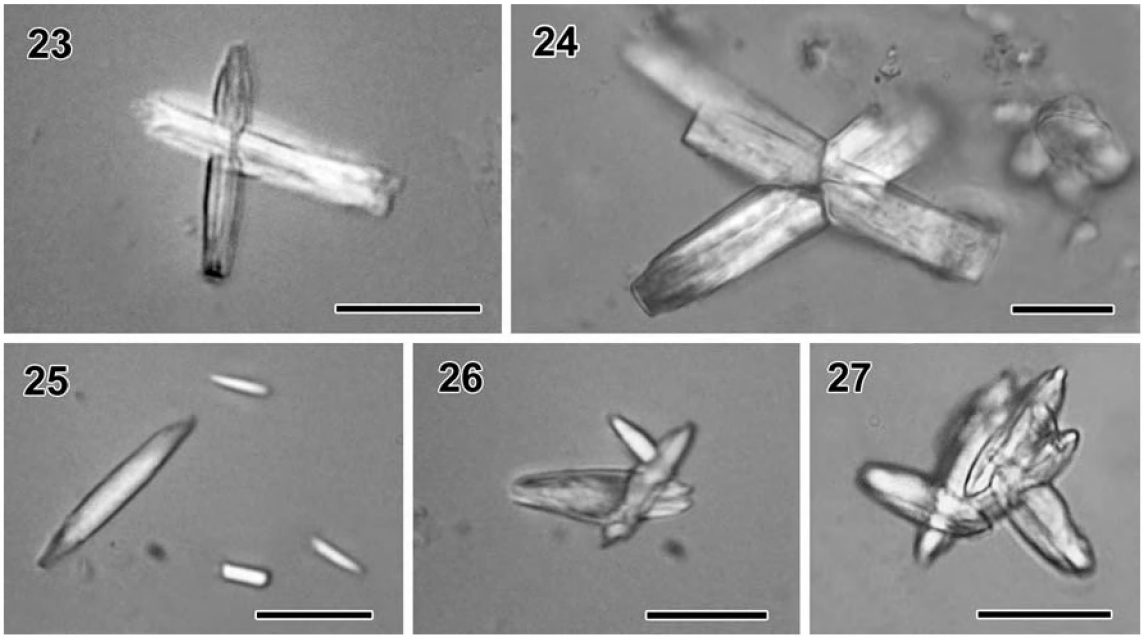
Figs 10-16. Broad hexagonal or diamond shaped prismatic crystals (Type-1b). Figs 10-12. Type-1b crystals in *Phyllodictyon orientale*. Fig. 10. Aggregate of crystals. Birefringence under polarizing optics demonstrates crystallinity of inclusions. Scale bar = 50 μm. Figs 11-12. Morphological variation of the crystals in a single cell. Scale bars = 25 μm. Figs 13-16. Type-1b crystals in *Cladophoropsis magnus*. Scale bars = 10 μm.



Figs 17-22. Needle or spindle shaped crystals (Type-2) in *Apjohnia laetevirens*. Figs 17-18. Dense accumulation of Type-2 crystals in the cells. Scale bars = 50 µm. Figs 19-22. Morphological variation of crystals within a single cell. Scale bars = 10 µm. Fig. 19. Needle shaped crystal with one attenuating end. Figs 20-21. Spindle shaped crystals with both ends attenuating. Fig. 22. Rod-shaped crystal without attenuating ends.

Broad hexagonal or diamond shaped prismatic crystals (**Type-1b**: Figs 10-16) were observed in *Chamaedoris peniculum*, *Cladophoropsis magnus*, *Phyllodictyon* (*P. orientale* and *P. pulcherrimum*) and *Struvea* (*S. gardineri*, *S. papuensis* and *S. plumosa*). In *Chamaedoris peniculum* the crystals are diamond-shaped and occur exclusively in the cells of the capitulum filaments with up to 5 crystals per cell; crystals are 12-24 µm in diameter, 18-35 µm long, with a l/w ratio of ca. 1.5. The diamond shaped crystals in *Cladophoropsis magnus* occur in all cells of the thallus with numbers ranging from ca. 20 to more than 100 per cell; crystals are 10-30 µm in diameter, 20-55 µm long, with a l/w ratio of 1.2-1.7. In the *Phyllodictyon* species, crystals are present in most cells (except the tenacular cells); the number of crystals per cell ranges between one and five. In *Phyllodictyon orientale*, *P. pulcherrimum* and *S. papuensis* the crystals are generally hexagonal, 15-25 µm in diameter, 20-65 µm long, with a l/w ratio of ca. 2. In *S. gardineri* the crystals are generally diamond shaped or triangular, 20-50 µm in diameter, 30-75 µm long, with a l/w ratio of 1.5-2. In *Struvea plumosa* crystals are diamond shaped, triangular or pentagonal and present in all cells, except the young laterals, with numbers per cell ranging from one to five; crystals are 5-27 µm in diameter, 8-32 µm long, with a l/w ratio of 1.2-1.5.

Needle or spindle shaped crystals with one or both ends attenuating to elongate rod-shaped crystals (**Type-2**: Figs 17-22) were found only in *Apjohnia laetevirens*. Crystals are present in all cells of the thallus and may exceed 1000 per cell, with diameters of 2-6 µm, and lengths up to 125 µm.



Figs 23-27. Clusters of elliptical or rod-shaped crystals (Type-3). Scale bars = 10 µm. Figs 23-24. Type-3 crystals in *Dictyosphaeria cavernosa*. Clusters of two and three rod-shaped crystals. Figs 25-27. Type-3 crystals in *Dictyosphaeria versluysii*. Elliptical crystalline structures, single or clustered.

Elongate elliptical to irregular rod shaped crystals (**Type-3**: Figs 23-27) differ from Type-1 crystals in their shape and the fact that they often form cruciate to star-shaped clusters. This type of crystal is present in the cells of *Dictyosphaeria cavernosa* and *D. versluysii* but was not found in *D. ocellata*. The number of crystals per cell is difficult to determine but is probably in the range of 1000 or more. Individual crystals are 1-3 µm in diameter and up to 20 µm long; the clusters are up to 25 µm in diameter.

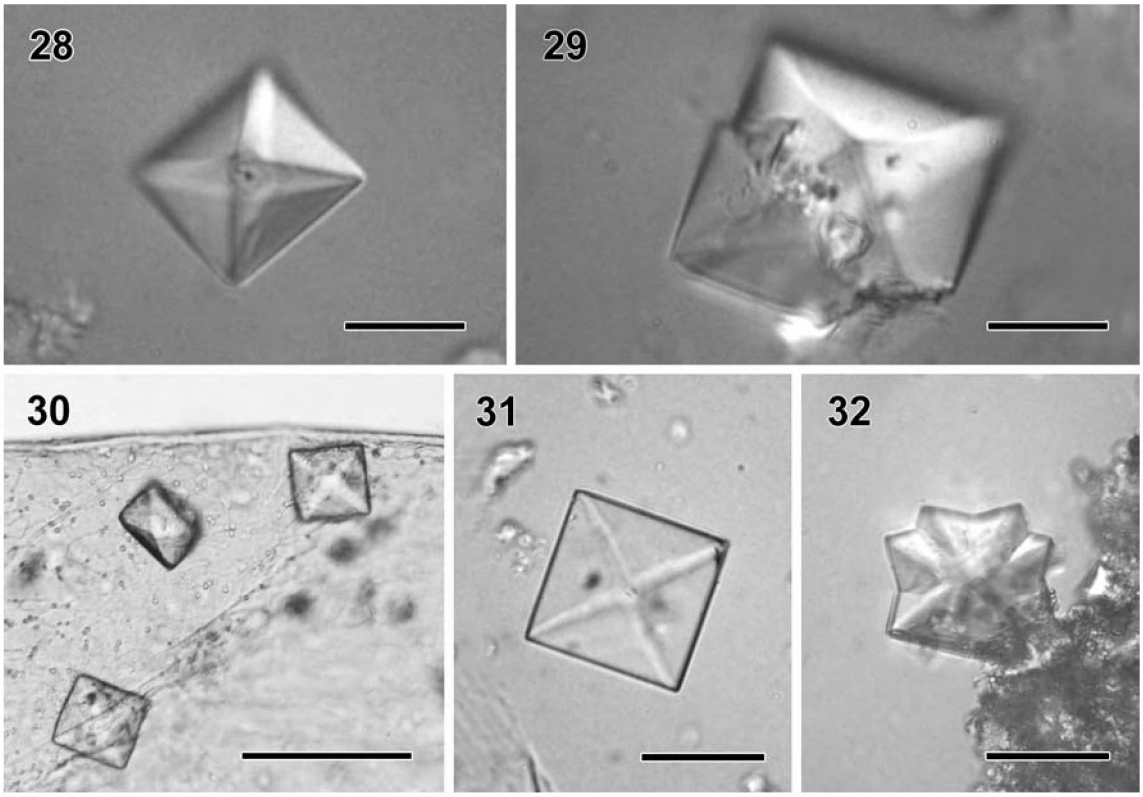
Octahedral crystals (**Type-4**: Figs 28-32) are present in *Valoniopsis pachynema*, where they occur in all cells of the thallus; the number of crystals per cell ranges from 100 to more than 1000; diameter 5-50 µm. Stellate morphologies resulting from two fusing crystals are sometimes found (Fig. 32). This type of crystal is less abundant in the cells of *Cladophora dotyana* and *Siphonocladus tropicus*; crystals in these species are 15-25 µm in diameter.

Globular aggregates of rod- or cone-shaped crystals (**Type-5**: Figs 33-35) are present in *Valonia fastigiata*, *V. macrophysa*, *V. utricularis* and *Ventricaria ventricosa*. The crystals could only be observed by dissecting the cell and viewing its contents under a light microscope. The crystals can be detected with brightfield microscopy but are especially noticeable when viewed with Nomarski contrast due to birefringence. The crystals stay intact when treated with sodium hypochlorite but dissolve in acetic acid and hydrochloric acid, suggesting their chemical composition to be calcium carbonate. The aggregates are 25-40 µm in diameter.

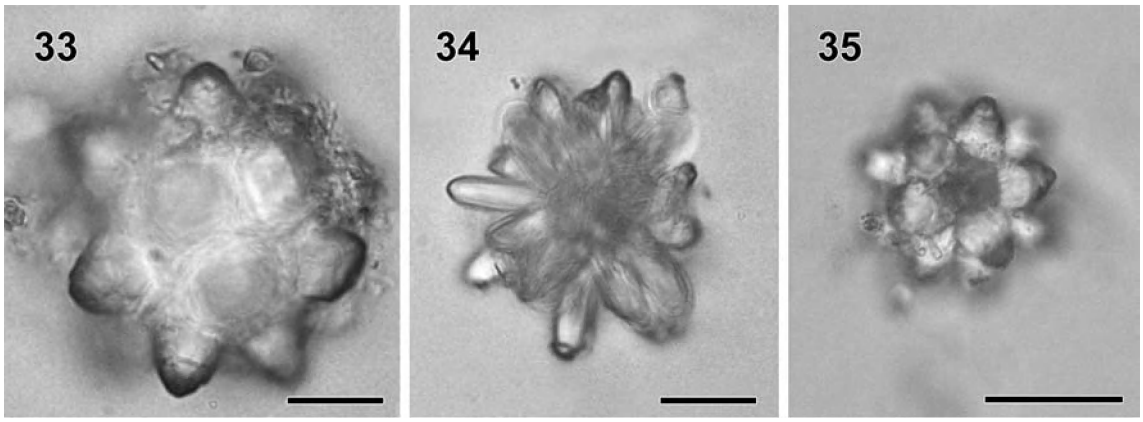
The colourless crystalline cell inclusions of Type-6 and -7 are not birefringent under polarized light and are therefore difficult to detect, especially when masked by the thick cell walls in some genera (e.g. *Valonia*). The inclusions can be observed by dissecting the cells and viewing the cell contents under a microscope. The structures dissolve when treated with sodium hypochlorite; they stain dark blue with methylene blue and dark brown with Lugol's iodine, suggesting a proteinaceous nature (dark blue staining with Lugol's iodine would indicate the presence of starch). Protein crystals stain easily due to their porous structure.

Cell inclusions of **Type-6** (Figs 36-44) are scattered among the chloroplasts. This type of crystal is abundant in cells of *Valonia aegagropila*, *V. fastigiata* and *V. utricularis*, and in the stipe cells of *Chamaedoris auriculata*, *C. delphinii* and *Struvea papuensis*. The crystals in these species are tetrahedral when small (diameter up to 40 µm) and grow into 4-armed structures with serrated edges, up to 230 µm across. Under the microscope these inclusions appear as 3-armed structures because the fourth arm is placed perpendicular to slide. In *Cladophoropsis herpestica* the crystals are less frequent and remain relatively small and tetrahedral, diameter up to 40 µm. The structures appear to have concentric bands, observable when stained with methylene blue. The bands replicate the crystal's morphology on a smaller scale; up to 5 bands per crystal were observed (Fig. 40).

Cubical cell inclusions (**Type-7**: Figs 45, 46) are present in the cells of *Cladophora prolifera*, *C. rugulosa* and *C. rupestris*. In *C. rugulosa* the crystalloids are especially abundant in the large basal cells. The diameters of the cubes are 5-15 (-20) µm in *C. prolifera* and *C. rupestris*, and up to 65 µm in *C. rugulosa*. In *C. rugulosa* two or more crystalloids are often fused in larger aggregates; frequently the structures are penetrated by crevices and are partially eroded (Fig. 45).



Figs 28-32. Octahedral crystals (Type-4). Figs. 28-29. Type-4 crystals in *Cladophora dotyana*. Scale bars = 10 µm. Figs. 30-32. Type-4 crystals in *Valoniopsis pachynema*. Fig. 30. Crystals scattered within a cell. Scale bar = 100 µm. Fig. 31. Surface view of an octahedral crystal. Scale bar = 25 µm. Fig. 32. Stellations resulting from two fusing octahedral crystals. Scale bar = 25 µm.

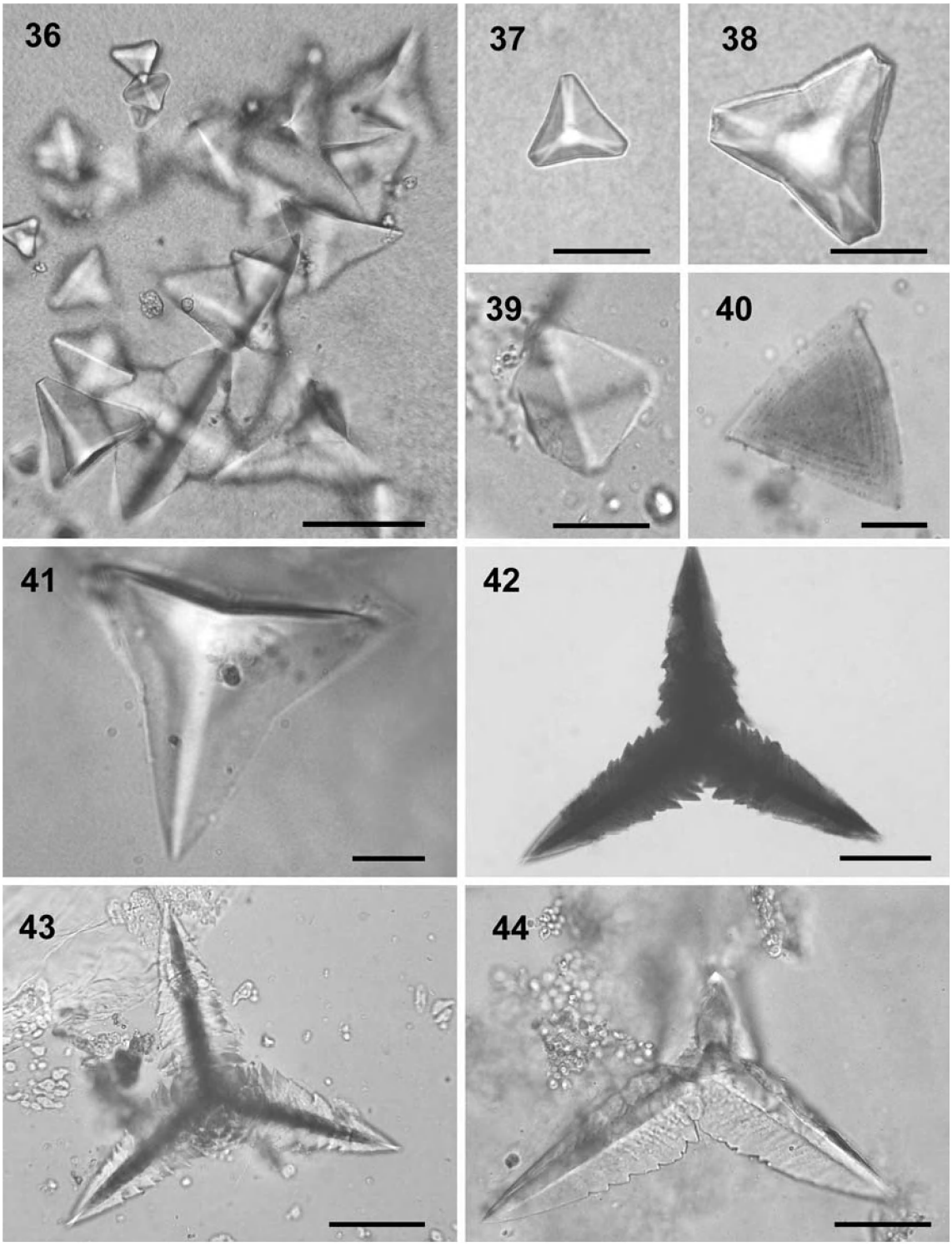


Figs 33-35. Globular aggregates of rod- or cone-shaped crystals (Type-5) in *Valonia* and *Ventricaria*. Figs 33-34. Type-5 crystals in *Valonia fastigiata*. Scale bars = 10 µm. Fig. 33. Globular aggregate of cone-shaped structures. Fig. 34. Globular aggregate of rod-shaped crystals. Fig. 35. Type-5 crystal in *Ventricaria ventricosa*: globular aggregate of cone-shaped structures. Scale bar = 25 µm).

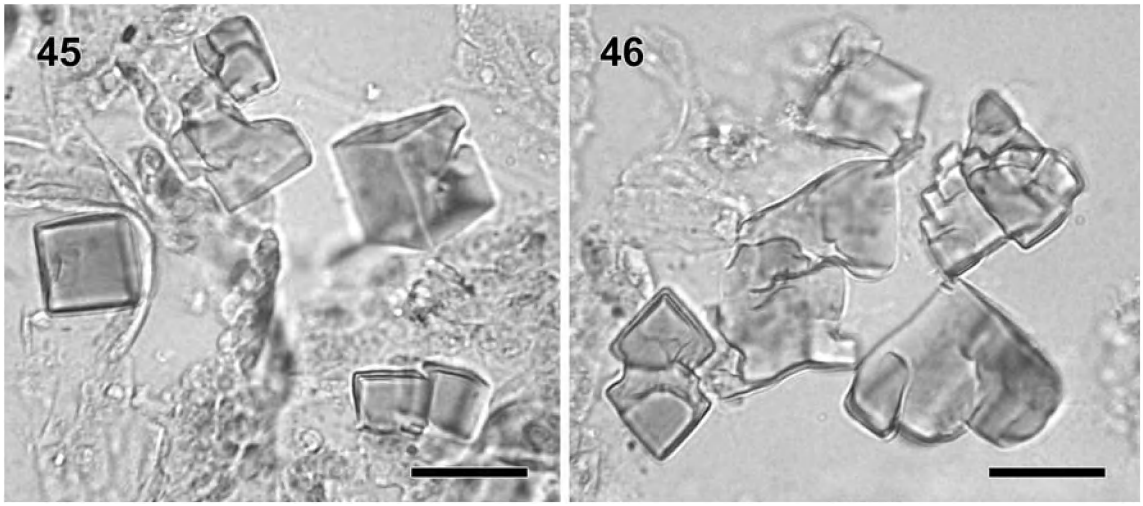
Star-shaped clusters of fine needle-shaped crystals (**Type-8**: Figs 47-49) are observed in a number of taxa (*Boodlea vanbosseae*, *Chaetomorpha aerea*, *C. brachygona*, *Chamaedoris auriculata*, *C. delphinii*, *Cladophora coelothrix*, *Microdictyon tenuius*, *Siphonocladus tropicus*, *Valonia aegagropila*, *V. fastigiata*, *V. macrophysa*, *Valoniopsis pachynema*, *Ventricaria ventricosa*). The structures appear bright under polarized light due to birefringence and can therefore be easily detected in taxa with relatively thin cell walls (e.g. some *Chaetomorpha* species, *Microdictyon* and *Siphonocladus*); in *Valonia* and *Ventricaria* dissection of the cells is needed to observe the inclusions. The crystalline structures stay intact when treated with hydrochloric acid, acetic acid and sodium hypochlorite. The clusters vary from being densely packed (Fig. 48) to loose aggregates of indefinite shape (Fig. 49); diameter of dense clusters 10-40 µm, loose aggregates up to 150 µm in diameter; needle-shaped crystals composing the clusters are straight or slightly curved, 0.2-1 µm in diameter, 10-35 µm long. The number of clusters per cell ranges between 1 and 7.

Discussion

Crystalline cell inclusions have previously been noticed in some members of the Cladophorophyceae but their taxonomic significance has never been examined. The needle-shaped crystals described in *Cladophoropsis membranacea* by Børgesen (1905: fig. 13; 1913: fig. 32, b) were also observed in this study and are categorized as CaOx crystals of Type-1a. The first record of protein crystalloids in the class was made by Klein (1882), who found cubical crystals in *Cladophora prolifera*. Later Chemin (1931) and Jónsson (1962) described tetrahedral protein crystals in *C. pellucida* and cubical protein crystals in *C. rupestris*. Recently van den Hoek & Chihara (2000: 96, fig. 44G) detected similar cell inclusions in Japanese *Cladophora* species without examining the chemical nature: tetrahedral crystals in *Cladophora sakaii* Abbott and cubical crystals in *C. ohkuboana* Holmes. Protein crystals with similar morphologies were also observed in the present study and are categorized as Type-6 and -7 protein inclusions.

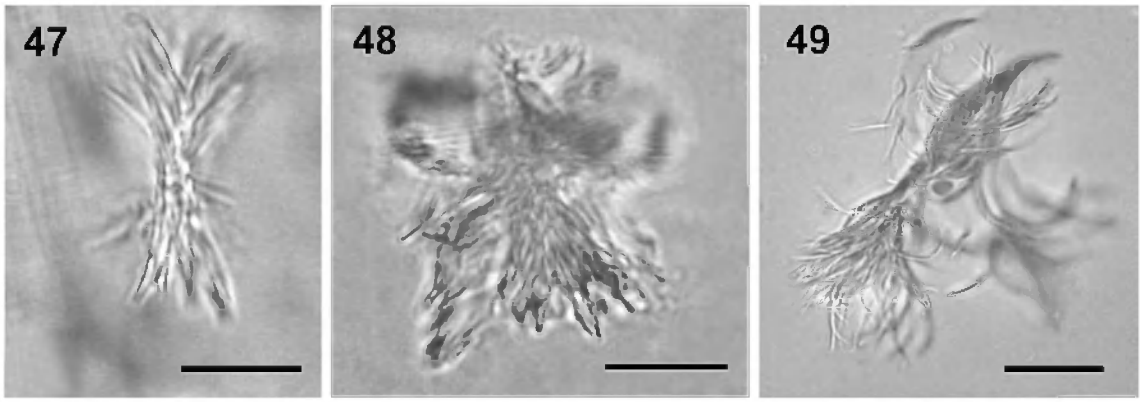


Figs 36-44. Tetrahedral cell inclusions (Type-6). Figs 36-38. Type-6 crystals in the stipe-cells of *Chamaedoris auriculata*. Fig. 36. Dense accumulation of type-6 crystals in the stipe-cell. Scale bar = 50 µm. Figs 37-38. 'Young' and 'mature' type-6 crystal. Scale bars = 25 µm. Figs 39-40. Type-6 crystals in *Cladophoropsis herpestica*. Fig. 39. Tetrahedral crystal eroded at one end. Scale bar = 25 µm. Fig. 40. Concentric bands within the structures observable when stained with methylene blue. Scale bar = 10 µm. Fig. 41. *Valonia aegagropila*. Tetrahedral type-6 crystal growing into a 4-armed star-shaped structure. Scale bar = 10 µm. Figs 42-43. *Valonia fastigiata*. 4-armed star-shaped structures (the 4th arm is not visible). Scale bars = 50 µm. Fig. 42. Dark blue staining with methylene blue. Fig. 43. Typical serrated edges of the star-shaped structures. Chloroplasts surrounding the crystalline structure. Fig. 44. *Valonia utricularis*. Serrated edges of the star-shaped structures. Chloroplasts surrounding the crystalline structure. Scale bar = 50 µm.



Figs 45-46. Cubical cell inclusions (Type-7) in the cells of *Cladophora rugulosa*. Scale bars = 25 µm. Fig. 45. Accumulation of cubical structures. Older structures are penetrated by crevices and are partially eroded. Fig. 46. Fusion of several cubical crystalloids forming larger aggregates.

The chemical nature of the various crystalline structures in this study is tentatively determined based on chemical solubility tests, staining methods and examination of birefringence under polarized light. Crystals of Type-1 to -4 are presumably composed of CaOx. CaOx crystals occur in a wide variety of organisms, including angiosperms and red and green algae (Khan 1995, Pueschel 2001). Plant cells make crystals of CaOx in an intriguing variety of shapes and their development is found to be genetically controlled (Franceschi & Horner 1980, Webb 1999). Two forms of CaOx crystals are found in biological systems: di-hydrated CaOx (mineralogical name: Weddellite) and mono-hydrated CaOx (mineralogical name: Whewellite). CaOx monohydrate crystals commonly appear as flat, elongated, six-sided prismatic crystals, corresponding to the crystals of Type-1a in the present study. CaOx di-hydrate crystals typically form octahedral crystals, corresponding to the crystals of Type-4 in this study. The morphological variation of the crystals of Type-1 to -4 has been observed in various related and non-related organisms. Needle-shaped crystals of Type-1a closely resemble the CaOx crystals found in the siphonous chlorophytes *Penicillus* (Friedmann *et al.* 1972) and *Chlorodesmis* (Ducker 1967), and the red alga *Antithamnion kylinii* (Pueschel 1995). Needle-shaped CaOx crystals, resembling Type-2 crystals in this study, are common in a wide variety of higher plants, where they are generally called rhaphides (Franceschi & Horner 1980; Prychid & Rudall 1999, 2000). The type-2 crystals in *Apjohnia* however, do not occur in bundles within a common organic matrix as rhaphides do in higher plants. The crystalline inclusions of Type-3 occur single or in clusters of 2-10 elongated crystals; these resemble the crystalline inclusions found in *Spongomorpha aeruginosa* (Linnaeus) van den Hoek (Acrosiphoniales) by Jónsson (1962), and the cruciate CaOx crystals found in *Spirogyra hatillensis* Transeau (Zygnematales) by Pueschel (2001). The octahedral Type-4 crystals found in *Valoniopsis pachynema*, *Cladophora dotyana* and *Siphonocladus tropicus* are similar to the CaOx di-hydrate crystals found on the surface of the lichen *Pyxine subcinerea* (Modenesi *et al.* 2001), or to renal stones composed of CaOx di-hydrate in mammals (Driessens & Verbeeck 1990).



Figs 47-49. Star-shaped clusters of fine needle-shaped crystals (Type-8). Fig. 47. *Chaetomorpha aerea*. Cluster of straight needle-shaped crystals. Scale bar = 10 µm. Fig. 48. *Siphonocladus tropicus*. Star-shaped cluster of needle-shaped crystals. Scale bar = 10 µm. Fig. 49. *Valonia macrophysa*. Cluster of curved needle-shaped crystals. Scale bar = 50 µm.

The globular aggregates of rod-shaped crystals (Type-5) are possibly composed of calcium carbonate based on the fact that the inclusions dissolve in acetic acid. In various species of green, brown and red algae the thallus is encrusted with calcium carbonate, occurring in two different crystalline states: calcite and aragonite (Borowitzka 1987; Simkiss & Wilbur 1989; Lobban & Harrison 1994). Aragonite is the most common form, and is deposited outside the cell-wall of some Chlorophyta (e.g. *Halimeda* and *Acetabularia*) and Phaeophyta (e.g. *Padina*), within the cell walls in some Rhodophyta (e.g. Gigartinales and Nemaliales), or in an organic matrix between the cells in some members of the Nemaliales. Calcite crystals are produced in the cell-walls of the Corallinales and in some Charophyceae. In some angiosperms and some members of the Peyssonneliaceae amorphous calcium carbonate occurs as cystoliths within cells (Watson & Dallwitz 1992 onwards; Boudouresque & Denizot 1975: 10, 38, figs 48, 49, 56, 57, 60; Womersley 1994: 153, figs 45, 46).

The colourless crystalline cell inclusions of Type-6 and Type-7 are presumably proteinaceous crystals. Jónsson (1962) demonstrated the proteinaceous nature of the cell inclusions in *Cladophora rupestris* and *C. pellucida* by xanthoprotein, biuret and Millon reactions. The concentric bands observed in the tetrahedral crystals of *Cladophoropsis herpestica* are comparable to the ones found in the protein crystals of *Haplogloia kuckuckii* (Phaeophyta) (Pueschel 1994: 95). Protein crystals are especially well known in the Rhodophyta where they are distributed among at least 11 orders (Pueschel 1992). Tetrahedral and cubical crystals, similar to the ones found in the present study, have been observed in the Ceramiaceae by Feldmann-Mazoyer (1941).

The chemical nature of the crystalline inclusions of Type-8 remains uncertain. Since the inclusions stay intact when treated with hydrochloric acid, they might be composed of silica. Star-shaped clusters of fine crystalline structures, similar to the crystals of Type-8, have been observed in *Spongomorpha aeruginosa* and *Acrosiphonia spinescens* (Kützing) Kjellmann (Acrosiphoniales) by Jónsson (1962).

The eight types of cell inclusions are plotted on a cladogram based on partial LSU rRNA sequence analysis (Leliaert *et al.* 2003) (Fig. 50). Although many species treated in the present study are missing in the phylogenetic analysis, the plotting of characters provides a general idea of the distribution of crystalline inclusions in the Cladophorophyceae. We restrain to draw conclusions about the evolution of these cellular inclusions for the following reasons. The absence of a particular crystal type in a taxon does not necessarily mean that the genes are absent or even that the product is not formed in a soluble form. An identical protein, for

example, may crystallize in one species but not in the second. Also various kinds of inclusions are not necessarily alternate states of a single character. Different shapes of protein crystals could be the result of differences of the same protein, or crystals of different morphologies could represent entirely different proteins (Pueschel, pers. comm.). Only CaOx crystals of Type-1a are characteristic for a single clade. The other types either occur in two or more separate lineages (types 1b, 4, 5, 6 and 8), or are only represented by a single taxon in the cladogram (types 3 and 7).

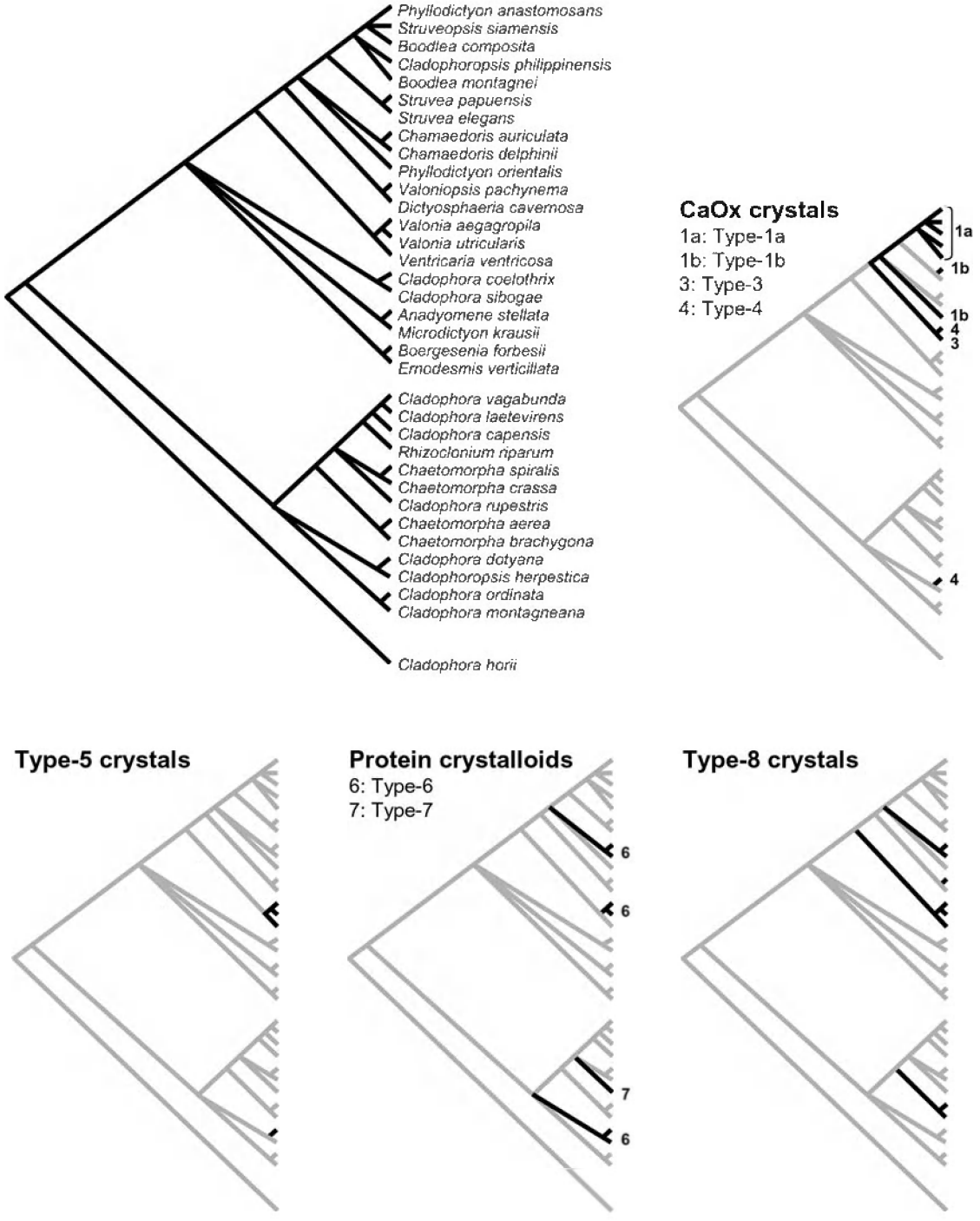


Fig. 50. Strict consensus maximum parsimony cladogram of the Cladophorophyceae based on partial large-subunit ribosomal RNA sequence analysis (Leliaert *et al.* 2003), with the different types of crystalline cell inclusions highlighted on different copies of the same plot.

The four types of CaOx crystals were found repeatedly in every specimen of a specific species, indicating that their presence is not environmentally dependent. Moreover the morphology of these crystals appears to be species- or genus-specific, indicating that their development would be genetically controlled and therefore have systematic value. Presence or absence of crystals can be used to distinguish between non-related species with similar thallus architectures, for example *Cladophoropsis sundanensis* and *Cladophora coelothrix*. Both species are characterized by a cushion-like growth form, presence of hapteroid rhizoids, delayed cross wall formation and have comparable cell dimensions. *Cladophoropsis sundanenis* can be distinguished from *Cladophora coelothrix* by the presence of elongate-rectangular crystals, which are absent in the latter. Some species in the genus *Cladophoropsis* possess CaOx crystals while in other species these crystals are absent. Molecular studies based on SSU and LSU rRNA gene sequences (Bakker *et al.* 1994; Hanyuda *et al.* 2002; Leliaert *et al.* 2003) demonstrate that *Cladophoropsis* is polyphyletic. One group of *Cladophoropsis* species is closely related to *Boodlea* and *Struvea*, while the other species are more closely related to certain *Cladophora* species. The first (i.e. *C. philippinensis*, *C. vaucheriiformis*, *C. membranacea*) can be characterized by the presence of CaOx crystals, whereas the other species (*C. javanica* and *C. herpestica*) lack this type of crystals. Additional species should be included in molecular analyses to test the usefulness of this character to distinguish between the two non-related *Cladophoropsis*-groups.

Jónsson (1962) demonstrated that the crystals found in adult thalli of *Cladophora pellucida* and *C. rupestris* were absent in germinating plants. Several authors suggest that protein crystals might have a storage function (Jónsson 1962; Wetherbee *et al.* 1984; Pueschel 1992, 1994). This hypothesis was confirmed by Pueschel & Korb (2001) who demonstrated that protein bodies in *Laminaria solidungula* were present in N-repleted conditions and absent from N-starved thalli. If the presence of proteinaceous inclusions is environmentally controlled, as the above studies suggest, their taxonomic application is undermined (Pueschel 1992).

As stated previously, morphological characters are scarce in the Cladophorophyceae. Many characters, such as growth form and branching pattern, have been found to be environmentally controlled and therefore have no value as taxonomic characters. The present study demonstrates that crystalline cell inclusions provide useful diagnostic characters at the specific level.

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Appendix 1: Species and specimens examined. Species with an * were found to enclose crystalline cell inclusion. Indication of collector, locality and herbarium [the following specimens are housed in GENT: Copp & PvR (E. Coppejans & W. Prud'homme van Reine), FL (F. Leliaert), HEC (E. Coppejans), KZN (E. Coppejans *et al.*), PH (F. Leliaert *et al.*), SEY (E. Coppejans *et al.*), Snellius-II (E. Coppejans *et al.*), SOC (F. Leliaert) and WA (T. Schils).

Anadyomene brownii (J. Gray) J. Agardh – Snellius-II 10516: Sumba, Indonesia.

Anadyomene plicata C. Agardh – Copp & PvR 13259: Madang, Papua New Guinea; HEC 6312: Port Moresby, Papua New Guinea.

Anadyomene stellata (Wulfen) C. Agardh – HEC 5450: Corsica.

**Apjohnia laetevirens* Harvey – Hussey s.n.: Port Elliot, S-Australia (NY); WA 138: Perth, W-Australia.

Boergesenia forbesii (Harvey) J. Feldmann – FL 628: Zanzibar, Tanzania; ODC 566: Dahab, Egypt; HEC 6334: Port Moresby, Papua New Guinea.

**Boodlea composita* (Harvey) Brand – Telfair s.n.: Mauritius (holotype, BM); Tilden 539: Oahu, Hawaii (NY); FL 927, FL 986, FL 1007: Zanzibar, Tanzania.

**Boodlea montagnei* (Harvey ex J. Gray) Egerod – Harvey, Algae Insul. Amicorum Exsicc. no. 89: Tonga (holotype, BM); Weber-van Bosse 1040: Flores, Indonesia (L 938 028 062); PH 646: Mactan Isl., The Philippines; FL 978: Zanzibar, Tanzania.

**Boodlea siamensis* Reinbold – Reinbold s.n.: Ko Chang Archipelago, Thailand (holotype, M); Børgesen 1068: St. Thomas, Virgin Islands (NY); FL 905: Mbudya Island, Tanzania.

**Boodlea vanbosseae* Reinbold – Reinbold s.n.: Lucipara Isl., Indonesia (holotype, M); Snellius-II 10117: Maisel Isl., Indonesia; SEY 603: Poivre Island, Seychelles; HEC 11411: Pemba Isl., Tanzania.

**Chaetomorpha aerea* (Dillwyn) Kützing – HEC 4187: N-France; FL 639: Zanzibar, Tanzania; KZN 908: KwaZulu-Natal, South Africa.

**Chaetomorpha brachygona* Harvey – Binney s.n.: Key West, Florida, U.S.A. (syntype, BM); Børgesen 1362, St. Croix, Virgin Island (BM); HEC 6096: Mombasa, Kenya; FL 981: Zanzibar, Tanzania.

Chaetomorpha crassa (C. Agardh) Kützing – HEC 5632: Mombasa, Kenya; PH 666: Siquijor, the Philippines; FL 983: Zanzibar, Tanzania.

Chaetomorpha gracilis Kützing – HEC 7317: Shimoni, Kenya; HEC 12944: Mnazi Bay, Tanzania.

Chaetomorpha spiralis Okamura – HEC 11621: Sri Lanka; KZN 814: Palm Beach, KwaZulu-Natal, South Africa; PH 239: Olango Island, The Philippines.

**Chamaedoris auriculata* Børgesen – Børgesen no. 5447: Dwarka, India (holotype, C); FL 906: Mbudya Island, Tanzania; SOC 344: S-Socotra; KZN 83: KwaZulu-Natal, South Africa.

**Chamaedoris delphinii* (Hariot) J. Feldmann & Børgesen – Ferlus s.n.: Fort-Dauphin, Madagascar (holotype, PC); Weber-van Bosse s.n.: Durban, South Africa (L 936 73 446); KZN 215: KwaZulu-Natal, South Africa.

**Chamaedoris peniculum* (Ellis & Solander) Kuntze – Børgesen 1575: St. Croix, Virgin Islands (NY); Howe 4430: Puerto Rico (NY); Vickers 34: Barbados (L 937 183 160); HEC 5032: Long Island, Bahamas.

**Chamaedoris orientalis* Okamura & Higashi – Yamada s.n.: Ryukyu, Japan (S); HEC 12289: Bulusan, The Philippines (21/04/98).

Cladophora capensis (C. Agardh) De Toni – FL 79: Kommetjie, South Africa; FL 169: Platboom, South Africa.

Cladophora catenata (Linnaeus) Kützing – KZN 398: Mabibi, KwaZulu-Natal, South Afica; KZN 767: Kosi Bay, KwaZulu-Natal, South Africa.

**Cladophora coelothrix* Kützing – HEC 9394: Mombasa, Kenya; KZN 321: Sodwana Bay, KwaZulu-Natal, South Afica; FL 953: Zanzibar, Tanzania.

**Cladophora dotyana* Gilbert – Gilbert 9214: Hokipa Park, East Maui, Hawaii (holotype, MICH); HEC 11240: Mafia Isl., Tanzania; PH 289: Bulusan, Sorsogon, The Philippines; KZN 1676: KwaZulu-Natal, South Africa.

Cladophora liebetruthii Grunow in Piccone – KZN 802: Palm Beach, KwaZulu-Natal, South Afica.

Cladophora montagneana Kützing – FL 900: Kunduchi, Tanzania.

Cladophora ordinata (Børgesen) van den Hoek – KZN 959: Trafalgar, KwaZulu-Natal, South Afica; FL 342: Port Edward, KwaZulu-Natal, South Africa.

**Cladophora prolifera* (Roth) Kützing – HEC 1790: S-Turkey.

**Cladophora rugulosa* G. Martens – HEC 11015: KwaZulu-Natal, South Africa; FL 225: KwaZulu-Natal, South Africa; KZN 819: KwaZulu-Natal, South Africa.

**Cladophora rupestris* (Linnaeus) Kützing – HEC 10781: N-France.

Cladophora sibogae Reinbold – HEC 5688: Mombasa, Kenya; FL 910: Mbudya Island, Tanzania.

Cladophora socialis Kützing – SEY 307: La Digue Island, Seychelles; FL 918: Mbudya Island, Tanzania.

**Cladophoropsis carolinensis* Trono – Yoshinaga s.n.: Nikumaroro Atoll, Kiribati (GENT).

**Cladophoropsis gracillima* Dawson – Dawson 3233: Punta Palmilla, Baja California Sur, Mexico (holotype, NY).

**Cladophoropsis javanica* (Kützing) P. Silva – Zollinger 2379: Java, Indonesia (PC); Taylor 46-287: Romurikku Isl., Marshall Islands (NY).

**Cladophoropsis herpestica* (Montagne) Howe – Hombron 3: New Zealand (PC); Womersley 234/b2: Elliston, S-Australia (MEL 3010); HEC 6001: Mombasa, Kenya.

**Cladophoropsis macromeres* Taylor – Taylor 903: Dry Tortugas, Florida (holotype, MICH); HEC 5624, HEC 8669B & HEC 9398: Mombasa, Kenya.

**Cladophoropsis magnus* Womersley – Womersley A 13,615: Smoky Bay, S. Australia (isotype, MEL 666096).

**Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgesen – s.n.: St. Croix, Virgin Islands (syntype, LD 7287); Papenfuss 10505: Oahu, Hawaii (UC 970829); Wynne 8209: Guadeloupe (MICH); van den Hoek 68/62: Curaçao (L 993 113 339); Womersley A56405: Cape Lannes, S-Australia (L 991 058 095).

**Cladophoropsis philippinensis* Taylor – Bartlett A-195: Little Santa Cruz Island, opposite Zamboanga, The Philippines (holotype, MICH); PH 567: Cebu, The Philippines.

**Cladophoropsis sundanensis* Reinbold – Weber-van Bosse s.n.: Indonesia (syntype, L 937 279 372); FL 975, FL 995 & FL 1000: Zanzibar, Tanzania.

**Cladophoropsis vaucheriiformis* (Areschoug) Papenfuss – FL 954 & FL 989: Zanzibar, Tanzania.

**Dictyosphaeria cavernosa* (Forsskål) Børgesen – s.n. Mokha, Yemen (holotype, C); FL 976: Zanzibar, Tanzania.

Dictyosphaeria ocellata (Howe) Olsen-Stojkovich – FL 630 & FL 667: Zanzibar, Tanzania.

**Dictyosphaeria versluysii* Weber-van Bosse – PH 634: Cebu, The Philippines; FL 993: Zanzibar, Tanzania; KZN 662: KwaZulu-Natal, South Africa.

**Ernodesmis verticillata* (Kützing) Børgesen – s.n.: St. Croix, Virgin Islands (holotype, L 937 183 51); Vickers 1533: Barbados (L 951 246 105); Dawson 3278: Baja California, Mexico (L 952 78 801).

Microdictyon kraussii J. Gray – HEC 10939: Durban, KwaZulu-Natal, South Africa; KZN 334: Sodwana Bay, KwaZulu-Natal, South Africa.

Microdictyon okamurae Setchell – Snellius-II 11644: Tukang Besi Islands, Indonesia; Snellius-II 11644: Salayer, Indonesia.

Microdictyon palmeri Setchell – Copp & PvR 13653: Madang Province, Papua New Guinea; HEC 4690: Hansa Bay, Papua New Guinea.

**Microdictyon tenuius* J. Gray – HEC 9808: Mafia Isl., Tanzania; HEC 10691: Zanzibar, Tanzania.

Microdictyon vanbosseae Setchell – Snellius-II 10887: Komodo Island, Indonesia.

**Phyllodictyon anastomosans* (Harvey) Kraft & Wynne – Harvey 582a: Fremantle, W-Australia (BM); HEC 6670: Laing Island, Papua New Guinea; FL 994: Zanzibar, Tanzania; SOC 253: Socotra.

**Phyllodictyon orientale* ('*orientalis*') (Gepp & Gepp) Kraft & Wynne – Gardiner, Sealark Exp'n s.n.: Amirante Islands (holotype, BM); HEC 6154: Bi Ya Doo Island, The Maledives; SEY 301: Bird Island, Seychelles; SEY 775: Plate Island, Seychelles.

**Phyllodictyon pulcherrimum* J.E. Gray – Howe 7228: Puerto Rico (NY); cancap 7403: Cape Verde Islands (L 997 062 499); Curtiss s.n.: Florida (*Microdictyon curtissiae* Taylor, Herb. Taylor 22712, MICH).

Rhizoclonium africanum Kützing – HEC 11291: Dar es Salaam, Tanzania; FL 725: Zanzibar, Tanzania.

**Siphonocladus rigidus* Howe – Howe 1502: Key West, Florida, USA (holotype, NY).

**Siphonocladus tropicus* (P. Crouan & H. Crouan) J. Agardh – Mazé 193: Guadeloupe (syntype, BM); Howe 4939: Jamaica (NY); HEC 9795: Mafia Isl., Tanzania; SOC 186: N-Socotra.

**Struvea elegans* Børgesen – Mortensen s.n.: between St. Thomas and St. Jan (syntype, C 1762); Taylor 313: Dry Tortugas, Florida (NY); HEC 10437: Port Moresby, Papua New Guinea.

**Struvea gardineri* A. Gepp & E. Gepp – Gardiner 10: Cargados Carajos (holotype, BM).

**Struvea papuensis* nom. prov. – HEC 4548, HEC 4696, HEC 7760: Laing Island, Papua New Guinea.

**Struvea plumosa* Sonder – Preiss s.n.: W-Australia (holotype, MEL 502116); Harvey 567a: Fremantle, W-Australia (MEL 666900); Womersley 169: Elliston, S-Australia (AK 144137).

**Struveopsis siamensis* (Egerod) P. Silva – ODC 665: Mbudya Island, Tanzania; FL 677: Zanzibar, Tanzania.

**Valonia aegagropila* C. Agardh – Bosc s.n.: Venezia, Italy (lectotype, LD 15978); HEC 9393: Mombasa, Kenya; FL 627, FL 688 & FL 990: Zanzibar, Tanzania.

**Valonia fastigiata* Harvey ex J. Agardh – Harvey 74: Sri Lanka (syntype, BM); Snellius-II 10810: Komodo Island, Indonesia; FL 688 & FL 729: Zanzibar, Tanzania.

**Valonia macrophysa* Kützing – FL 355 and KZN 90: KwaZulu-Natal, South Africa.

**Valonia utricularis* (Roth) C. Agardh – Copp & PvR 13511: Madang, Papua New Guinea; FL 922 and FL 957: Zanzibar, Tanzania.

**Valoniopsis pachynema* (G. Martens) Børgesen – s.n.: Sumatra, Indonesia (lectotype, L 936 181 388); HEC 11581: Sri Lanka; SEY 212: Bird Isl., Seychelles; FL 698 & FL 1006: Zanzibar, Tanzania.

**Ventricaria ventricosa* (J. Agardh) Olsen & J. West – FL 952: Zanzibar, Tanzania.

Chapter 5

A taxonomic re-assessment of the genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis*

Abstract – This present study presents a taxonomic re-assessment and revision of the genera *Boodlea* Murray & De Toni, *Chamaedoris* Montagne, *Cladophoropsis* Børgesen, *Phyllodictyon* Gray, *Struvea* Sonder and *Struveopsis* Rhyne & Robinson. The taxonomy of these genera has been primarily based on thallus architecture and some other characters, including tenacular cell types and mode of cell division. Although many authors have commented on the unclear boundaries between some of the genera (e.g. *Boodlea* and *Phyllodictyon*), their systematic histories are relatively separate. The mutual relationships and affinity with other genera has long been doubtful and the different genera have been placed in two or more separate families. The clustering of *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* in a well supported monophyletic group, the non-monophyly of a number of included genera, in combination with the fuzzy morphological boundaries and the presence of a number of shared derived morphological supports the recognition of a single genus. Based on priority, the oldest name, *Chamaedoris*, should be selected, but, in order to avoid disadvantageous nomenclatural changes we propose to conserve the name *Cladophoropsis*. Given the apparent morphological variety in the newly defined genus, six sections are distinguished: *Cladophoropsis* (including the species *C. kenyensis*, *C. macromeres*, *C. magna*, *C. membranacea*, *C. philippinensis*, *C. sundanensis* and *C. composita*), *Spongocladia* (incuding *C. vaucheriiformis*); section *Rigidae* (including *C. rigida*), *Phyllodictyon* (including *C. mexicana*, *C. orientalis* and *C. pulcherrima*), *Struvea* (including *C. elegans*, *C. gardineri*, *C. papuensis* and *C. plumosa*) and *Chamaedoris* (including *C. auriculata*, *C. delphinii*, *C. arbuscula* and *C. peniculum*). The application of the morphological species concept in the group is often problematic because of the limited number of morphological characters and the considerable phenotypic plasticity. Therefore a good understanding of this morphological variability (which is possible through the examination of a large number of specimens) is essential for establishing reliable (morphological) species circumscriptions. Detailed descriptions and illustrations are provided for the 20 recognized species, including two new species *C. kenyensis* and *C. papuensis*. Lectotypification of 15 taxa (including many synonyms) is made in this paper. Molecular evidence based on ITS and LSU sequence data in combination with a detailed morphological study indicate that the taxa "*Boodlea composita*", "*Phyllodictyon anastomosans*" and "*Struveopsis siamensis*" constitute a species complex. The conception of traditionally recognized taxa in this species complex is presumably clouded by a combination of different factors: ecologically induced phenotypic plasticity, developmental variability, hybridisation, and cryptic, genetic differentiation. For now, a single species, *Cladophoropsis composita*, is recognized. Awaiting the true nature of the morphological entities in the *C. composita* complex (different species or growth forms of the same species), the different morphological types are referred to as phenodemes.

Contents of chapter 5

1. Introduction

The genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis* are generally placed in the Siphonocladaceae Schmitz (Silva *et al.* 1996) but their mutual relationships and affinity with other genera has long been doubtful. Børgesen (1925) allied *Boodlea* with *Cladophoropsis* based on the delay of cross wall formation at the base of the laterals and created the family Boodleaceae. Egerod (1952) considered *Boodlea* to be closely related to *Struvea* based on similar mode of anastomosis by tenacular cells, while *Cladophoropsis* was allied with *Siphonocladus* based on the segregative mode of cell division (cleavage of the multinucleate protoplast into walled, rounded portions which later expand into new cells). *Struveopsis* has been related to a number of genera, including *Apjohnia*, *Boodlea*, *Cladophoropsis*, *Ernodesmis*, *Struvea* and *Willeella* by Rhyne & Robinson (1968), or to *Cladophora* by Kraft & Wynne (1996). *Phyllodictyon* has recently been resurrected and split off from *Struvea* based on differences in mode of cell division (Kraft & Wynne 1996).

Based on immunological distances, Olsen-Stojkovich (1986) and Olsen-Stojkovich *et al.* (1986) demonstrated that *Boodlea composita*, *Phyllodictyon anastomosans*, *Cladophoropsis membranacea* and *Chamaedoris peniculum* form a tightly associated clade. More recent phylogenetic studies based on sequence analyses of rDNA internal transcribed spacers (Kooistra *et al.* 1993), SSU rRNA (Wysor 2002) and partial LSU rRNA (Leliaert *et al.* 2003) confirm the immunological studies and reveal an extreme close relationship between the genera *Boodlea*, *Chamaedoris*, *Cladophoropsis* (excluding *C. herpestica*), *Phyllodictyon*, *Struvea* and *Struveopsis*. The tight clustering of these genera is not surprising given that taxonomic and phenetic studies demonstrate numerous morphological similarities and extreme vague boundaries between these genera (with the exception of *Chamaedoris* which can be easily distinguished) (Børgesen 1913; Egerod 1952; Olsen-Stojkovich 1986; Kooistra *et al.* 1993; Leliaert *et al.* 1998).

This study aims to (1) re-assess the genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis* based on morphological and molecular evidence, (2) examine whether or not the separate recognition of these genera is justified, (3) assess the morphological diversity and plasticity, (4) determine the number of recognized morpho-species and to provide their accurate descriptions and illustrations.

2. Material and methods

Extensive field collections were made in various regions of the (sub)tropical Indo-West Pacific from 1980 to 2003 and are deposited in GENT; these herbarium numbers are prefixed by the "Copp & PvR" (seaweeds from Papua New Guinea, collected by Eric Coppejans and Willem Prud'homme van Reine) "FL" (collections of Frederik Leliaert); HEC (herbarium of Eric Coppejans), "HOD" (herbarium of Olivier Dargent); KZN (collections from KwaZulu-Natal, South Africa), "MAS" (collections from Masirah, Oman of Tom Schils), "ODC" (collections of Olivier De Clerck), "PH" (Philippine collections of Leliaert, Liao and Dargent), "SEY" (Seychelles collection of Coppejans, Kooistra and Audiffred), "sMM" (Socotra collection of Tom Schils), "Snellius-II" (collections from the Snellius-II expedition) or "SOC" (Socotra collection of Leliaert). Many other collections worldwide, including historical collections and type specimens, were studied from AKU, B, BISH, BM, BR, GB, L, LD, M, MEL, MICH, NSW, NY, O, PC, S, SAP, UC, UPS and W (herbarium abbreviations follow Holmgren *et al.* 1990).

Two new species are being described in this chapter. Effective publication of new taxa in theses (e.g. a PhD dissertation) is allowed according to the International Code of Botanical Nomenclature (2000), Art. 29 as long as the printed matter is distributed (through sale, exchange, or gift) to the general public or at least to botanical institutions with libraries accessible to botanists generally. However, there have been debates among taxonomists if this practice is favourable (see for example a discussion on the Taxacom Listserv in 1997: http://biodiversity.bio.uno.edu/mail_archives/taxacom/). In order to avoid later nomenclatural confusion we indicate the new names as provisional (sp. nov. prov. or nom. nov. prov.). Similarly, the new combinations made and the new sections proposed are provisional names (comb. nov. prov. and stat. nov. prov.).

Liquid-preserved material and rehydrated herbarium specimens were examined with a light microscope, after portions were prepared on glass microscopic slides and stained with 1% methylene blue. Drawings were made with a camera lucida on a Leitz-Diaplan bright field light microscope. Photographs were taken with an Olympus-DP50 digital camera mounted on the microscope. Calcium oxalate crystals were examined using differential interference (Nomarski) contrast.

To assess the morphological variability and possible morphological overlap in the species complex *Cladophoropsis herpestica-javanica* and the *Boodlea* (*Cladophoropsis*) *composita* complex, Principal Component Analysis (PCA) were carried out using the FORTRAN program CANOCO (Ter Braak 1988).

The species are presented alphabetically within each section. Type specimens which have been examined are indicated with an exclamation mark after the herbarium abbreviation. Distribution data and habitat description of the species are based on personal observations, data from specimen labels and verifiable literature data.

Phylogenetic analyses of the partial LSU rDNA dataset with only specimens of clade B6 included (Leliaert *et al.* 2003) were performed using PAUP 4.0* beta version 10 (Swofford 2002). *Valonia aegagropila* and *Valoniopsis pachynema* were used as outgroup taxa. Gaps were treated as missing. Maximum parsimony (MP) analyses were carried out using a general heuristic search, with 100 random sequence additions, TBR swapping and MULTREES options; branches were collapsed if it was possible for them to have zero length. For the neighbour-joining (NJ) analyses, a Jukes-Cantor model, was used. Bootstrapping (Felsenstein, 1985) was performed in PAUP* using 1000 replicates for the MP and NJ analysis.

3. History of the genera

Chamaedoris

Chamaedoris ['χαμαι' = low growing flower, 'δορις' = sea goddess, wife of the sea god Nereus in the Greek mythology] was described by Montagne (1842) to accommodate *Penicillus annulatus* Lamarck, a homotypic synonym of *Corallina peniculum* Ellis & Solander. The original genus delineation is very similar to the one used to date: thalli consisting of clustered, annulated stipes, each producing an apical capitulum, composed of branched and entangled filaments. According to Børgesen (1912: 59) cell division in the apical pole of the stipe and in the capitulum filaments takes place by segregative cell division. It is now known that the main mode of cell division in the capitulum filaments is by centripetal invagination of the cell walls while segregative cell division only occurs occasionally, often in response to cell wounding. Most taxonomic work on the genus has been performed by Børgesen (1912, 1933, 1940) and

Olsen-Stojkovich (1986). In the course of time only two new species (*C. auriculata* and *C. orientalis*) have been described and one species (*C. delphinii*) transferred from *Siphonocladus* to *Chamaedoris*.

Struvea and *Phyllodictyon*

The genus *Struvea* was founded by Sonder (1845: 49) in a paper in which he described the Australian algae collected by Preiss; the name was chosen in honour of a Russian ambassador, H. de Struve. The only species described, *S. plumosa*, became better known by the illustrations of Kützing (1856: Tab. 90) and Harvey (1958, pl. 32). Knowledge of the genus has been gained primarily through the monograph of Murray & Boodle (1888b) and the works of Børgesen (1912, 1913). To date16 additional species have been described in, or transferred to *Struvea*. The genus was later conserved by Silva (1952: 297) versus *Struvea* Reichenbach, a synonym of *Torreya* Arnott (Taxaceae).

The genus *Phyllodictyon* ['φύλλο'= blade, 'δίκτυον' = net] was created by Gray (1866: 69-71) to accommodate *P. pulcherrimum* J.E. Gray, collected by A. Menzies in the Gulf of Mexico. The genus was thought to be closely allied with *Microdictyon* (both placed in the Microdictyonemeae J.E. Gray, a group of the Confervaceae). Gray (1866: 43) believed that *Struvea* was allied to the "unicellular Algae" (referring to the aberrant cell structure, now known to be caused by segregative cell divisions), and thus unrelated to *Phyllodictyon*. *P. pulcherrimum*, the only species in the genus was soon transferred to *Struvea* by Murray & Boodle (1888b: 281), based on similarities in thallus architecture, and recently returned to *Phyllodictyon* by Kraft & Wynne (1996) on the basis of mode of cell division (see next paragraph). The genus *Pterodictyon* ['πτερο' = wing or blade, 'δίκτυον' = net] was created in the same paper as *Phyllodictyon* (Gray 1866: 70) to accommodate *Cladophora anastomosans* Harvey (1859), collected by Harvey at Fremantle, Western Australia. Gray (l.c.) regarded the genus closely related to *Phyllodictyon*, differing only in cell dimensions and shape of the lamina. *Pterodictyon anastomosans* was later transferred to *Struvea* by Piccone (1884b: 20), and recently placed in *Phyllodictyon* by Kraft & Wynne (1996). The genus name *Pterodictyon* was also found to be illegitimate because the name was already used earlier for a form-genus of fossil stem, probably from a lycopod (Kraft & Wynne 1996: 138).

Kraft & Wynne (1996) resurrected the genus *Phyllodictyon* and distinguished it from *Struvea* based on different modes of cell division. In *S. plumosa* (the type of *Struvea*) the blade cells divide by segregative cell division (SCD), while in *P. anastomosans* and *P. pulcherrimum*, cell division is accomplished by centripetal wall ingrowths (CI). Kraft & Wynne (l.c.) restricted the genus *Struvea* to two species (*S. plumosa* and *S. elegans*), while the other *Struvea* species were transferred to *Phyllodictyon*. However, we believe that the taxonomic significance of mode of cell division on a generic level is questionable based on the following evidence. 1) Phylogenetic studies have demonstrated that SCD evolved several times independently in the Siphonocladales, and mode of cell division cannot be used to typify monophyletic groups (Leliaert *et al.* 2003). 2) Several species whose cells normally divide by CI occasionally exhibit SCD, e.g. *Chamaedoris peniculum* (Børgesen 1912) and *Cladophoropsis membranacea* (La Claire 1982). In *Chamaedoris* CI is the main mode of cell division in the capitulum filaments, while the initial cell divisions in the stipe are segregative. 3) In *Struvea gardineri* and *Phyllodictyon papuense*, the mode of cell division is segregative in the initial stages of lamina development while in the older blades, cells divide by CI. Similarly in *Chamaedoris auriculata*, *C. delphinii* and *C. orientalis* Okamura & Higashi, the stipe initially divides by SCD, while the capitulum filaments divide by CI.

In a phylogeny based on partial LSU rRNA, *S. elegans* and *P. papuense* always cluster together, while two other *Phyllodictyon* species (*P. orientale* and *P. anastomosans*) are situated in different sub-clades within the *Cladophoropsis*-complex (Leliaert *et al.* 2003).

Cladophoropsis

The genus *Cladophoropsis* was created by Børgesen (1905) who assigned seven species to it, previously placed in the genus *Siphonocladus* Schmitz. Børgesen (l.c.) however only made one new combination, *C. membranacea*. The other members (*S. brachyartrus*, *S. fasciculatus*, *S. modonensis*, *S. psyttaliensis*, *S. voluticula* and *S. zollingeri*) were left as *Siphonocladus* and were only transferred later (along with three additional species) to *Cladophoropsis* by Reinbold (1905) and Wille (1910) (see diagram). The original circumscription of the genus – cushion-like thalli composed of unilateral to irregular branch systems with laterals lacking basal cross walls – is still generally accepted today. Two other genera, *Spongocladia* and *Spongodendron*, are considered to be congeneric with *Cladophoropsis* (Murray and Boodle 1888a; Papenfuss 1950), although the merger of *Spongocladia* and *Cladophoropsis* has not been accepted by some authors (Millar & Kraft 1994; Silva *et al.* 1996). Recently Hanyuda *et al.* (2002) demonstrated the very close relationship between *Cladophoropsis vaucheriiformis* (*Spongocladia*) and *C. membranacea* based on 18S rRNA gene sequences.

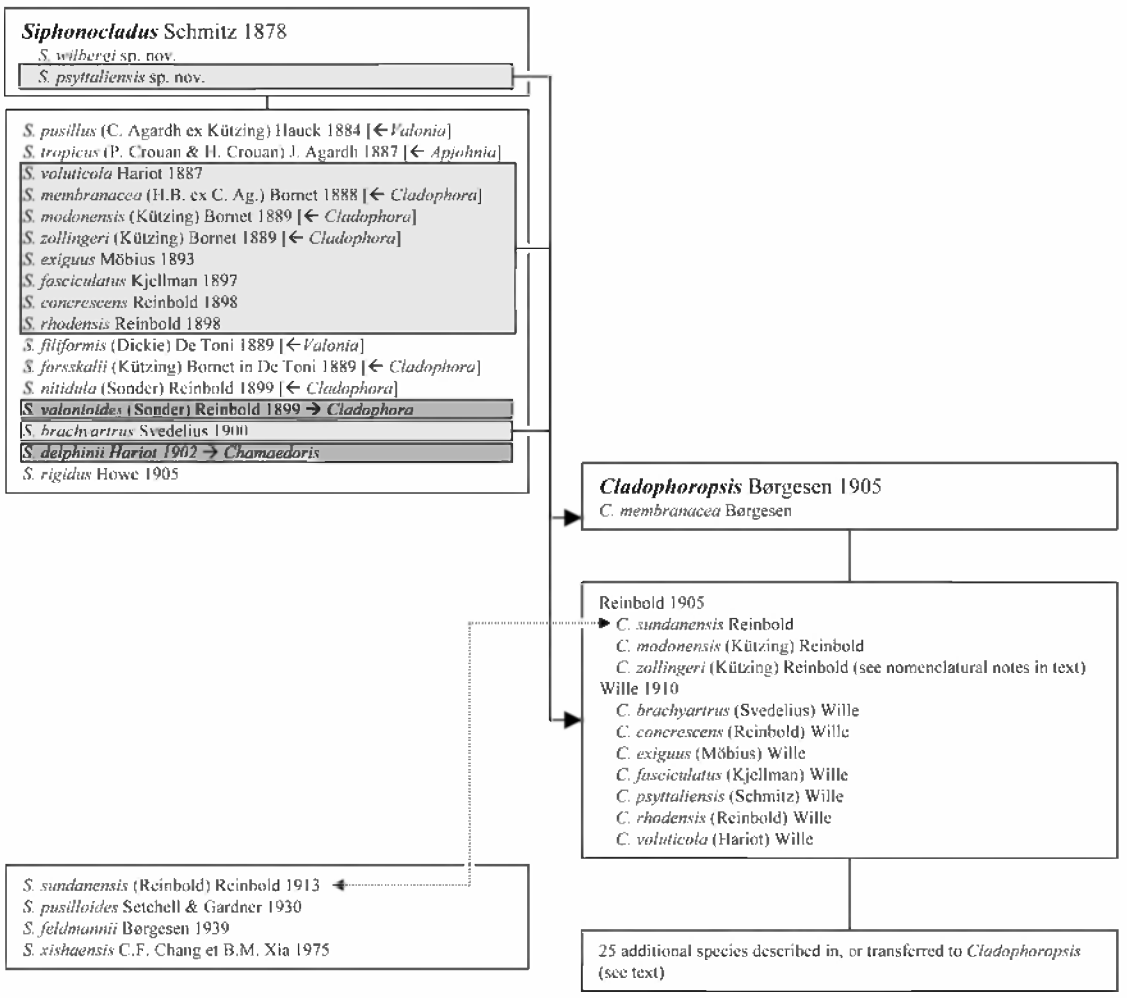

Diagram showing the nomenclatural relationship between *Cladophoropsis* and *Siphonocladus*.

Despite the extreme simple thallus architecture, 36 different species have been described or transferred to *Cladophoropsis* (Index Nominum Algarum). New species have been defined based on differences in branching pattern, cell dimensions and presence or absence of tenacular cells and rhizoids. The number of species that should be recognized however remains debatable. Womersley (1984) credited the genus with about 20 species, while Olsen-Stojkovich (1986) remained ambiguous with 4 to 29 species. Many authors therefore emphasized the need of a monographic treatment of the genus and pointed out that many of the described species may prove to be untenable (Egerod 1971, 1975; Womersley 1984; Sartoni 1992).

Børgesen (1905) was indecisive about the systematic position of his new genus. Originally, *Cladophoropsis* was placed in the Cladophoraceae. Later Børgesen considered segregative cell division to be characteristic for the genus and therefore included it successively in the Valoniaceae (Børgesen 1913), Boodleaceae (Børgesen 1925) and finally in the Siphonocladaceae (Børgesen 1948). Segregative cell division is currently considered to occur only in certain *Cladophoropsis* species (van den Hoek 1984; Womersley 1984; Millar & Kraft 1994), often in response to wounding (La Claire 1982). van den Hoek (1984) regarded *Cladophoropsis* to be morphologically related to *Cladophora* section *Repentes*, based on similar branching pattern, presence of rhizoids and tenacular cells. Phylogenetic studies based on ITS, SSU and LSU rRNA gene sequences have demonstrated that *Cladophoropsis* is polyphyletic and that morphological characters in the class are generally unsuitable for retrieving evolutionary relationships, owing to repeated convergence and parallel evolution (Kooistra *et al.* 1993, Bakker *et al.* 1994; Hanyuda *et al.* 2002; Wysor 2002; Leliaert *et al.* 2003). Most *Cladophoropsis* species fall within a genus complex including *Boodlea* and *Struvea*, while *C. herpestica* (including *C. javanica*) is more closely related to the *Cladophora* section *Longi-articulatae*.

Circumscription of *Cladophoropsis* to date

Cladophoropsis as presently conceived is polyphyletic as mentioned above. One group of *Cladophoropsis* species (including the type species *C. membranacea*, *C. philippinensis*, *C. sundanensis* and *C. vaucheriiformis*) is situated in the siphonocladalean lineage (Hanyuda *et al.* 2002; Leliaert *et al.* 2003) and closely related to the genera *Boodlea*, *Phyllodictyon*, *Struveopsis*, *Struvea* and *Chamaedoris*. These *Cladophoropsis* species can either be seen as reduced forms of *Boodlea*-, *Phyllodictyon*-, *Struvea*- or *Chamaedoris*-type architectures, or the *Cladophoropsis*-type morphology can be considered as an ancestral state from where the more complex architectural types have evolved (Leliaert *et al.* 2003). Most *Cladophoropsis* s.s. species and nearly all taxa in the related genera can be characterized by the presence of prismatic calcium oxalate (CaOx) crystals (Leliaert & Coppejans 2004) and the occasional occurrence of segregative cell division. *Cladophoropsis* s.s. most probably does not consist of a natural group as implied by ITS gene sequence analyses (Kooistra *et al.* 1993, Wysor 2002, unpublished pers. obs.).

Cladophoropsis herpestica (including *C. javanica*, see Appendix 2) is unrelated to *Cladophoropsis* and is located in the cladophoralean lineage within a clade of *Cladophora* section *Longi-articulatae* [including *C. dotyana* Gilbert, *C. japonica* Yamada, *C. ohkuboana* Holmes, *C. pellucida* (Hudson) Kützing, *C. sakaii* Abbott and *C. pellucidoidea* van den Hoek]. *C. herpestica* can be regarded as reduced form of a *Cladophora*-type architecture (Leliaert *et al.* 2003). The species lacks CaOx crystals but the cells contain tetrahedral protein crystals, similar to those found in some species of *Cladophora* section *Longi-articulatae* (Jónsson 1962; van den Hoek & Chihara 2000; Leliaert & Coppejans 2004). *C. herpestica* is furthermore characterized by rhizoids sprouting from the proximal pole of nearly every cell of the thallus (including the

subapical cells). This type of rhizoid formation is also found in some species of the *Cladophora* section *Longi-articulatae* (e.g. *C. minisakaii*: van den Hoek & Chihara: 108, fig. 49). Rhizoids sprouting from the proximal pole of the cells also occur in some *Cladophoropsis* s.s. species, but only in the basal parts of the thallus. Based on this combined molecular and morphological evidence we propose to return *C. herpestica* to the genus *Cladophora*; species description and illustrations are provided in Appendix 2.

Historical relationship of *Cladophoropsis* with *Siphonocladus*

The genus *Siphonocladus* was created by Schmitz (1879) to accommodate two new species, *S. wilbergi* and *S. psyttaliensis*, with filamentous branched thalli and laterals lacking basal cross walls. In the following years 17 additional species were described or moved (mainly from *Cladophora* or *Valonia*) to *Siphonocladus* (Fig. 1). Later Børgesen (1905) re-defined the genus *Siphonocladus* and suggested to transfer the majority of its species to his new genus *Cladophoropsis* (see above). Børgesen (l.c.) distinguished *Siphonocladus* from *Cladophoropsis* by its large clavate cells with basal annular constrictions producing laterals in all directions by segregative cell division. Ten *Siphonocladus* species were transferred to *Cladophoropsis* (Børgesen 1905, Reinbold 1905, Wille 1910); one other species, *S. delphinii*, was transferred to *Chamaedoris* by Feldmann & Børgesen (in Børgesen 1940), and *S. valonioides* was returned to *Cladophora* by Kützing (1849: 391). Only three additional *Siphonocladus* species have been described after 1905. To this day the separate recognition of *Cladophoropsis* and *Siphonocladus* has been generally accepted but the taxonomic boundaries and the relationship between both genera have become unclear.

Of the nine *Siphonocladus* species recognized today, only five [the type species, *Siphonocladus wilbergi* (= *S. pusillus*), *S. tropicus*, *S. filiformis*, *S. pussilloides* and *S. feldmannii*] meet the genus criteria as circumscribed by Børgesen (1905). Two of the remaining species, *S. forsskalii* (Kützing) Bornet in De Toni and *S. nitidula* (Sonder) Reinbold, are characterized by a typical *Cladophora*-type architecture and need to be returned to that genus. The systematic position of *S. rigidus* has long been questionable. The species was originally described in *Siphonocladus*, based on the segregative cell division and the multiseriate filaments although Howe (1905) was not completely confident about this systematic position considering the numerous differences between his new species and *Siphonocladus tropicus*. The possible affinity of *S. rigidus* with *Cladophoropsis* was briefly suggested by Børgesen (1913, footnote on p. 46-47). In this paper we propose to transfer *S. rigidus* to *Cladophoropsis* based on the following morphological grounds. 1) The thallus architecture is essentially similar to that of several other *Cladophoropsis* s.s. species. Cells formed by segregative cell division each produce one lateral which are unilaterally organized and lack basal cross walls. Because the filaments in *S. rigidus* are relatively broad, the daughter vesicles formed by segregative cell division are not always organized linearly (as is the case in *C. sundanensis* and *C. vaucheriiformis*) but lay perpendicular or in rows of two ore more. These oblique or longitudinal cell divisions result in multiseriate filaments which are apparently similar to *Siphonocladus tropicus*. 2) Tenacular cells and prismatic calcium oxalate crystals characterize many *Cladophoropsis* s.s. species and closely related genera, but do not occur in *S. pusillus* nor *S. tropicus*.

In a phylogenetic study of the Cladophorophyceae, Leliaert *et al.* (2003) demonstrated that *S. tropicus* is closely related with the monospecific genera *Ernodesmis* and *Boergesenia*, and more distantly related with *Cladophoropsis* (excl. *C. herpestica*). *Ernodesmis*, *Boergesenia* and *Siphonocladus* are all characterized by inflated, club-shaped cells with basal annular

constrictions but differ in their mode of cell division, and consequently in their thallus architecture.

Boodlea

The genus *Boodlea*, named in honour of Leonard Boodle (a fellow worker and friend of George Murray), was created by Murray & De Toni (in Murray 1889: 245) to assign *Cladophora coacta* Dickie, collected along the coast of Japan during the "Challenger" expedition. *Boodlea* was originally circumscribed as sponge-like thalli composed of a three-dimensional reticulum, reinforced through anastomosis by type-3 tenacular cells. The genus was distinguished from *Struvea* by the lack of a stipe and the irregular, three-dimensional branching, and from *Microdictyon* by the presence of type-3 tenacular cells[1]. Murray (1889) suggested to transfer *Microdictyon montagnei* Harvey ex J.E. Gray (possessing type-3 tenacular cells) to *Boodlea*, but the new combination was only made later by Egerod (1952: 332, footnote). To date, eight additional species have been described or transferred to *Boodlea* (*B. composita*, *B. kaenana*, *B. mutabile*, *B. paradoxa*, *B. siamensis*, *B. struveoides*, *B. trukensis* and *B. vanbosseae*) and four forms have been described for *B. composita* (f. *contracta*, f. *elongata*, f. *irregularis* and f. *robusta*). *B. kaenana* and *B. siamensis* have been reduced to synonyms of *B. composita* by Egerod (1952: 362) and Børgesen (1946: 16) respectively; *B. paradoxa* was proposed as a synonym of *B. montagnei* by Papenfuss & Egerod (1957: 83-84).

The distinction between *Boodlea* (three-dimensional net-like thalli lacking a stipe) and *Struvea* or *Phyllodictyon* (stipitate blades composed of a two-dimensional reticulum) has been generally accepted to date. However, many authors commented on the vague boundaries between the two genera (see *C. composita* complex, below). Egerod (1952, 1975) already noticed that the initial developmental stages of *B. composita* are indistinguishable from *S. anastomosans*, and stated "one might even question whether the genus *Struvea*, or at least the species *S. anastomosans*, exists at all or whether it represents but a stage on the way to becoming something else". Moreover, not all *Boodlea* species fit in the original and widely accepted circumscription. *B. montagnei* and *B. struveoides* for example, have been described as monostromatic blades, and the latter even develops a distinct stipe. A phylogeny based on partial LSU sequences confirms the unclear boundaries between the two genera and demonstrated that *P. anastomosans* is more closely related to *Boodlea* than to other *Phyllodictyon* or *Struvea* species (Leliaert *et al.* 2003).

Nereodictyon was created by Gerloff (1960) to accommodate a single species, *N. imitans* (provisionally identified as *Struvea anastomosans*). Since its original description, the species name has only been mentioned sporadically from tropical East and West Africa (see Lawson 1980 and Silva *et al.* 1996). As will be discussed below, all *Boodlea* taxa (except *B. vanbosseae*) and *Nereodictyon imitans* fall within the morphological variation of the *C. composita* complex (see there). *B. vanbosseae* falls within the circumscription of the *Cladophora* section *Repentes* and should be transferred to that genus (see appendix).

The genus *Microdictyon* was originally allied with *Anadyomene* based on its blade-like, astipitate thalli (Børgesen 1925). Later the genus was thought to be related with *Boodlea* based on similarities in branch pattern (Børgesen 1930, 1934, 1940) or similarities in anastomosis, resulting in reticulate thalli (Setchell 1929). To date, tenacular cells (type-3) are considered to

[1] Note that at that time the term "tenacula" was only used for the small, specialized cells which were produced at the tips of the terminal cells (type-3 tenacular cells). The type-1 tenacular cells (characteristic for the genus *Microdictyon*) were referred to as "unmodified segments with a crenulate thickened membrane or ring at the tip" (Setchell 1929).

be the principal character to distinguish *Microdictyon* and *Boodlea* as proposed by Egerod (1952). The two genera are not closely related as confirmed by a phylogeny based on partial LSU sequences (Leliaert *et al.* 2003).

Struveopsis and *Pseudostruvea*

The genus *Struveopsis* was described by Rhyne & Robinson (1968: 468) to include two species, *S. chagoensis* and *Cladophoropsis robusta* Setchell & Gardner, characterized by stipitate thalli, delayed formation of cross walls at the bases of laterals, lack of tenacular cells, and cells dividing by segregative cell division (SCD). Rhyne & Robinson's conception of SCD however was incorrect since they associated the phenomenon of delayed cross wall formation with SCD, referring to an illustration of Børgesen (1913: 44, fig. 29).

The genus *Pseudostruvea* was described by Egerod (1975: 47) to accommodate two species, *P. siamensis* from Thailand and *Cladophoropsis robusta* Setchell & Gardner. Apparently unaware of the publication of Rhyne & Robinson (1968), Egerod made the new combination *Pseudostruvea robusta* and included *Willeella mexicana* Dawson (1950) as a synonym. Sartoni (1992: 315) had already noticed this, but it was Silva *et al.* (1996) who reduced *Pseudostruvea* to a synonym of *Struveopsis*. It remained uncertain, however, that their type species, *S. chagoensis* and *P. siamensis*, are conspecific. Only one additional species, *P. covalamensis* Iyengar (1980) [*Struveopsis covalamensis* (Iyengar) P. Silva] has been described in the genus.

4. Grounds for the recognition of a single genus

The extreme close relationship between the genera *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* has been demonstrated by phenetic and molecular evidence (Olsen-Stojkovich 1986; Olsen-Stojkovich *et al.* 1986; Kooistra *et al.* 1993; Wysor 2002; Leliaert *et al.* 2003). Furthermore, several authors have commented on the vague morphological boundaries between *Cladophoropsis*, *Boodlea*, *Phyllodictyon* and *Struveopsis* (Børgesen 1913; Egerod 1952, 1975; Leliaert *et al.* 1998). Due to these fuzzy genus circumscriptions, there are a number of species crossing generic boundaries. For example, *Boodlea* traditionally differs from *Phyllodictyon* in the formation of three-dimensional reticulate thalli lacking a stipe, while *Phyllodictyon* is characterized by monostromatic reticulate, stipitate blades. Mature thalli of *Phyllodictyon anastomosans*, however, form three-dimensional blades anastomosing with other blades and eventually form three-dimensional net-like thalli with obscure stipes. Some *Boodlea* species (e.g. *B. montagnei* and *B. struveoides*) on the other hand, typically form monostromatic blades; *B. struveoides* even develops a distinct stipe. *Struveopsis siamensis* differs from *P. anastomosans* and *B. composita* only by the lack of tenacular cells, but branching patterns in these three taxa are nearly identical. Moreover, under sheltered conditions, *B. composita* almost fails to form tenacular cells (see Fig. 24). *Cladophoropsis* differs from *Boodlea* by irregular to unilateral branch systems, cells producing mostly a single lateral, and infrequent anastomosis; the branches in *Boodlea* are predominately opposite, and anastomosis by means of tenacular cells is more abundant. In culture conditions, *B. composita* exhibits thalli with irregular to unilateral branch systems and scarce anastomosis, similar to *Cladophoropsis membranacea* (Kooistra, unpublished obs.). Some *Cladophoropsis* species, on the other hand, frequently produce opposite laterals (e.g. *C. magna* and *C. philippinensis*, Figs 9 and 12) or form tenacular cells (*C. membranacea*, Fig. 11C). Under certain culture conditions

(e.g. elevated temperatures and calm conditions), *C. membranacea* forms reticulate thalli (Wysor 2002). *Phyllodictyon* has recently been resurrected and split off from *Struvea* based on differences in mode of cell division (Kraft & Wynne 1996). In *Struvea*, cell division is strictly segregative while in *Phyllodictyon* cells divide by centripetal invagination of the cell walls. In *Phyllodictyon gardineri*, however, both types of cell division occur and the generic placement of this species is therefore ambiguous. Unlike the other genera, *Chamaedoris* can be regarded as a well defined genus characterized by conspicuous stipes with annular constrictions, bearing apical whorls of branching filaments forming a capitulum. With the exception of the apomorphic character "laterals in whorls", all other characters are also found in the other genera of the clade: tenacular cells in all genera except *Struveopsis*, annulated stipes in *Phyllodictyon*, *Struvea* and *Struveopsis*, unilateral branching pattern in *Cladophoropsis*.

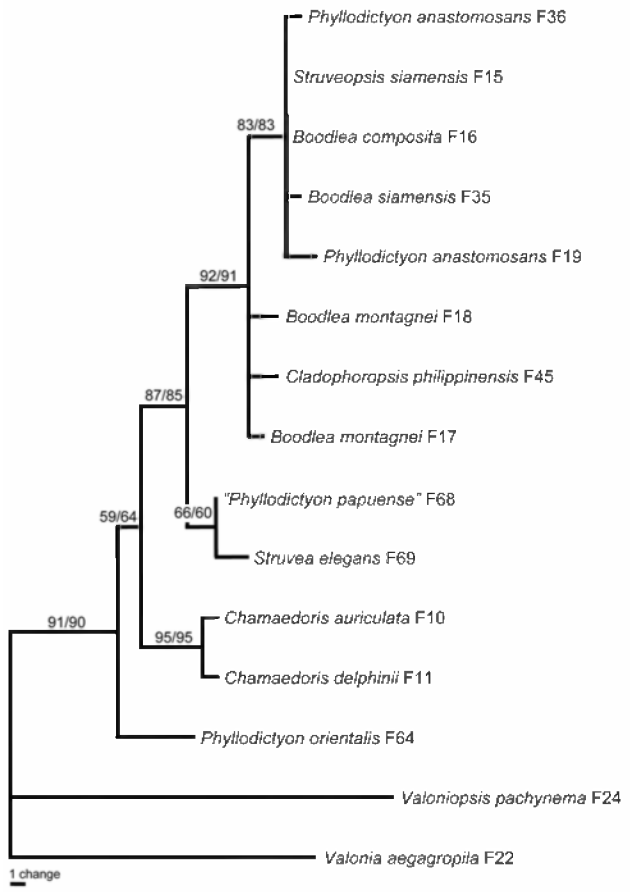

Fig. 1. Single MP tree inferred from partial large subunit rDNA sequence data (gaps treated as missing). Tree length = 85 steps, CI = 0.82, RI = 0.88. Bootstrap percentages (MP/NJ) are indicated above branches.

A phylogenetic tree inferred from partial large subunit rDNA sequence data (chapter 3, Leliaert *et al*. 2003) has a well supported clade (B6) consisting of all *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* (excluding *C. herpestica*) species. Some new analyses were carried out, using the same dataset but only including the specimens of clade B6, and *Valonia aegagropila* and *Valoniopsis pachynema* as outgroup taxa. In this partial dataset, only 11 positions with ambivalent alignment (positions 480-490) had to be removed prior to phylogenetic analysis. Of the 451 included nucleotide positions, 71 were variable and 20 parsimony-informative. MP analyses of the 15 taxa yielded a single MP tree of 85 steps (CI = 0.92, RI = 0.88) (Fig. 1). Phylogenetic trees constructed with MP and NJ methods gave similar topologies and show that neither *Boodlea* nor *Phyllodictyon* are monophyletic. *Struveopsis* (only represented by a single species, *S. siamensis*) falls within a clade comprising

Boodlea composita, *B. siamensis* and *Phyllodictyon anastomosans*. *Struvea elegans* groups together with an undescribed species which is morphologically somewhat intermediate between *Phyllodictyon* and *Struvea*. In this species (provisionally named *Phyllodictyon papuense*) segregative cell division [which is the sole mode of cell division in *Struvea* according to Kraft & Wynne (1996)] occurs only in the initial stages of the thallus development while in mature blades, cell division takes place by centripetal invagination of the cell walls (like in *Phyllodictyon*). Non-monophyly has furthermore been demonstrated in *Cladophoropsis* (*C. membranacea* and *C. sundanensis*) on the basis of ITS sequence analyses (Kooistra *et al.* 1993; Wysor 2002).

Although the comparison of genetic distance between genera (or other taxonomic ranks) may not have any taxonomic implications [especially given that different rates of sequence evolution are found throughout the phylogenetic tree of the Cladophorophyceae (chapter 3, Leliaert *et al.* 2003)], large differences in genetic variation could be an indication of "oversplitting" or "overlumping" (Johns & Avise 1998). It is remarkable that genetic variation of partial LSU rRNA sequences between members of the genera *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* (maximum pairwise sequence divergence of 3.5 %) is less than the variation found between two *Cladophora dotyana* isolates (South Africa and the Philippines) (pairwise sequence divergence of 4.8 %), and is far less than between all taxa of *Cladophora* s.s., as circumscribed by van den Hoek & Chihara, 2000: 22) (maximum pairwise sequence divergence of 24 %) (Table 1). Thus, from the perspective of sequence divergence in the partial LSU rDNA molecule, the genera in clade B6 tend to be oversplit as compared to the genus *Cladophora*. It remains to be determined (e.g. by calibration of evolutionary rates) if these disparities in genetic divergence are merely attributable to differences in rates of sequence evolution in the Cladophorophyceae.

Table. 1. Divergence levels within the "*Boodlea composita*"-clade (including *Boodlea composita*, *B. siamensis*, *B. montagnei*, *Phyllodictyon anastomosans*, *Struveopsis siamensis* and *Cladophoropsis philippinensis*); within the *Cladophoropsis* clade (including the above taxa and *Chamaedoris auriculata*, *C. delphinii*, *Phyllodictyon orientalis*, *P. papuense* and *Struvea elegans*); between two *Cladophora dotyana* isolates; and within *Cladophoropsis* s.s. (van den Hoek & Chihara 2000: 22), corresponding with lineage A in Leliaert *et al.* (2003: fig. 1). Calculations based on the sequence data of Leliaert *et al.* (2003), with ambiguous sites excluded and gaps treated as missing.

	n	Uncorrected pairwise sequence divergences: min.-max. (av.)	Jukes-Cantor pairwise sequence divergences: min.-max. (av.)
"*Boodlea composita*"-complex	8	0 – 0.010 (0.005)	0 – 0.010 (0.005)
Cladophoropsis clade	13	0 – 0.034 (0.016)	0 – 0.035 (0.016)
Cladophora dotyana	2	0.047	0.048
Cladophora s.s.	14	0.010 – 0.207 (0.156)	0.010 – 0.243 (0.176)

The genus complex (*Struvea–Phyllodictyon–Boodlea–Struveopsis–Chamaedoris–Cladophoropsis*) can be characterized by a number of shared derived morphological characters: (1) The thalli are composed of densely branched, entangling filaments, often forming a two- or three-dimensional reticulum. (2) The reinforcement of the thallus is generally achieved by type-3 tenacular cells (as defined by Olsen-Stojkovich 1986: 28, fig. 5), with the exception of *Struveopsis* and some *Cladophoropsis* species where this feature may have been lost

secondarily. (3) Prismatic calcium oxalate crystals are found in the cells of most taxa; this type of crystals presumably evolved on a single occasion and was subsequently lost in *Struvea elegans*, *Chamaedoris auriculata* and *C. delphinii* (chapter 4; Leliaert & Coppejans 2004). (4) Laterals are produced almost immediately after the division of an apical or intercalary cell, single or in opposite pairs. Cross wall formation at the base of the laterals is markedly delayed, and in most *Cladophoropsis* species cross walls are even never formed. Delay of cross wall formation also characterizes the non related *Cladophoropsis herpestica* (moved to *Cladophora* below) and the *Cladophora* sections *Repentes* and *Aegagropila*. (5) Segregative cell division, either organized as in *Struvea plumosa*, or through cell wounding as in *Cladophoropsis membranacea*, has been documented in most representatives.

The clustering of *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* in a well supported monophyletic group, the non-monophyly of a number of included genera, in combination with the fuzzy morphological boundaries and the presence of a number of shared derived morphological characters supports the recognition of a single genus. In accordance with articles 11 and 14.5 of the International Code of Botanical Nomenclature (2000), the oldest name *Chamaedoris* should be selected. However, we believe that this would lead to disadvantageous nomenclatural changes, firstly because of the small number of species currently placed in *Chamaedoris*, secondly because, within the genus complex, only *Chamaedoris* can be easily distinguished by the characteristic stipitate capitula. We think that the name *Cladophoropsis* should be preferred because of the more simple and basic thallus architecture and the larger number of comprised taxa. *Cladophoropsis* would then have to be proposed for conservation against *Chamaedoris*, *Struvea*, *Phyllodictyon*, *Boodlea*, *Nereodictyon*, *Struveopsis* and *Pseudostruvea* in accordance to articles 14 and 56 of the International Code of Botanical Nomenclature (2000).

Given the apparent morphological variety in the newly defined genus *Cladophoropsis*, we propose to distinguish six sections, based on morphological and molecular evidence (Table 2). Only the sections Spongocladia and Chamaedoris correspond entirely with their former genus. The section *Cladophoropsis* contains the former taxa of the genus plus taxa within the *C. composita* complex and the new species *C. kenyensis*. The section *Phyllodictyon* contains two of its former taxa plus *C. mexicana* (previously placed in *Willeella*, *Cladophoropsis* or *Struveopsis*). The section *Struvea* contains two of its former taxa, one species previously placed in *Phyllodictyon*, and a new species, *C. papuensis*. The new section *Rigidae* contains a single species, *C. rigida*, originally described in *Siphonocladus*. It must be noted that the circumscriptions of the sections are subject to changes based on future molecular evidence.

Table 2. Survey of morphological characters of the six sections of *Cladophoropsis*.

Section and included species [old names, if different, between brackets]	Thallus morphology	Cell division	Lateral production	Special features
Cladophoropsis *C. composita* complex [*Boodlea composita*, *B. montagnei*, *B. struveoides*, *Nereodictyon imitans*, *Phyllodictyon anastomosans*, *Struveopsis siamensis*] *C. kenyensis* *C. macromeres* *C. magna* *C. membranacea* *C. philippinensis* *C. sundanensis*	stipitate blades or cushion-like thalli	CI[1] (occasionally SCD[2])	laterals initially single or opposite, older cells generally producing additional branches, perpendicular or opposite to the first ones	
Spongocladia *C. vaucheriiformis* [*Spongocladia vaucheriiformis*]	clumps of variable morphology	CI and SCD	laterals single; filaments siphonous in many parts of the thallus	growing in symbiosis with a sponge
Rigidae *C. rigida* [*Siphonocladus rigidus*]	cushion-like	SCD	laterals single; generally unilaterally organized	filaments often composed of 2-3 contiguous cell rows as a result of oblique cell divisions
Phyllodictyon *C. mexicana* [*Cladophoropsis robusta*] *C. orientalis* [*Phyllodictyon orientale*] *C. pulcherrima* [*Phyllodictyon pulcherrimum*]	stipitate blades	CI (occasionally SCD)	laterals initially opposite, older cells producing additional laterals in the same plane, resulting in flabellate branches	two species with type-4 tenacular cells
Struvea *C. elegans* [*Struvea elegans*] *C. plumosa* [*Struvea plumosa*] *C. gardineri* [*Phyllodictyon gardineri*] *C. papuensis* ["*Phyllodictyon papuense*"]	stipitate blades	SCD (sometimes CI in older blades)	laterals opposite	
Chamaedoris *C. auriculata* [*Chamaedoris auriculata*] *C. delphinii* [*Chamaedoris delphinii*] *C. arbuscula* [*Chamaedoris orientalis*] *C. peniculum* [*Chamaedoris peniculum*]	stipitate capitula, stipe with annular constrictions	SCD & CI	laterals initially single; older cells sometimes producing a second branch	type-3 tenacular cells generally formed laterally

[1] Centripetal invagination of cell walls.
[2] Segregative cell division.

5. Criteria used for the distinction of species in *Cladophoropsis* s.l.

The twelve main criteria used for the distinction of the species in *Cladophoropsis* are summarized below. Many of these criteria have also been found to be taxonomically important in the genus *Cladophora* (van den Hoek 1963, 1982a).

(1) *Thallus architecture* is extremely diverse in *Cladophoropsis* and ranges from mat forming thalli composed of loosely entangled filaments (e.g. section *Cladophoropsis*), three-dimensional, reticulate cushion-like thalli (e.g. some *C. composita* morphological types), stipitate blades (e.g. sections *Phyllodictyon* and *Struvea*), to stipitate capitula (e.g. section *Chamaedoris*). One species, *C. vaucheriiformis*, lives in association with a sponge (*Halichondria* sp.) and forms tough clumps of variable morphology.

(2) *Mode of cell division*. Two modes of cell division occur in *Cladophoropsis*. In some species cell division is mainly by centripetal invagination of the cell walls (CI) (e.g. *C. macromeres*, *C. magna*, *C. orientalis* and *C. pulcherrima*), while other species divide exclusively by segregative cell division (SCD) (e.g. *C. rigida*, *C. elegans* and *C. plumosa*). However, in a number of species, this distinction, is not always clear-cut. In many species which normally divide by CI, segregative cell division occurs occasionally, often in associating with cell wounding (La Claire 1982). In some other species (*C. gardineri*, *C. papuensis*), segregative cell division occurs only in the initial stages of the blade development. Similarly in most species of the section *Chamaedoris*, the initial divisions in the stipe cell are segregative, while the capitulum filaments divide mainly by CI. Segregative cell division normally results in the simultaneous formation of three to several cells, while CI normally generates two new cells. In a number of species, however, apical cells may divide into 3 to 6 cells by more or less simultaneous invagination of the cell walls (e.g. *C. membranacea*, C. *philippinensis and C. composita* complex). In both cases (SCD or CI) cell division is almost immediately followed by the development of more or less equally developing, unilateral or opposite, laterals.

(3) *Branching systems*. A wide variety of branching systems is observed in *Cladophoropsis*. Branching mode is primarily determined by the mode of cell division (see above), the number of laterals produced per cell and the orientation of the laterals. In most species, one or two (opposite) laterals are formed almost immediately after cell division; older cells may produce secondary laterals which may be orientated in the same plane (opposite or flabellate branches) or perpendicular to the first laterals. The production of a single lateral per cell results in unilateral or irregular branch systems; single laterals may eventually displace the main axis resulting in pseudodichotomous main branch systems (e.g. *C. membranacea* and *C. composita*). Branching order is generally related with age of the thallus and therefore this character can only be used when comparing mature thalli. Angle of ramification may be informative in some cases, though very variable.

(4) *Delay of cross wall formation*. In all species, cross wall formation at the base of the laterals is delayed. The extend of delay varies greatly, and in the section *Cladophoropsis* cross walls are often never formed. The extend of delay can be expressed by the maximum length/width ratio of laterals in open connection with the mother cell.

(5) *Cell enlargement*. In most *Cladophoropsis* species, cells increase in thickness with age (i.e. in basipetal direction). The extent of cell enlargement differs between different taxa, and this increase in thickness can be expressed as the ratio of the apical cell diameter and the diameter of the basal branches.

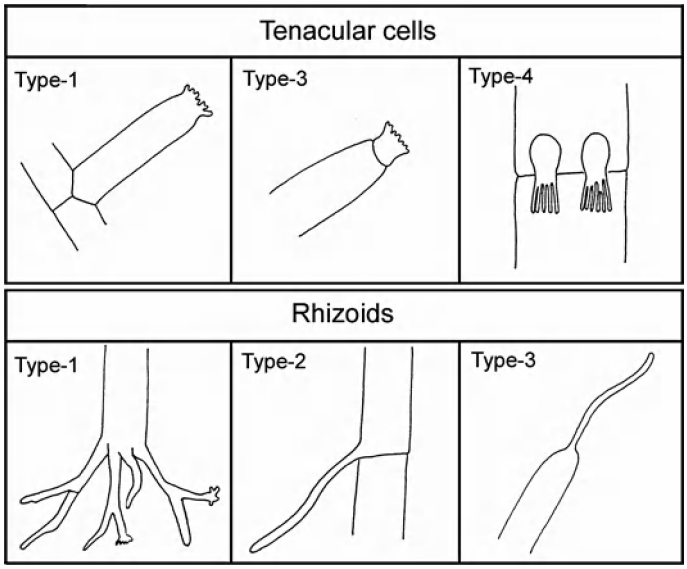

Fig. 2. Types of attachment/reinforcement structures in *Cladophoropsis*. **Type-1 tenacular cells**: crenulate adhesion pads formed distally (or laterally) on apical or lateral cells; **Type-3 tenacular cells**: small tenacular cells produced distally or laterally on apical, lateral or intercalary cells; **Type-4 tenacular cells**: small tenacular cells formed intracellular between neighbouring cells of the same filament; **Type-1 rhizoids**: branching, multicellular rhizoids arising from the proximal pole of the stipe or basal cell, realizing the attachment to the substratum (septa are generally absent in young rhizoids and only formed later in the older ones); **Type-2 rhizoids**: sprouting from the proximal pole of the cells in any part of the thallus; **Type-3 rhizoids**: sprouting from the tips of apical cells.

(6) *Attachment and reinforcement of the thallus*. Structures reinforcing the thallus also often realize the attachment of the thallus to the substratum. Stipitate thalli (sections *Chamaedoris*, *Struvea* and *Phyllodictyon*) and some cushion-like thalli (e.g. *C. magna*) attach to the substratum by branching, multicellular rhizoids arising from the proximal pole of the stipe or basal cells (type-1 rhizoids). This type of attachment is also found in most *Cladophora* species and in many other Cladophorophyceae genera. Most cushion-forming species attach to the substratum by tenacular or rhizoidal cells which develop in any part of the thallus. Some species (e.g. *C. macromeres* and *C. philippinensis*) have only been found unattached or loosely entangled with other macro-algae. Thalli may be reinforced by entangling or interweaving of the filaments, by specialized structures (tenacular or rhizoidal cells) or a combination of the two. Entangling of filaments in the section *Cladophoropsis* is often aided by the curved or sinuous cells or branch systems (e.g. *C. magna*). Six types of attachment/reinforcement structures can be distinguished in the genus (Fig. 2). Three of the four types of tenacular cells, as defined by Olsen-Stojkovich (1986), occur in *Cladophoropsis*. **Type-1 tenacular cells**: crenulate adhesion pads formed distally or laterally on apical cells (or lateral in open connection with the mother cell), generally attaching to the substratum but occasionally also anastomosing with adjacent filaments; e.g. *C. composita*. **Type-3 tenacular cells**: small tenacular cells produced distally or laterally on apical, lateral or intercalary cells, anastomosing with adjacent filaments (e.g. sections *Chamaedoris*, *Struvea*, *Phyllodictyon*, *C. composita* and *C. rigida*); sometimes also attaching to the substratum. **Type-4 tenacular cells**: small tenacular cells formed between neighbouring cells of the same filament; e.g. *C. orientalis* and *C. pulcherrima*. Three types of rhizoids can be distinguished. **Type-1 rhizoids**: branching, multicellular rhizoids arising from the proximal pole of the stipes or basal cells, realizing the attachment to the substratum. Septa are generally absent in young rhizoids and only formed later in the older ones. **Type-2 rhizoids**: rhizoids with or without basal cross walls, sprouting from the proximal pole of the cells in any part of the thallus, reinforcing the thallus by entanglement with filaments, or

attaching to the substratum by hapteroid structures at the tips of these rhizoids. **Type-3 rhizoids**: unbranched, septate or aseptate rhizoids, sprouting from the tips of apical cells, entangling or anastomosing with adjacent filaments, or attaching to the substratum by terminal hapteroid structures.

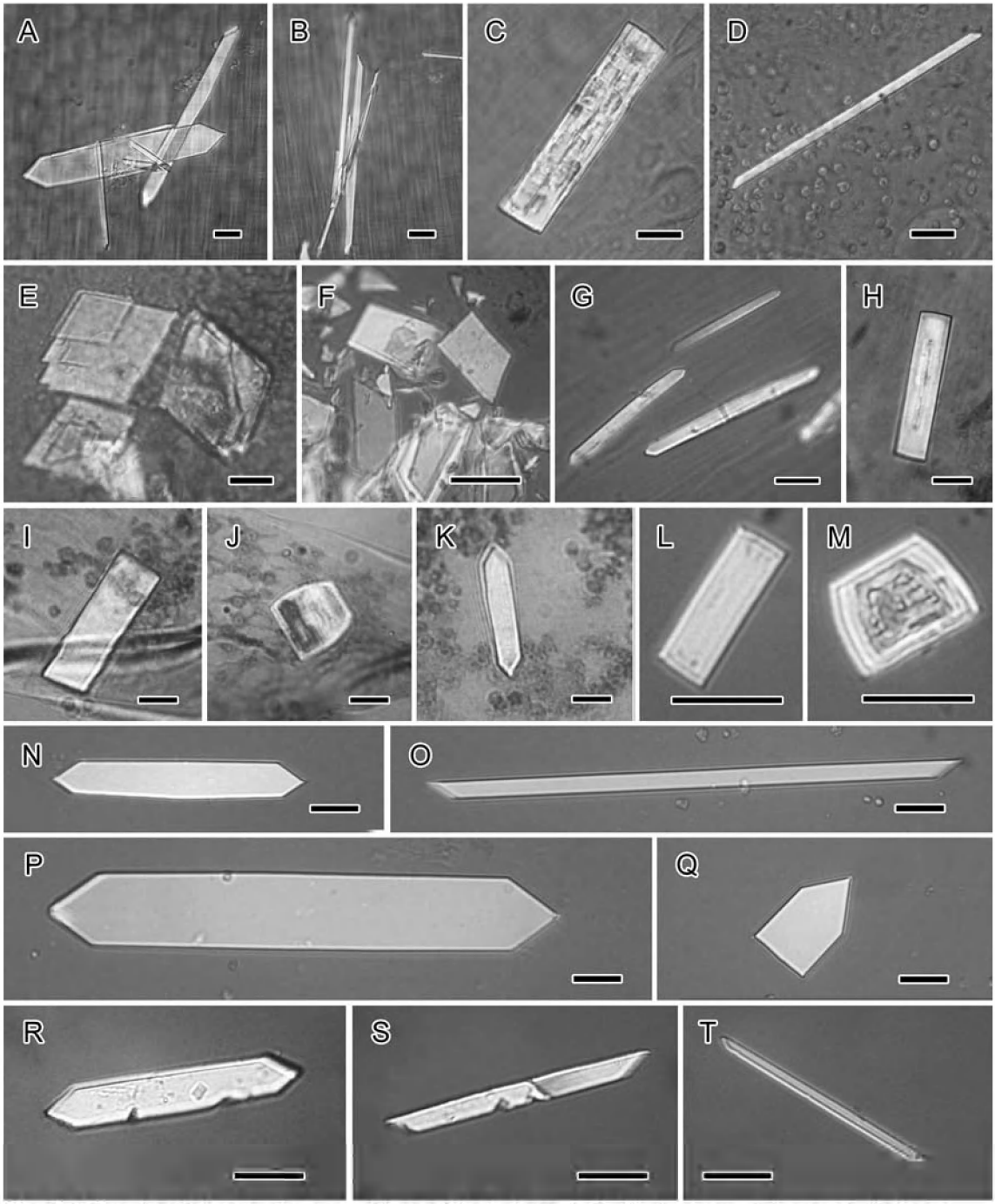

Fig. 3. Prismatic calcium oxalate crystalline cell inclusions. **A-B.** *Cladophoropsis kenyensis* (holotype, GENT); **C-D.** *C. macromeres* (holotype, MICH); **E.** *C. magna* (isotype, MEL 3012); **F-K.** *C. membranacea* [F: CmCI TF PdH2 (GENT), G: lectotype (LD), H-K: holotype of *Boodlea trukensis* (BISH)]; **L-M.** *C. sundanensis* (lectotype, L); **N-Q.** *C. philippinensis* (holotype, MICH); **R-T**: *C. composita* complex (lectotype of *Cladophora anastomosans*). Scale bars = 10 µm.

(8) *Cell shape*. Most cells in the *Cladophoropsis* species are cylindrical or subcylindrical. Some species have cells which are conspicuously curved or sinuous, facilitating entanglement of the filaments (e.g. *C. magna*). In a number of species the stipe cells and cells of the main axes may be conspicuous clavate (e.g. *C. composita* phenodeme *struveopsis*), or tapering towards both extremities (e.g. *C. plumosa*).

(9) *Cell diameter* is an important character, though very variable. The distinction between delicate species (e.g. *C. sundanensis*) and robust species (e.g. *C. philippinensis*) is obvious but the existence of a series of taxa with intermediate sizes (e.g. *C. sundanensis* – *C. membranacea* – *C. macromeres*) makes the use of this character on itself often problematic.

(10) *Annular constrictions* has been traditionally widely used as a taxonomic character in the Cladophorophyceae. In some species annular constrictions in the stipe cell (or cells of the main axes) are always present (e.g. *C. plumosa*, *C. gardineri* and all species in the section *Chamaedoris*) while in other taxa this character does not seem to be constant (e.g. *C. orientalis* and *C. composita* complex).

(11) *Thickness of cell walls* is a useful but often highly variable character too. In some species all cells (including the apical and subapical cells) are very thick walled and consequently the thalli have a stiff texture (e.g. *C. rigida* and *C. vaucheriiformis*). In most species the thickness of the cell walls increases with age, resulting in the basal cells of the thallus being generally thick walled, but in some delicate species such as *C. membranacea* and *C. sundanensis* even the basal cells remain thin walled.

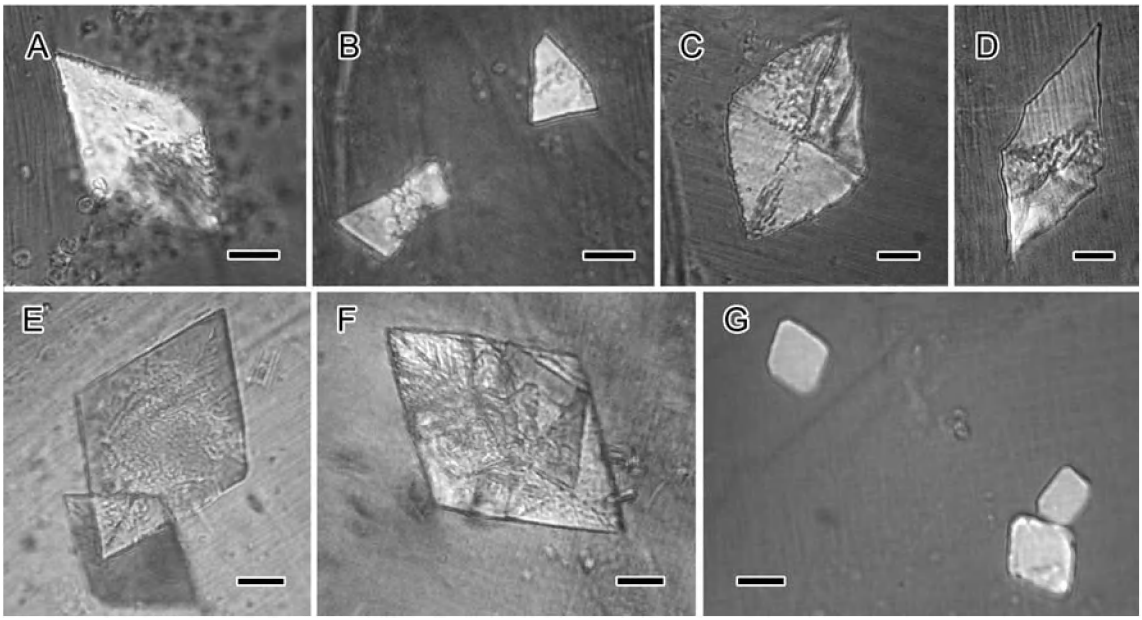

Fig. 4. Prismatic calcium oxalate crystalline cell inclusions. **A-B.** *Cladophoropsis orientalis* (holotype); **C-D.** *C. pulcherrima* [C: lectotype of *Phyllodictyon ramosa* (BM); D: holotype of *C. pulcherrima* (BM)]; **E-F.** *C. gardineri* (holotype, BM); **G.** *C. plumosa* (MEL 666898). Scale bars = 10 µm.

(12) *Crystalline cell inclusions* have recently been described in various genera of the Cladophorophyceae, including *Cladophoropsis* (Leliaert & Coppejans 2004). Three types of crystals with a different chemical nature occur in the genus: prismatic calcium oxalate crystals, occurring in most species (Figs 3, 4), tetrahedral protein crystals in *C. gardineri*, *C. papuensis* (Fig. 63), *C. auriculata* and *C. delphinii*, star-shaped clusters of fine needle-shaped crystals (possibly silica) in *C. auriculata* and *C. delphinii*. The shape of the calcium oxalate crystals is

generally constant within a species; in some taxa however (e.g. *C. membranacea*) crystal shape is variable and different forms may co-occur, within a single thallus or cell.

(13) The colour of the thallus corresponds to the density of the reticulum of chloroplasts. In the dark green cells of *C. philippinensis*, for example, the chloroplasts form an almost closed parietal layer while in the light green cells of *C. sundanensis* the chloroplasts form an open parietal reticulum (Fig. 5). In most species, however, thallus colour is variable and may vary depending on the habitat. The density of the chloroplast reticulum may also vary within a single thallus. This has been demonstrate by Horiguchi *et al.* (1998) who studied differences in chloroplast morphology between inner, dark-habituated cells, and the light-exposed surface cells of the ball-forming *Cladophora aegagropila* (Linnaeus) Rabenhorst.

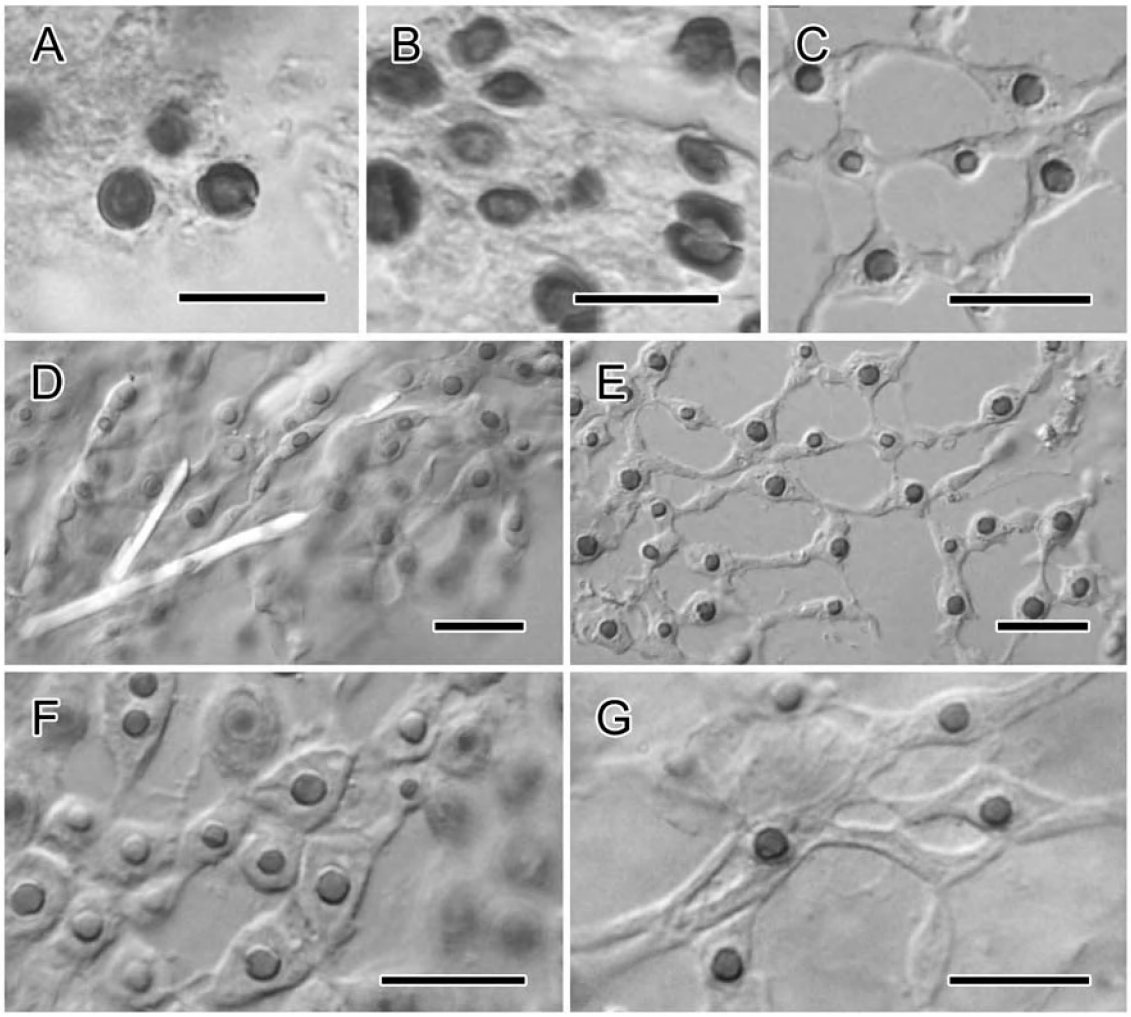

Fig. 5. A. Chloroplasts of *Cladophoropsis macromeres* with bilenticular pyrenoids (holotype, MICH); **B.** Chloroplasts of *C. magna* with bilenticular pyrenoids (holotype, ADU); **C-E.** Chloroplasts of *C. membranacea* forming an open parietal network (PH 115); **D.** Calcium oxalate crystals lying between the chloroplasts; **F.** Chloroplasts of *C. philippinensis* forming a relative closed parietal network (PH 567); **G.** Chloroplasts of *C. vaucheriiformis* forming an open parietal network (FL 989). Scale bars = 10 µm.

6. Key to the species of *Cladophoropsis* s.l.

1.a. Thallus forming erect, stipitate blades or capitula[1], single or clustered, attached to the substratum at a single point, by rhizoids developing at the base of the stipe 2

1.b. Thallus forming astipitate blades, cushions, mats or clumps of variable morphology, attached to the substratum at multiple points, by rhizoids or tenacular cells[2] developing from cells in any part of the thallus, or unattached 17

2.a. Thallus forming stipitate capitula which may be plane, globose or oblong; stipe with numerous annular constrictions over the entire length, often epiphytized by crustose coralline rhodophytes 3

2.b. Thallus forming stipitate, reticulate blades composed of filaments, branching essentially in a single plane; stipe with or without annular constrictions 6

3.a. Thallus 5-20 cm high; capitulum oblong, obovate or pyriform (more rarely globose); capitulum filaments developing from a central axis composed of 14-28 apical cells; diameter of capitulum filaments 320-490 µm ..... *C. arbuscula* (p. 226)

3.b. Thallus smaller than 12 cm; capitulum plane or globose; capitulum filaments developing from the distal end of the stipe cell or from an apical cell or two superimposed ones; diameter of capitulum filaments smaller than 220 µm 4

4.a. Capitulum flat, auriculate; capitulum filaments developing from the distal end of the stipe cell and from 1-3 superimposed, apical cells ..... *C. auriculata* (p. 219)

4.b. Capitulum globose or flat and cup-shaped; superimposed, apical cells absent or up to three 5

5.a. Capitulum globose; capitulum filaments only developing from the distal end of the stipe; capitulum filaments lacking prismatic calcium oxalate crystals ..... *C. delphinii* (p. 223)

5.b. Capitulum flat, cup-shaped (sometimes subglobose); capitulum filaments developing from the distal end of the stipe or from 1 to 3 superimposed, apical cells; diamond-shaped calcium oxalate crystals present in the capitulum filaments ..... *C. peniculum* (p. 229)

6.a. Branching in the blade strictly opposite (except in some terminal branch systems where a cell occasionally produce a single lateral, or in old blades where branch systems may become irregular); maximum 2 number of laterals per cell 7

6.b. Branching in the blade unilateral, opposite, flabellate, or three-dimensional, never exclusively opposite 12

7.a. Cells of the blade dividing by centripetal wall ingrowths; intercalary cell divisions occurring at regular intervals; elongate to needle-shaped calcium oxalate crystals present in most cells of the thallus 8

7.b. Cells of the blade dividing by segregative cell division[3] (at least in young blades); cells with or without calcium oxalate crystals, diamond-shaped when present 9

8.a. All laterals lying strictly in a single plane ..... *C. composita* complex (*delicatula* phenodeme)

8.b. All laterals lying in a single plane but but some cells with a young, initiating lateral perpendicular to the main branching plane ..... *C. composita* complex (young plant of the *anastomosans* phenodeme)

9.a. Cells of the blade dividing exclusively by segregative cell division; branching systems strictly opposite 10

9.b. Segregative cell division only occurring in young blades; cells in old blades dividing by centripetal wall ingrowths; branching systems initially strictly opposite, becoming irregular in mature blades 11

10.a. Stipe cell subcylindrical, generally less than 1300 µm in widest diameter; apical cells of the blade 190-315 µm in diameter; cells lacking calcium oxalate crystals ..... *C. elegans* (p. 201)

10.b. Stipe cell very broad in the middle, markedly attenuating towards both extremities, generally more than 1800 µm in widest diameter; apical cells of the blade 600-1500 µm in diameter; diamond-shaped calcium oxalate crystals present in most cells of the blade .. *C. plumosa* (p. 214)

11.a. Blade with a closed[4], crenate margin, stipe cells with basal annular constrictions, 1500-2000 µm in diameter; adjacent filaments frequently attached laterally by two or three type-3 tenacular cells born on a single apical or intercalary cell ..... *C. gardineri* (p. 206)

11.b. Blade with an open margin[5]; stipe cells lacking annular constrictions, 380-700 (-820) µm in diameter; type-3 tenacular cells generally borne singly (only occasionally in pairs) on apical cells .... *C. papuensis* (p. 210)

12.a. All branches of the blade produced in a single plane; branching opposite to flabellate 13

12.b. Branches of the blade not strictly formed in a single plane; cells initially producing a single lateral or an opposite pair of laterals, older cells generally forming laterals perpendicular to the first ones..... 15

13.a. Tenacular cells (type-3) very rare or absent; type-4 tenacular cells absent, branch cells producing up to 4 laterals; apical cells 950-1120 µm in diameter; most cells containing rectangular to irregular calcium oxalate crystals ..... *C. mexicana* (p. 184)

13.b. Structural reinforcement of the blade by numerous type-3 tenacular cells; type-4 tenacular cells produced at the proximal poles of the basal cells of the main axes and attaching to the cell below; branching opposite or flabellate, cells producing up to 6 laterals; most cells containing diamond-shaped calcium oxalate crystals 14

14.a. Thallus up to 7 cm high; apical cells (70-) 90-170 (-200) µm in diameter .. *C. orientalis* (p. 186)

14.b. Thallus up to 36 cm high; apical cells 200-380 µm in diameter ..... *C. pulcherrima* (p. 192)

15.a. Stipe cell clavate, short (l/w ratio 5-7), lacking annular constrictions; apical cells 220-400 (-560) µm in diameter; adjacent cells occasionally anastomosing[6] by type-1 or -3 tenacular cells ... *C. kenyensis*

15.b. Stipe cell clavate or subcylindrical, long (l/w ratio 12-36), with or without annular constrictions; apical cell diameter in average smaller than 200 µm 16

16.a. Stipe cell subcylindrical, without annular constrictions; cells of the blade frequently anastomosing by type-3 tenacular cells .... *C. composita* complex (*anastomosans* phenodeme) (p. 135)

16.b. Stipe cell clavate, generally with basal annular constrictions; type-3 tenacular cells absent (or extremely rare) ..... *C. composita* complex (*struveopsis* phenodeme) (p. 167)

17.a. Thallus living in symbiosis with a sponge, forming large, tough clumps of variable morphology (prostrate mats, with or without short, papillous protuberances; upright forms with subcylindrical, finger-like, dichotomously branched, fastigiate processes; irregularly branching processes, with pointed tips; thick blade-like outgrowths); laterals single; filaments siphonous[7] in many parts of the thallus ..... *C. vaucheriiformis* (p. 171)

17.b. Thallus forming astipitate reticulate blades, or cushions, composed of entangling filaments 18

18.a. Cells dividing by segregative cell division; filaments often composed of 2-3 contiguous cell rows as a result of oblique cell divisions; laterals single ..... *C. rigida* (p. 180)

18.b. Cell division by centripetal wall ingrowths (occasional segregative cell division occurs in response to cell wounding); branching unilateral, opposite or three-dimensional 19

19.a. Thallus forming astipitate reticulate blades or cushions composed of reticulate or entangling filaments; branching of the main filaments generally opposite; delay of cross wall formation at the base of laterals limited (l/w ratio of laterals in open connection with the mother cell smaller than 7) 20

19.b. Thallus forming cushions composed of entangling filaments; branching of the main filaments generally unilateral or irregular (more rarely opposite); delay of cross wall formation marked (maximal l/w ratio of laterals in open connection with the mother cell 40-80) 25

20.a. Thallus forming astipitate, reticulate, unistratose blades .... *C. composita* complex (*montagnei* phenodeme) (p. 154)

20.b. Thallus forming three-dimensional cushions composed of reticulate blades or entangling filaments 21

21.a. Thalli composed of clustered blades; apical cell diameter 220-400 (-560) µm .. *C. kenyensis* (p. 113)

21.b. Thalli with or without an internal blade-like structure; apical cell diameter in average smaller than 200 µm 22

22.a. Thalli composed of loosely entangling filaments; ultimate branch systems composed of regularly, opposite branching filaments, thallus reinforcement mainly by entangling of filaments, type-3 tenacular cells rare or absent 23
22.b. Thalli composed of tightly interwoven filaments, forming a three-dimensional reticulum with or without an internal blade-like structure; ultimate branch systems composed of unilateral, pseudodichotomous or opposite branching filaments, thallus reinforcement mainly by anastomosis of adjacent cells by type-3 tenacular cells 24

23.a. Cells of the main axes subcylindrical, without annular constrictions; type-3 tenacular cells infrequent ..... *C. composita* complex (*composita* phenodeme) (p. 144)
23.b. Cells of the main axes generally clavate with annular constrictions; type-3 tenacular cells absent .... *C. composita* complex (*struveopsis* phenodeme) (p. 167)

24.a. Cushion-like thalli with an internal blade-like structure .... *C. composita* complex (*anastomosans* phenodeme) (p. 135)
24.b. Cushion-like thalli forming a three-dimensional reticulum without an internal blade-like structure ..... *C. composita* complex (*siamensis* phenodeme) (p. 157)

25.a. Mat-forming thalli composed of loosely entangling filaments; basal cell conspicuous, clavate, sinuous, with annular constrictions ..... *C. magna* (p. 118)
25.b. Cushion- or mat-forming thalli lacking stipe cells without conspicuous basal cells 26
26.a. Thalli unattached or loosely entangled with other macro-algae..... 27
26.b. Thalli attached to the substratum by tenacular or rhizoidal cells sprouting from cells in any part of the thallus..... 28

27.a. Laterals single, unilaterally organized; apical cell diameter (140-) 280-360 (-400) µm; diameter of the main filaments 280-510 µm ..... *C. macromeres* (p. 116)
27.b. Laterals single or opposite, irregularly organized; apical cell diameter 300-670 (-860) µm; diameter of the main filaments 430-750 (-1300) ..... *C. philippinensis* (p. 124)

28.a. Apical cell diameter (70-) 110-290 (-340) µm ..... *C. membranacea* (p. 120)
28.b. Apical cell diameter (40-) 60-120 (-140) µm ..... *C. sundanensis* (p. 127)

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[1] Capitulum: three-dimensional structure, composed of branching and anastomosing filaments, borne on top of a stipe.
[2] Tenacular cell: specialized cell achieving attachment (anastomosis) with adjacent cells. *Type-1 tenacular cells*: crenulate adhesion pads formed distally or laterally on apical or lateral cells. *Type-3 tenacular cells*: small tenacular cells produced distally or laterally on apical, lateral or intercalary cells. *Type-4 tenacular cells*: small tenacular cells formed between neighbouring cells of the same filament.
[3] Segregative cell division: a form of cell division in which a multinucleate protoplast divides into several, rounded daughter protoplasts, which subsequently become surrounded by a wall. Since this mode of cell division occurs rapidly, cells which are in the process of division are usually relatively rare. Therefore it may be necessary to examine several specimens in order to observe segregative cell division.
[4] Closed, crenate blade margin: formed as a result of the marginal blade filaments that curve upwards, and produce unilateral, adaxial laterals only.
[5] Open blade margin: margin consisting of free (not anastomosing) apical and lateral cells.
[6] Anastomosis: attachment or connection of two cells by tenacular or rhizoidal cells.
[7] Siphonous: long tubular cells lacking cross walls.

7. Descriptions of the sections and species

Cladophoropsis Børgesen, 1905

Cladophoropsis has to be proposed for conservation against *Chamaedoris*, *Spongodendron*, *Struvea*, *Phyllodictyon*, *Boodlea* (*nomina rejicienda*).

Chamaedoris Montagne, 1842: 261 [Type: *C. annulata* (Lamarck) Montagne (nom. illeg.), homotypic synonym of *Chamaedoris peniculum* (Ellis & Solander) Kuntze].

Scopularia Chauvin, 1842: 122 (non *Scopularia* Lindley, 1834, *in* Edwards's Bot. Reg. 20: 1834, nom. rej. vs. *Holothrix* Lindley, Gen. Sp. Orchid. Pl.: 257) [Monospecific genus. Type: *S. annulata* (Lamarck) Chauvin (nom. illeg.), homotypic synonym of *Chamaedoris peniculum*].

Struvea Sonder, 1845: 49 [*nom. cons.* vs. *Struvea* H.G.L. Reichenbach, 1841, Deut. Bot. Herb.Buch, Syn.: 222, 236 (Silva 1952: 297) (= *Torreya* Arnott 1838, Ann. Nat. Hist. 1: 130, *nom. cons.* vs. *Torreya* Raf. 1818, Amer. Monthly Mag. & Crit. Rev. 3: 356)] [Type: *S. plumosa* Sonder].

Spongocladia J.E. Areschoug, 1854: 202 (*nom. rej.* vs. *Cladophoropsis* Børgesen, Papenfuss 1950: 211) [Type: *S. vaucheriiformis* J.E. Areschoug].

Phyllodictyon J.E. Gray, 1866: 69 [Type: *P. pulcherrimum* J.E. Gray].

Spongodendron G. Zanardini, 1878: 37 [Type: *non designatus*. Zanardini described two species in this genus, *S. crassum* and *S. dichotomum*. *S. crassum* is regarded as a synonym of *Spongocladia vaucheriiformis* Areschoug by Murray & Boodle (1888a: 175), which was in its turn transferred to *Cladophoropsis* by Papenfuss (1958). *S. dichotomum* was first transferred to *Spongocladia* by Murray & Boodle (1888a), and later to *Cladophoropsis* by Papenfuss (1958)].

Boodlea Murray & De Toni, *in* Murray, 1889: 245 [Type: *B. coacta* (Dickie) Murray & De Toni (*Cladophora coacta* Dickie)].

Cladophoropsis Børgesen, 1905: 288 [*nom. cons.* vs. Spongocladia J.E. Areschoug, 1854 (Papenfuss 1950: 211)] [Lectotype: *C. membranacea* (Hofman Bang ex C. Agardh) Børgesen (according to Papenfuss, 1950: 211) (*Conferva membranacea* Hofman Bang ex C. Agardh)].

Nereodictyon Gerloff, 1960: 616 [Type: *N. imitans* Gerloff, 1960: 616].

Struveopsis Rhyne & Robinson, 1968: 468 [Type: *S. chagoensis* Rhyne & Robinson].

Pseudostruvea Egerod, 1975: 47 [Type: *P. siamensis* Egerod].

7.1. Section *Cladophoropsis*

Thallus forming mats, cushions or stipitate blades; attached to the substratum by rhizoids sprouting from the proximal pole of the basal cells or stipe cell (if present) or by type-1 or type-3 tenacular cells and rhizoids formed in any part of the thallus. Cell division by centripetal wall ingrowths. Growth by apical and intercalary cell divisions, formation of laterals and cell elongation. Cells producing a single lateral or a pair of opposite laterals; older cells generally producing secondary laterals, opposite or perpendicular to the first ones, resulting in three-dimensional branch systems. Reinforcement of the thallus by entangling of the filaments and in most species by anastomosis of adjacent filaments by type-1 or -3 tenacular cells.

Seven species (including the *C. composita* species complex) are ranged under this section. The differences between the species are listed in Table 3.

Table 3. Survey of characters of the seven species in the section *Cladophoropsis*.

	C. kenyensis	*C. macromeres*	*C. magna*	*C. membranacea*	*C. philippinensis*	*C. sundanensis*	*C. composita* complex
Thallus morphology	cushion-like thalli composed of clustered stipitate blades.	mat-forming thalli composed of loosely entangling filaments.	mat-forming thalli composed of loosely entangling filaments.	cushion-like or mat-forming thalli composed of tightly interwoven filaments.	cushion-like thalli composed of loosely entangled filaments.	cushion-like thalli composed of tightly interwoven filaments.	variable, ranging from stipitate blades to cushion-like thalli.
Stipe cell, shape and cell dimensions	clavate, lacking annular constrictions, 370-740 µm in diam., l/w ratio 5-7	not observed	clavate, sinuous, with annular constrictions, 750-1200 µm in widest diam., l/w ratio 25-46	absent	absent	absent	present or absent, shape and cell dimensions variable
Thallus attachment	type-1 rhizoids; type-1 and -3 tenacular cells	unattached	unknown	type-1 rhizoids; type-3 tenacular cells	unattached	type-1 and -3 rhizoids; type-3 tenacular cells	type-1 rhizoids; type-1 and -3 tenacular cells
Organization of branch systems	laterals initially opposite; older cells often producing a 3rd (to 5th) lateral	laterals single, unilaterally organized	laterals single or opposite, unilaterally to irregularly organized	laterals initially single; older cells occasionally producing a second, opposite lateral	laterals single or opposite, irregularly organized	laterals single or opposite, irregularly organized	laterals initially single or opposite; older cells often producing a 3rd and 4th lateral.
Delay of cross wall formations at the base of the laterals: max. l/w ratio of laterals in open connection with the mother cell	l/w ratio up to 2.4	cross walls not formed; l/w ratio up to 45	cross walls not formed; l/w ratio up to 80	cross walls only formed in some older branches; l/w ratio up to 55	cross walls only formed in some older branches; l/w ratio up to 60	l/w ratio up to 40	l/w ratio up to 6
Thallus reinforcement	loosely entangling of filaments; anastomosis occasionally by type-1 or -3 tenacular cells	loosely entangling of filaments; anastomosis occasionally by type-3 tenacular cells	loosely entangling of filaments	tightly interweaving of filaments; anastomosis occasionally by type-3 tenacular cells	interweaving of filaments; anastomosis occasionally by type-3 tenacular cells	tightly interweaving of filament; anastomosis occasionally by type-3 rhizoids and type-3 tenacular cells	loosely to tightly interweaving of filaments; anastomosis by type-1 and -3 tenacular cells.
Apical cell diameter (µm) and l/w ratio	220-400 (-560) l/w ratio 2.2-8 (-14)	(140-) 280-360 (-400) l/w-ratio up to 60	170-700 µm l/w ratio 15-35	(70-) 110-290 (-340) l/w ratio 1.7-70	300-670 (-860) l/w ratio 3-40	(40-) 60-120 (-140) l/w ratio 1.5-80	(40-) 80-220 (-280) l/w ratio 1-10 (-18)
Main filament diameter (µm)	(370-) 450-880 (-1050)	280-510	(400-) 500-800	(90-) 220-260 (-280)	430-750 (-1300)	(80-) 180-250	(120-) 160-750 (-930)
Shape of the prismatic calcium oxalate crystals	elongate hexagonal or trapeziform to needle-shaped	elongate rectangular or trapeziform to needle-shaped	diamond-shaped	broad to elongated hexagonal, trapeziform or rectangular, often with curved faces	large, elongate hexagonal or trapeziform	broad to elongate rectangular, often with curved faces	elongate hexagonal or trapeziform to needle-shaped

Cladophoropsis kenyensis Leliaert & Coppejans, sp. nov. prov. Figs 3A-B, 6, 7

Holotype: Mwamba Beach, Mombasa, mid- to low intertidal rock pools, epilithic, leg. Coppejans, 5.ix.1991, HEC 8669a (GENT).

Description:
Thallus yellow green, forming a crisp, stiff, prostrate cushion, 3-10 cm in diameter, 1-3 cm high, composed of clustered stipitate blades, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe and by type-1 or -3 tenacular cells produced in the terminal branch systems of the blades.
Stipes clustered, lacking annular constrictions, branched, bearing several blades at their distal poles. Young lamina ovate in outline, with a conspicuous central axis, composed of regularly opposite branch systems lying more or less in a single plane. Mature lamina more irregular in outline, 8-18 mm broad, 17-24 mm long, with an obscure central axis, plane but branch systems not restricted to a single plane, (Figs 6A, 7A).
Formation of a lamina initiated by division of a distal stipe cell and formation of one or two opposite laterals. Further development of the blade by a repetitive process of cell division, formation of laterals, elongation and enlargement. Cell division exclusively by centripetal invagination of the cell walls; growth mainly by apical cell divisions. Apical cells dividing into 2 cells or simultaneously into 3-4 (-6) cells, followed by the formation of a pair of opposite laterals, or a series of opposite laterals. Older cells possibly producing a 3rd and 4th lateral, perpendicular to the first opposite pair, resulting in three-dimensional branch systems; occasionally a 5th lateral is produced resulting in verticillate branches (Fig. 7C). Formation of cross walls somewhat delayed; laterals in open connection with the mother cell commonly up to 600 µm long (l/w ratio 2.4). Older branches laterally inserted with a steep cross wall cutting it off from the parent cell; this cross wall soon becomes partly fused with the cell above the parent cell. Blade filaments branching up to the 4th order. The diameter of the basal (stipe) cells 0.8-3 times that of the apical cells. Angle of ramification 30°-75°.
Structural reinforcement of the lamina limited; adjacent filaments sporadically attach by type-1 or -3 tenacular cells produced (sub)terminally on the apical cells or laterals in open connection with the mother cell, or occasionally laterally or basally on intercalary cells (Figs 6E, 7D-H). In mature blades, in average 1-4 % of the apical cells producing a type-3 tenacular cell; type-1 tenacular cells even less frequent.
Apical cells cylindrical with rounded tips, 220-400 (-560) µm in diameter, l/w ratio 2.2-8 (-14). Cells of the terminal branch systems cylindrical, (200-) 240-560 (-650) µm in diameter, l/w ratio 1.6-8.5. Cells of the central axis cylindrical to slightly clavate, (370-) 450-880 (-1050) µm in diameter, l/w ratio (2-) 4-13. Stipe cells clavate (Fig. 7B), 370-740 µm in diameter, l/w ratio 5-7. Type-3 tenacular cells 85-170 µm in diameter, 110-220 µm long.
Cell walls relatively thick, 4-8 (-14) µm in the terminal branch systems, 18-40 (-65) µm in the stipe and basal blade cells.
Zoidangia are transformed apical cells with lateral conical projections (Fig. 6F).
Chloroplasts small, polygonal or round, 3-4 µm in diameter, each with a single pyrenoid, ca 2.5 µm in diameter, forming an open to more or less closed parietal reticulum.
Prismatic calcium oxalate crystals present in most cells of the thallus, number of crystals per cell ranging from a few to over 50, crystals elongate hexagonal, trapeziform to needle-shaped, 2-14 µm broad, up to 95 µm long, l/w ratio 3.6-24 (Fig. 3A-B).

Ecology: *C. kenyensis* grows epilithic in mid to low intertidal rock pools.

Geographical distribution: *C. kenyensis* is only known from the area around Mombasa, Kenya.

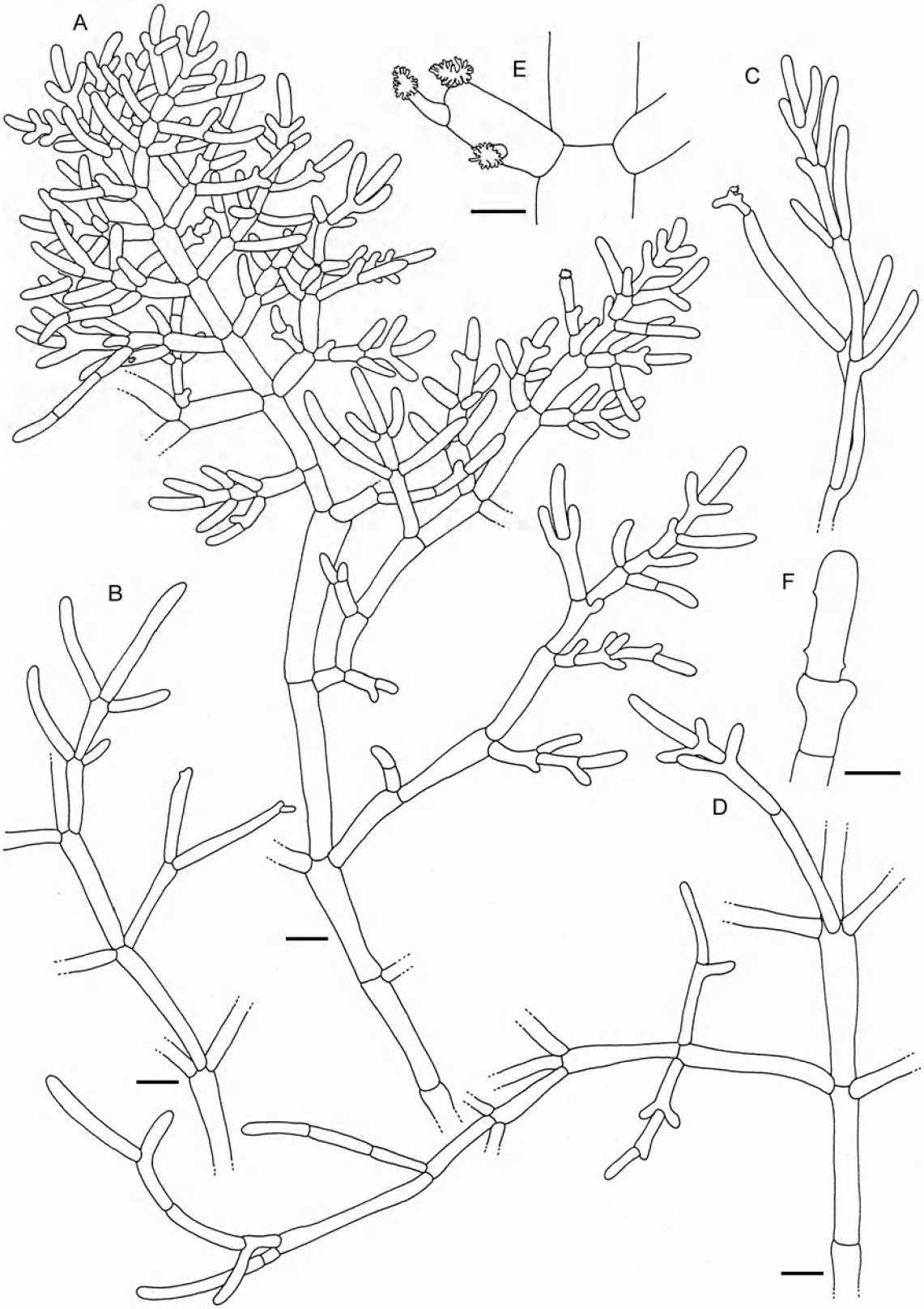


Fig. 6. *Cladophoropsis kenyensis* (holotype, GENT). **A-C.** Terminal, mainly opposite branches; **D.** Basal branches; **E.** Type-3 tenacular cells; **F.** Sporangium with lateral conical projections. Scale bars: A-D = 1 mm; E = 200 µm; F = 500 µm.

Specimens examined: **Indian Ocean: Kenya**. Iwatine Bay, N of Mombasa, mid intertidal rock pool, epilithic, (leg. Coppejans, 10.ix.1992, HEC 9404); Mwamba Beach, Mombasa, mid to low intertidal rock pools, epilithic, (leg. Coppejans, 5.ix.1991, HEC 8669a: holotype); Vipingo, 35 km N of Mombasa, (leg. Coppejans, 29.vii.1989, HEC 8187).

Note: *C. kenyensis* has a similar gross morphology as some morphological types in the *C. composita* complex (e.g. *anastomosans* and *struveopsis* phenodemes), characterized by stipitate blades clustering together and forming cushion-like thalli. *C. kenyensis* can be distinguished from the above taxa mainly by the much coarser filaments (Table 3).

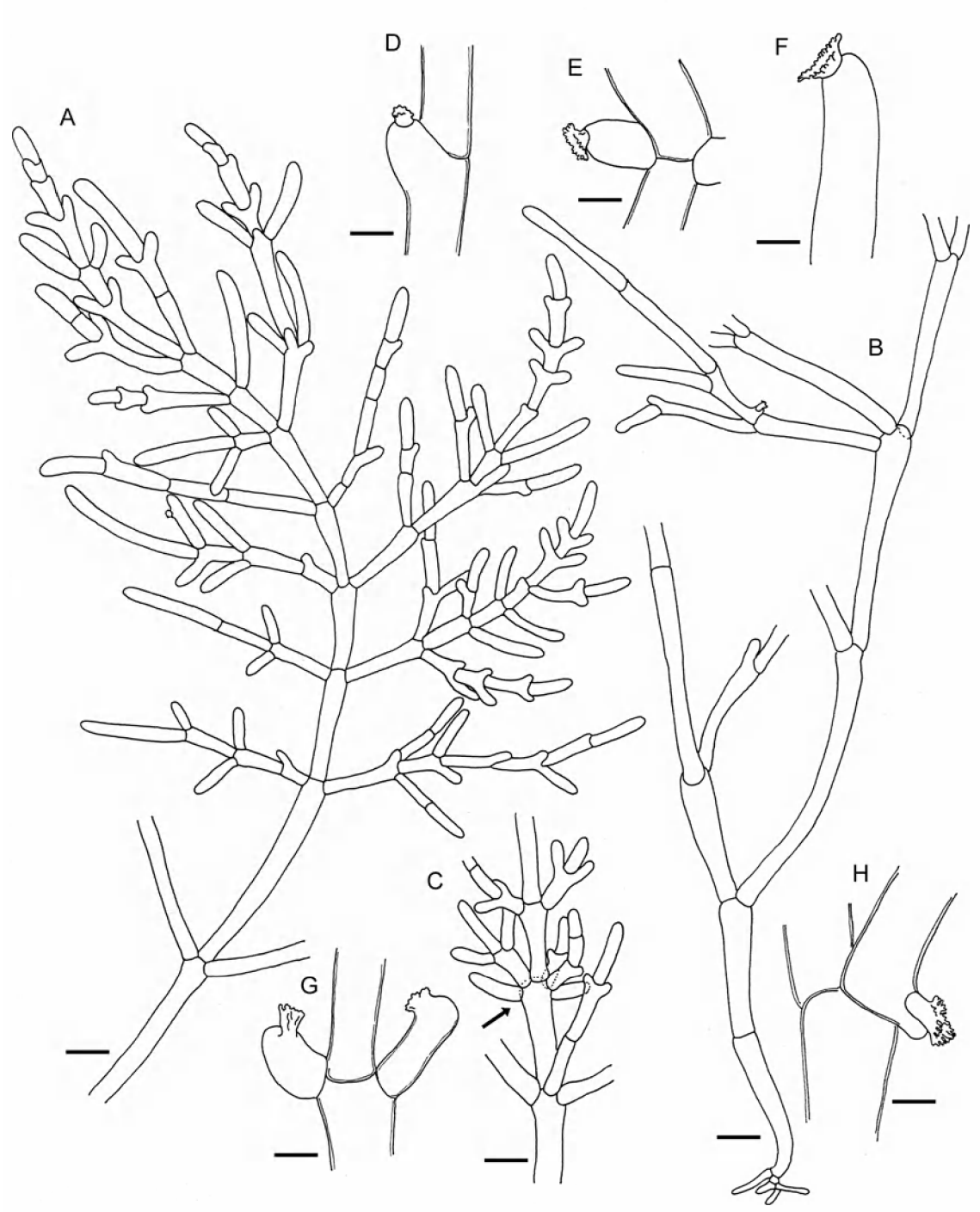


Fig. 7. *Cladophoropsis kenyensis* (holotype, GENT). **A.** Terminal, mainly opposite branches; **B.** Basal branches and stipe cell with type-1 rhizoids; **C.** Cells in the central part of the thallus producing up to 5 laterals (arrow); **D-F.** Type-3 tenacular cells; **G.** Type-1 tenacular cells; **H.** Type-3 tenacular cells produced at the basal pole of a cell. Scale bars: A-C = 1 mm; D-H = 200 µm.

Cladophoropsis macromeres Taylor Figs 3C-D, 5A, 8

Cladophoropsis macromeres Taylor, 1928: 64, pl. 4, figs 15, 16 [Holotype: Fort Jefferson (Garden Key), Dry Tortugas, Florida, U.S.A., leg. Taylor 903, MICH!; paratype: same locality, leg. Taylor 1143, NY!].

Description:
Thallus bright green, forming loose lying mats, up to 15 cm across and 2-10 (-15) cm thick, composed of loosely entangled, coarse filaments.
Cell division by centripetal invagination of the cell walls. Growth mainly by apical cell division, followed by cell elongation and limited cell enlargement. The diameter of the thickest part of the main axes about 1-1.3 times that of apical cells. Newly formed cells producing one lateral at the apical pole. Laterals generally lacking basal cross walls (l/w ratio of laterals in open connection with the mother cell up to 45). Ultimate branch systems unilateral to irregular. Branching limited to the first order. Angle of ramification 20°-55°.
Structural reinforcement of the thallus limited, by loosely entangling of the filaments and occasionally by anastomosis of cells by tenacular cells (intermediate forms between type-3 tenacular cells and type-2 rhizoids, Fig. 8D-E), produced laterally or basally on the intercalary cells, 40-50 µm in diameter, 170-260 µm long; in average less than 1 % of the cells forming a tenacular cell.
Apical cells cylindrical, straight, or slightly curved or sinuous, (140-) 280-360 (-400) µm in diameter, up to 22 mm long, l/w-ratio up to 60. Laterals 220-300 µm in diameter, up to 5 mm long, l/w-ratio up to 17. Main axes cylindrical, straight or slightly curved, 280-510 µm in diameter, 100-5500 µm long, l/w-ratio: 2.3-18. Cell walls 2-4 µm thick in the ultimate branches; up to 10 µm thick in main axes.
Chloroplasts polygonal or rounded, forming an open to dense parietal reticulum, 7-10 µm in diameter. Most chloroplasts with a single large pyrenoid, 3.8-6.4 µm in diameter (Fig. 5A).
Elongate prismatic calcium oxalate crystals present in most cells of the thallus, elongate rectangular or trapeziform to needle-shaped, numbers ranging from 1 to several per cell; crystals 1-14 µm broad, up to 150 µm long, l/w ratio 1.5-55.
Ecology: *C. macromeres* grows in sheltered intertidal pools down to the shallow subtidal (down to 5 m depth), free floating, loosely attached to the substratum, or entangled with other attached macro-algae.

Geographical distribution: *C. macromeres* is a common species in the Caribbean Sea and Gulf of Mexico (Littler & Littler, 2000) and has been recorded from the Canary Islands (Gil-Rodriguez *et al.* 1985: 102, fig. 2).

Specimens examined: **Caribbean Sea: Bonaire**. locality unknown (leg. Baart 13-1, 12.vii.1972, L 8280). **Gulf of Mexico: USA**. Fort Jefferson (Garden Key), Dry Tortugas, Florida, (leg. Taylor 903, 21.vi.1925, MICH 10593, holotype of *Cladophoropsis macromeres*; leg. Taylor 1143, 7.vi.1926, NY, paratype).

Note: *C. macromeres* is most easily confused with *C. philippinensis*, *C. magna* and *C. membranacea*. It differs from *C. philippinensis* by the thinner filaments and by the more regular branching pattern with maximum one lateral per cell. *C. magna* can be distinguished from *C. macromeres* by the presence of diamond shaped calcium oxalate crystals. *C. macromeres* differs from *C. membranacea* by the filaments being about twice as thick (Table 2).

General references: Taylor (1960: 118, pl. 2, fig. 2); Littler & Littler (2000: 330, figs on p. 331).

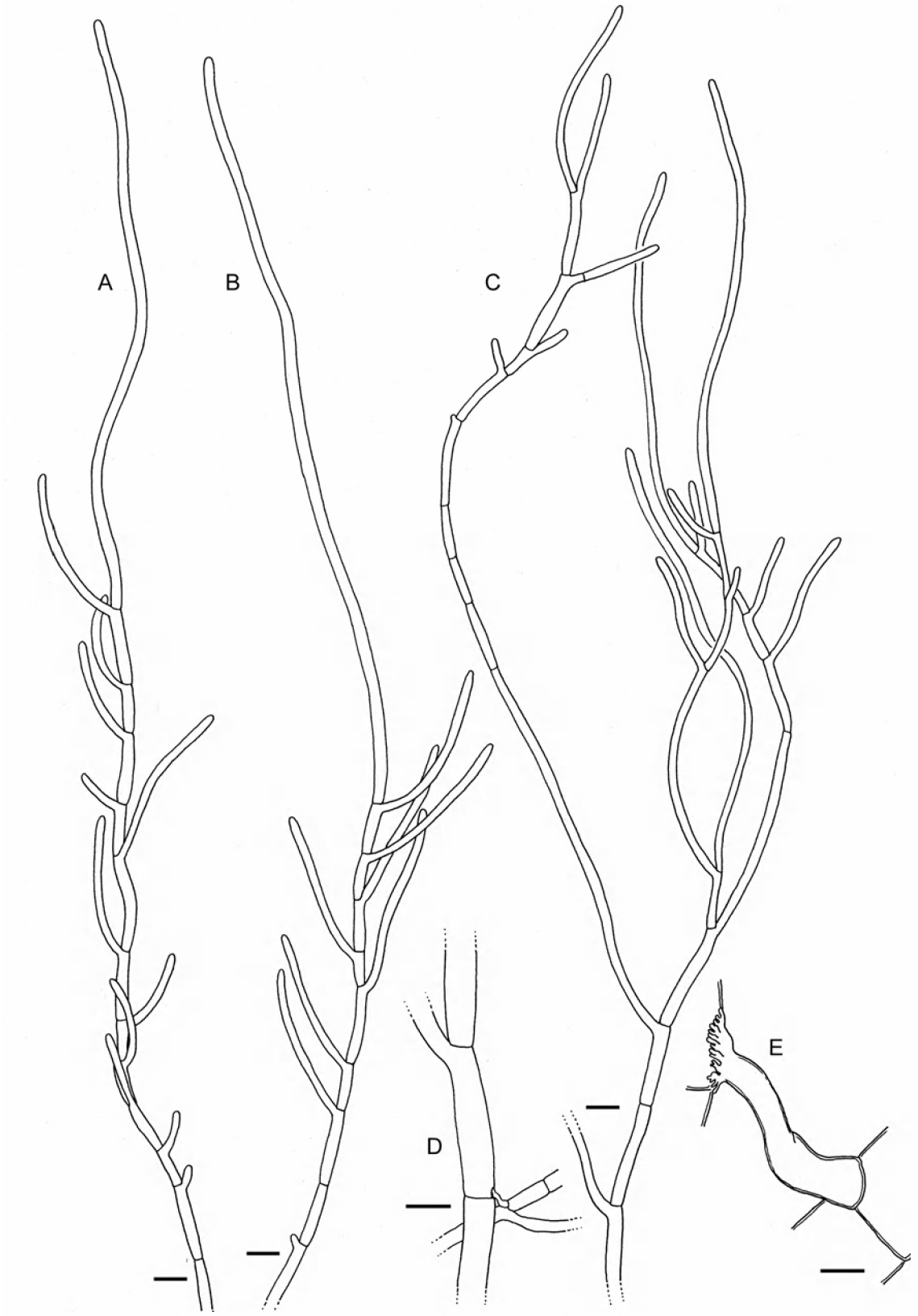


Fig. 8. *Cladophoropsis macromeres*. **A-C.** Unilateral to irregular terminal branch systems; **D.** Anastomosis by a type-3 tenacular cell; **E.** Detail of type-3 tenacular cell. (A-B: paratype, Taylor 1143, NY; C-E: holotype, MICH). Scale bars: A-C = 1 mm; D = 500 µm; E = 50 µm.

Cladophoropsis magna Womersley Figs 3E, 5B, 9

Cladophoropsis magna Womersley, 1955: 390, fig. 7 ("*C. magnus*") [Holotype: Smoky Bay, west coast of Eyre Peninsula, South Australia, Australia, leg. H.B.S. Womersley A13615, 21.i.1951, ADU; isotypes distributed under numbers A13615 and A13616, MEL! 3012, 666096 and 666097].

Description:
Thallus light to medium green, forming large, free floating masses, up to 50 cm across and 7 cm thick, composed of loosely entangled, coarse filaments. Attachment probably by rhizoids produced at the proximal pole of the large stipe cells (type-1 rhizoids) (several stipe cells were found in the material, all with torn basal parts, Figs 9A, D, arrows); tenacular cells absent.
Cell division by centripetal invagination of the cell walls. Growth by apical and intercalary cell division, followed by cell elongation and limited cell enlargement. The diameter of the thickest part of the main axes about 1.5-3.2 times that of apical cells.
Young thallus consisting of a single large cell with basal annular constriction, up to 43 mm long (Fig. 9D). The apical part of this cell dividing into 4-6 cells, the basal part remaining undivided and forming the stipe cell. Newly formed cells producing one lateral at their distal pole; older cells in the basal part of the thallus occasionally producing a second, often opposite, lateral. Laterals not displacing the main axes, lacking basal cross walls and remaining considerably thinner than the mother cell. Laterals often developing from short axial cells which are clustered in groups of three to seven (Figs 9B-C). These clusters of short branched cells alternate with long undivided cells. Thallus branching up to the 3rd or 4th order. Angle of ramification 25°-90°.
Apical cells subcylindrical, markedly sinuous, diameter very variable within a single plant; apical cells of the first and second order branches 170-350 µm in diameter at the base, increasing towards their apices to 500-700 µm; apical cells of the higher order branches 200-250 µm in diameter; length 13.8-17.5 mm; l/w ratio 15-35. Cells of the ultimate branch systems, 150-300 µm in diameter, 1.8-15 mm long, l/w ratio 4-30. Cells of the main filaments, first and second order laterals subcylindrical, often with a few annular constrictions, (400-) 500-800 µm in diameter, 0.7-16 mm long, l/w ratio 1.5-30. Stipe-cells generally unbranched, clavate, sinuous, with numerous annular constrictions over the entire length, diameter near the base 300-500 µm, increasing distally to 750-1000 (-1200) µm, l/w ratio 25-46.
Cell walls 2-8 µm thick in the ultimate branches, up to 20 (-36) µm thick in basal cells and stipe.
Chloroplasts polygonal or rounded, 6-16 µm in diameter, forming an open to dense parietal reticulum. Most chloroplasts with a single large pyrenoid, 3.8-7.6 µm in diameter (Fig. 5B).
Diamond-shaped calcium oxalate crystals present in all cells of the thallus, including the stipe cell; numbers ranging from a few to ca. 100 per cell; crystals single or clustered, resulting in jagged angles (Fig. 3E), 10-30 µm in diameter, 20-55 µm long, l/w ratio 1.2-1.7.

Ecology: *C. magna* has only been collected from drift collections, but probably grows attached subtidally (Womersley 1984).

Geographical distribution: *C. magna* is only known from Smoky and Denial Bay, west coast of Eyre Peninsula, South Australia.

Specimens examined: **Pacific Ocean: Australia**. Denial Bay, South Australia, (leg. Tieskens s.n., MEL 3011); Smoky Bay, Eyre Peninsula, South Australia, (leg. Womersley A 13615, A13616, 21.i.1951, MEL 3012, MEL 666096, MEL 666097 and NY, isotypes).

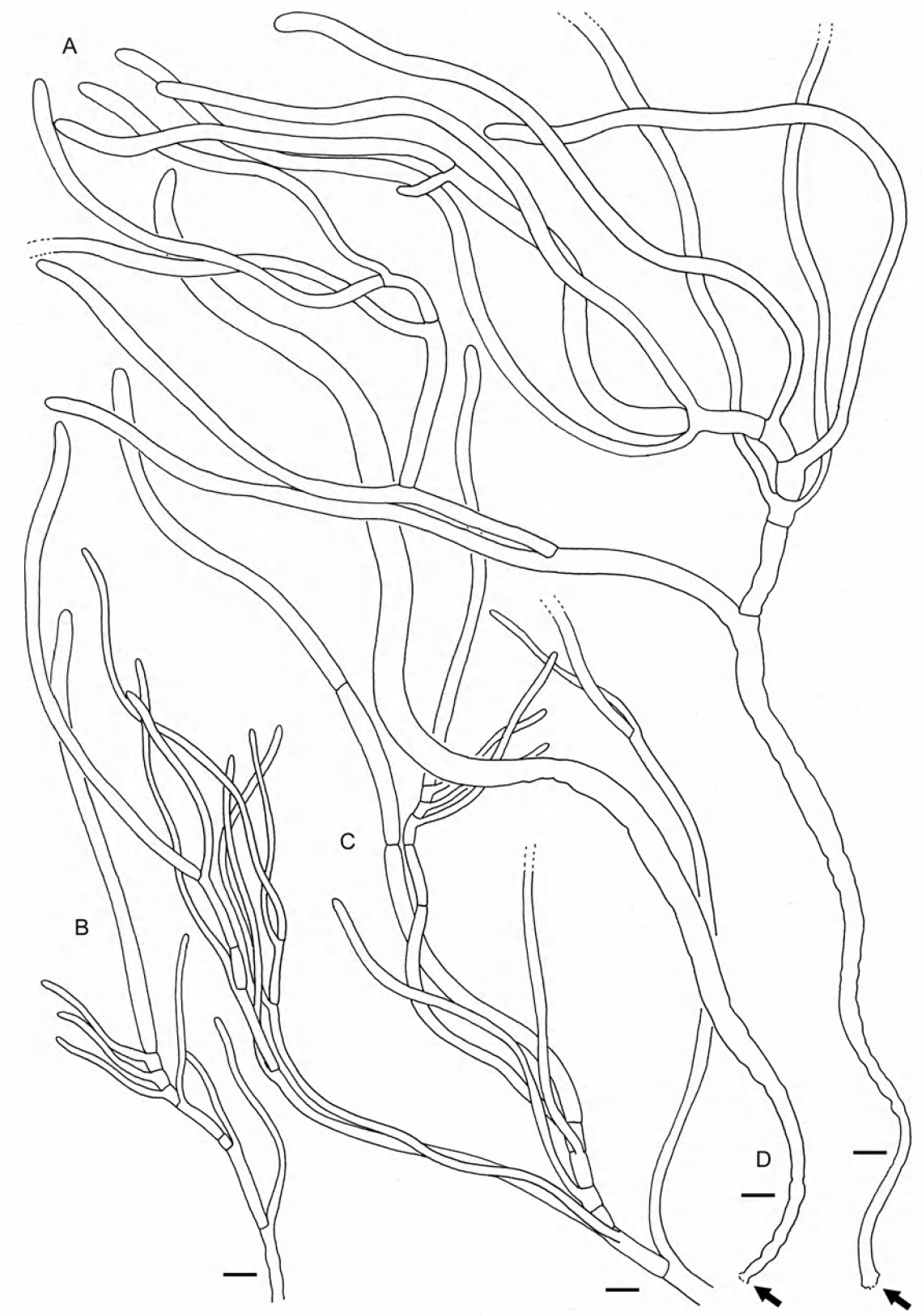


Fig. 9. *Cladophoropsis magna* (isotype, MEL 666096) **A.** Thallus consisting of a large basal stipe cell with annular constrictions, giving rise to terminal branch systems; basal attachment structures missing (arrow); **B-C.** Terminal branch systems; **D.** Young thallus consisting of a single, large cell with basal annular constrictions; basal attachment structures missing (arrow). Scale bars = 1 mm.

Note: *C. magna* can easily be distinguished from the other coarse species in the section *Cladophoropsis* by the conspicuous stipe cells with annular constrictions and the presence of diamond-shaped crystalline cell inclusions (Table 3). Surprisingly the conspicuous stipe cells were not mentioned nor depicted by Womersley (1955, 1984). Annulated stipe cells, in combination with diamond-shaped calcium oxalate crystals have also been observed in *C. peniculum*, *C. orientalis*, C. *pulcherrima*, *C. gardineri* and *C. plumosa* (Leliaert & Coppejans 2004).

General reference: Womersley (1984: 185, figs 58C, 59D).

Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen

Figs 3F-K, 5C-E, 10, 11

Conferva membranacea Hofman Bang ex C. Agardh, 1824: 120-121 [Lectotype: St. Croix, Virgin Islands, collector unknown, LD! 7287. St. Croix is indicated as type locality in the original prologue. Several specimens of this species from that locality are present in LD; one of these, labeled "Conf. membranacea Hoffm, Ins St. Crucis" from the Agardh herbarium is here indicated as lectotype].

Cladophora membranacea (Hofman Bang ex C. Agardh) Kützing, 1843: 271.

Aegagropila membranacea (Hofman Bang ex C. Agardh) Kützing, 1854: 145.

Siphonocladus membranacea (Hofman Bang ex C. Agardh) Bornet, *in* Askenasy, 1888: 6.

Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen, 1905: 289, figs 8-13.

Boodlea kaenana Brand, 1904: 190, pl. VI, figs 36-39 [Lectotype: Kaenana point, Hawaii, leg. J.E. Tilden 146, Herb. Stockmayer ex Herb. Brand, B! 09449; isolectotype: B! 09450].

Cladophoropsis gerloffii Nizamuddin, 1988: 229-234, figs 1-3 [Holotype: Andulus Beach near Tripoli, Libya, leg. M. Nizamuddin N-1905, B Alg35585].

Boodlea trukensis Trono, 1972: 49, pl. 4 [Holotype: reef between Falo and Moen Island, Truk Group, Caroline Islands, leg. E.G. Meñez, Doty no. D23458.2, 29.vii.1960, BISH! 510376].

Description:

Thallus light to medium green, forming compact spongy cushions, up to 12 cm across or moss-like mats, up to 50 cm across, 2-5(-10) cm high, often sediment-trapping, composed of much ramified, tightly interwoven or loosely entangled filaments. Attachment to the substratum by branching, multicellular rhizoids arising from the proximal pole of the basal cells (type-1 rhizoids, Fig. 10G); also by type-3 tenacular cells which are produced distally or laterally on apical or intercalary cells in any part of the thallus, occasionally by rhizoids sprouting from the proximal pole of the cells (type-2 rhizoids).

Cell division by centripetal invagination of the cell walls or by segregative cell division. Growth mainly by apical cell division and subsequent cell elongation, also by intercalary cell division in the basal parts of the thallus. The diameter of the thickest part of the main axes about 1-1.5 times that of the apical cells. Cell division followed by formation of a single lateral at the distal pole of the newly formed cell (Fig. 10A-C). Cells sometimes dividing simultaneously into 3 to 6 cells followed by the formation of more or less equally developing laterals. Older cells frequently producing a second, generally opposite, lateral (Indo-Pacific representatives) (Fig. 11B). Laterals not displacing the main axis. Formation of cross walls at the proximal pole of newly formed laterals markedly delayed, or cross walls absent; laterals in open connection with the mother cell up to 750-5000 µm long, l/w ratio 8-55. Older branches laterally inserted with a

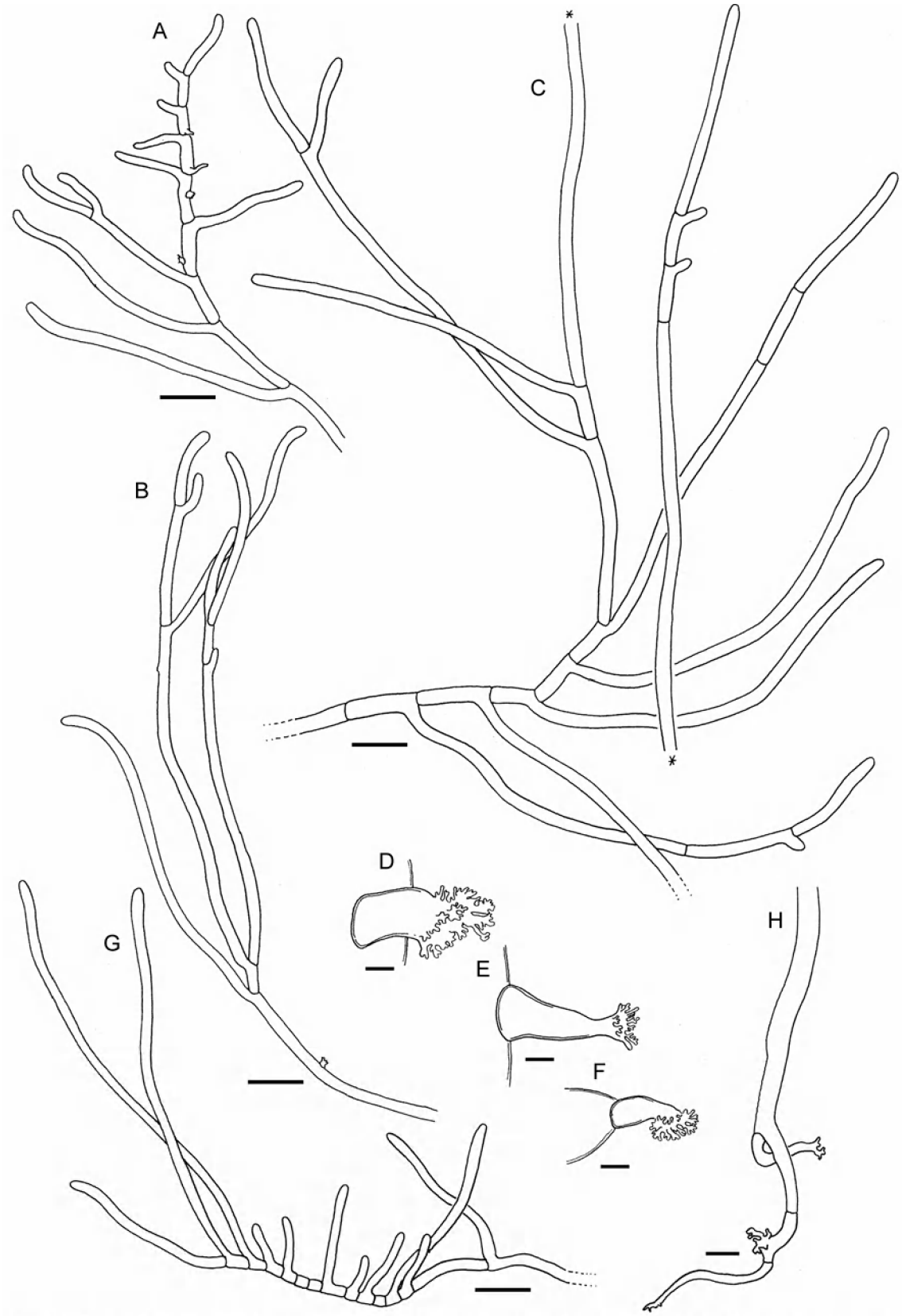


Fig. 10. *Cladophoropsis membranacea*. **A-C.** Unilateral to irregularly organized terminal branch systems; type-3 tenacular cells and short type-2 rhizoids produced by some cells; **D-F.** Type-3 tenacular cells; **G.** Unilateral terminal branch system; **H.** Branched type-1 rhizoids arising from the lower poles of the basal cells. (A-F: lectotype, LD; G: L 996 222 055; H: L 993 113 339). Scale bars: A-C = 500 µm; D-F = 50 µm; G = 500 µm; H = 200 µm.

steeply inclined cross wall cutting it off from the parent cell. Terminal branch systems unilaterally or irregularly organized; basal branch systems with a more irregular organization. Thallus branching up to the 2nd or 3rd (sometimes 4th) order. Angle of ramification 30°-90°.
Structural reinforcement of the thallus mainly achieved by interweaving of the filaments; adjacent cells occasionally anastomosing by means of type-1 or -3 tenacular cells (Figs 10 D-F; 11C). In average 2-8 % of the cells producing a tenacular cell.
Zoidangia formed by transformation of apical or intercalary cells in the terminal branch systems which form a few ob-conical outgrowths, each with an apical pore.
Apical cells cylindrical, straight or curved, dimensions very variable, even within a single thallus, (70-) 110-290 (-340) µm in diameter, 0.7-12.5 (-17.5) mm long, l/w ratio 1.7-70. Cells of the terminal branch systems cylindrical, (90-) 140-290 µm in diameter, 180-5000 µm long. Basal filaments cylindrical, (90-) 220-260 (-280) µm in diameter, 250-1700 (-3000) µm long, l/w ratio 1.3-12. Tenacular cells 80-120 µm in diameter, 180-290 µm long. Cell walls ca. 2 µm thick in the terminal branches, up to 5-10 µm thick in the basal filaments.
Chloroplasts polygonal, elongated to star-shaped, forming an open parietal reticulum, 2.5-7 µm in diameter with strands spanning up to 20 µm. Each chloroplast containing a single pyrenoid, 1.4-2.6 µm in diameter (Fig 5C-E).
Prismatic calcium oxalate crystals extremely variable in morphology, broad to elongated hexagonal, trapeziform or rectangular, often with curved faces (Fig. 3F-K), present in most cells of the thallus; numbers per cell ranging from 1-30 in the apical cells to more than 200 in the cells of the main axes. Crystals 1.5-10 µm broad, up to 60-90 µm long, l/w ratio 1-15 (-40).

Ecology: *C. membranacea* grows epilithic or epiphytic as cushion or mat-forming thalli, or is loose-lying as Aegagropila-like clumps, in exposed or sheltered intertidal to shallow subtidal habitats (occasionally down to -10m depth).

Distribution: *C. membranacea* is widely distributed in the tropical to subtropical seas and especially common in the Atlantic Ocean. In the western Atlantic it is reported from as far north as Bermuda and as far south as southern Brazil (Wynne 1998). In the eastern Atlantic the species is reported from the Canary Islands (Børgesen 1925), the Cape Verde Islands, and the tropical West-African coast, as well as in the Mediterranean sea. *C. membranacea* has occasionally been reported from the Indo-West Pacific (Kooistra 1993). The Hawaiian record of this species (Egerod 1952: 356, fig. 3) turns out to be a misapplied name for *Cladophora catenata* (Linnaeus) Kützing after examination of the reference specimens collected by Papenfuss (10502, 10503, 10504, 10505, 10505, 10775, 10776 in UC).

Specimens examined: **Atlantic Ocean: Canary Islands**. Fare de Maspalomas, Gran Canaria, (leg. van der Strate CmCI GC MP1 & CmCI GC MP2, i.1998, GENT); Punta del Hidalgo, Tenerife, (leg. van der Strate CmCI TF PdH1 & CmCI TF PdH2, i.1998, GENT); Punta del Rincón, Fuerteventura, (leg. van der Strate CmCI FV PdR1 & CmCI FV PdR2, i.1998, GENT); Faro de Orchilla, Hierro, (leg. Cancap 2 Expedition 455, 6.ix.1977, L 996 225 796); **Cape Verde Islands**. Sal Island, Pedra da Lume, (leg. van der Strate CmCVI Sal PdL1 and CmCVI Sal PdL2, vii.1998, GENT); Branco, north coast, (leg. Cancap 7 Expedition 9621, 5.ix.1986, L 996 222 039); Branco, south coast, (leg. Cancap 7 Expedition 9697, 5.ix.1986, L 996 222 055); **Carribean Sea: Barbados**. Hasting Rocks, (leg. Vickers, s.n., 16.xii.1898, BR); unknown locality, (leg. Vickers 26, 1905, PC); **Bermuda**. Shark Hole, Harrington Sound: shallow subtidal, (leg. Schneider 92-4-2, 20.vi.1992, NY); Hungry Bay, Hamilton Island, (leg. Taylor & Bernotowicz 49-463, 26.iii.1949, BR); Hungry Bay, Hamilton Island, (leg. Collins 7021, iv.1912, BR); **Curaçao**. Boco Grandi, (leg. van den Hoek 68/62, 23.v.1968, L 993 113 339); Sint Michiels-baai, (leg. van den Hoek 68/22bis, 14.v.1968, L 993 113 322); Playa Chikitu: infralittoral fringe, (leg. van den Hoek 68/17, 11.v.1968, L, 993 113 308); **Guadeloupe**. Petit Havre, (leg. Wynne 8209, 25.ii.1987, MICH); **Puerto Rico**. Caja de Muertos, (leg. Howe 7471, 8.vii.1915, NY); Cayo Icacos, (leg. Pagan 5252, 22.i.1966, NY); Guanica Harbor, low intertidal, (leg. Howe s.n., 1.vii.1915, L 938 095 652); Playa Talloboa, south coast of Guayanilla, (leg. Diaz-Piferrer 1333, 1959, L 996 224 552); Salinas Bay, near Guánica, (leg. Howe 2680, 29.vi.1903, BR); **Virgin Islands**. St. Croix, (leg. collector unknown s.n., Herbarium Agardh, LD 7287: lectotype of *C. membranacea*); St. Croix, (leg. collector unknown, LD 7285 & 7307); **Gulf of Mexico: USA**. West Summerland Key, Florida, (leg. Prud'homme van Reine 2508, 30.vii.1991, L 992 035 589); Key

West, Florida, (leg. Messina 225, PC); **Indian Ocean: Seychelles**. La Digue Island, near Anse Union: intertidal granite boulders, (leg. Coppejans *et al.*, 23.xii.1992, SEY 306); **Sri Lanka**. Beruwela, intertidal rock platform, in front of Confifi Beach Hotel: sheltered and exposed side of the reef crest, epilithic on horizontal substratum, (leg. Coppejans, 25.i.1997, HEC 11813b); Hikkaduwa, in front of Reefcomber Hotel: intertidal fossil reef, exposed to strong surf, epilithic on horizontal rock substratum, (leg. Coppejans, 12.i.1997, HEC 11671); Midigama beach, west of Weligama: infralittoral fringe, epilithic on horizontal substratum, (leg. Coppejans, 10.i.1997, HEC 11641); **Mediterranean Sea: Spain**. Balearium minorum, (leg. Wittrock & Nordstedt 317, 1870, NY); **Pacific Ocean: Caroline Islands**. unknown locality, (leg. Hallier s.n., B 09451, M); reef between Falo and Moen Island, Truk Group, (leg. Meñez, Doty no. D23458.2, 29.vii.1960, BISH! 510376: holotype of *Boodlea trukensis*); **Hawaii.** Hanauma Bay, Oahu, (leg. Eubank 704, 12.i.1942, UC 940 373); Kaenana point, (leg. Tilden 146, B 09449: holotype of *Boodlea kaenana*; B 09450: isotype); **Indonesia.** Flores, (leg. Weber-van Bosse 1068, xii.1888, L 937 279 433); **Martinique.** Pointe des Nègres, (leg. Hamel & Hamel-Joukov 61, iv.1930, B 34440, L 939 028 260); **Marshall Islands**. Parry Island, Eniwetok Atoll: seaward reef flat, (leg. Dawson 13669, 20.viii.1955, AKU, VWL13669); **The Philippines**. Bingag, Danis, Panglao Island, Bohol: intertidal, epilithic or epiphytic, loosely attached to substratum, (leg. Leliaert *et al.*, 10.viii.1998, PH 115); Hilangagan, Punta Maria, Borongan, Samar, epilithic, (leg. Cordero, Yamboa & de la Cruz PNH 124807, 30.xi.1977, L 366099); Malibago Bluewater Resort, Mactan Island: intertidal sandy reef flat with dead coral boulders, unattached, (leg. Leliaert *et al.*, 27.viii.1998, PH 569b); Tulapos, Enrique Villanueva, Siquijor: intertidal reef flat, loosely attached to substratum, (leg. Leliaert *et al.*, 7.viii.1998, PH 670); **Solomon Islands.** Guadalcanal, Kopiu, on reef rim, (leg. Bailey 737, 5.x.1965, L 211518); New Georgia, Matiu Island, lower intertidal, (leg. Womersley & Bailey 396, 28.viii.1965, L 211513); **Tahiti.** Papeivi Pass, (leg. Setchell & Parks 5214, 24.vi.1922, NY); **Tonga.** unknown locality, (leg. Graeffe s.n., S).

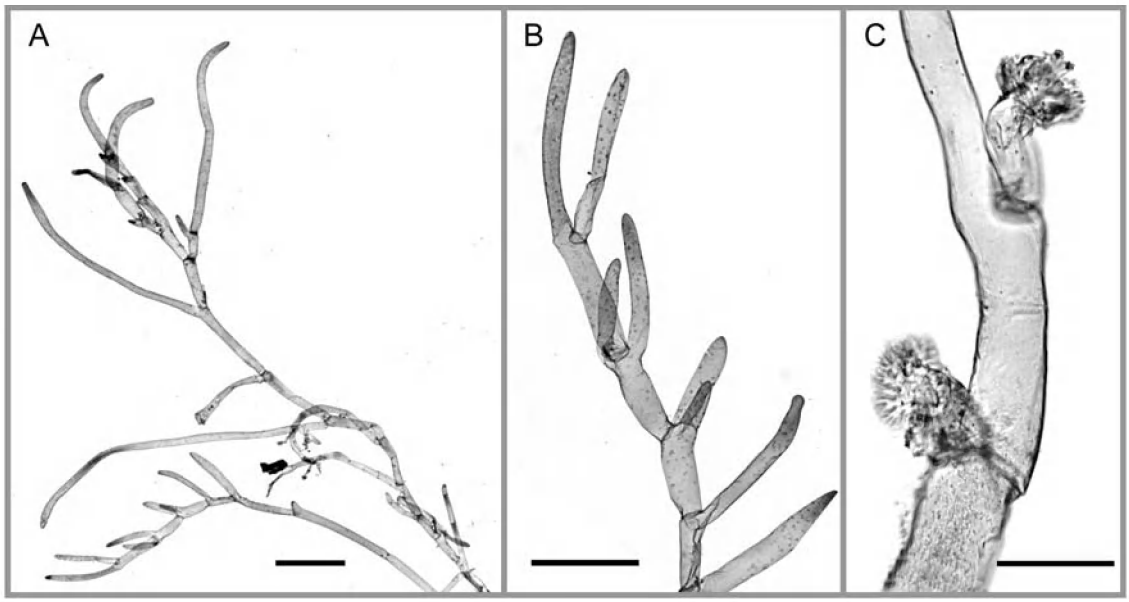


Fig. 11. *Cladophoropsis membranacea* (holotype of *Boodlea kaenana*, B) **A.** Unilateral to irregularly organized terminal branch systems; **B.** Detail of terminal branches showing cells producing a second, opposite lateral; **C.** Intermediates between type-1 and -3 tenacular cells. Scale bars: A = 1 mm; B = 500 µm; C = 100 µm.

Notes:

C. membranacea is the type of the genus and has been studied thoroughly by Børgesen (1905, 1913). Børgesen (1913: 44-45, figs 28-29) argues that the cell-division in *C. membranacea* takes place only by segregative cell division whereas in an earlier publication (1905) he regarded this mode of cell division as uncommon and a possible response to wounding, a phenomenon that was later confirmed by La Claire (1982).

C. membranacea can be confused with *C. sundanensis* and *C. macromeres* because of its intermediate cell dimensions (Table 2).

Nizamuddin (1988: 229-234, fig 1-3) distinguished *C. gerloffii* from *C. membranacea* on the basis of differences in branching pattern, position of rhizoidal and tenacular cells, and the slightly larger cell diameter. These characters are now known to be extremely variable in *C. membranacea*; therefore there is no reason to distinguish *C. gerloffii* from *C. membranacea*.

The close morphological affinity of *C. membranacea* with *Boodlea composita* has been confirmed by molecular evidence based on ITS sequence analysis (Kooistra *et al.* 1993, Wysor 2002). These studies have demonstrated that *C. membranacea* is more closely related to *Boodlea composita* and *Phyllodictyon anastomosans* (*C. composita* complex) than to the morphologically similar *C. sundanensis*. Recently, van der Strate *et al.* (2002) demonstrated, based on ITS sequences and amplification differences of microsatellite loci, that *C. membranacea* consists of at least three cryptic species in the Atlantic Ocean.

The Indo-Pacific representatives resemble the Atlantic plants in thallus morphology and architecture, mode of thallus reinforcement and crystal morphology, but differ by the cells regularly producing opposite pairs of laterals (Fig. 11B) (in the Atlantic plants generally one lateral is formed per cell and opposite laterals are rare). Indo-Pacific plants (often referred to as *B. kaenana* or *B. trukensis*) may therefore be confused with irregular thalli of the *C. composita* complex (*siamensis* or *composita* phenodemes) from which they can be distinguished by their crystal morphology. Both rectangular and elongate hexagonal crystals occur in *C. membranacea* (both morphologies often occurring within the same thallus or cell), whereas in the *P. anastomosans* complex only elongate hexagonal to needle-shaped crystals occur. The evolutionary relationship between the Indo-Pacific and the Atlantic *C. membranacea* plants remains uncertain.

Two specimens of *Boodlea kaenana* collected by Mrs. J.E. Tilden from Kaena point, Hawaii are present in B. The most intact specimen is here designated as lectotype. Both specimens are mixed with a *Cladophora* (probably *C. coelothrix*). Egerod (1952: 362) considered *B. kaenana* to be within the limits of *B. composita*.

General references: Børgesen (1905: 275-290, figs 8-13; 1913: 42-48, figs 26-33; 1925: 24, fig. 1); Littler & Littler (2000: 332, figs on p. 333); Littler *et al.* (1995: 2, fig. on p. 2); Taylor (1960: 117-118, pl. 2, fig. 1, pl. 3, fig. 2).

Cladophoropsis philippinensis Taylor

Figs 3N-Q, 5F, 12

Cladophoropsis philippinensis Taylor, 1961: 58, figs 1-6 [Holotype: Little Santa Cruz Island, near Zamboanga City, Mindanao, Philippines, leg. H.H. Bartlett 195, MICH!].

Description:

Thallus light to dark green, forming large masses or tufts, free floating or loosely attached to the substratum, 5-20 cm across, 1-3 cm thick, composed of stiff, loosely entangled, often curved branch systems.

Cell division by centripetal invagination of the cell walls. Growth by division of apical and intercalary cells, followed by cell elongation and limited cell enlargement. The diameter of the thickest part of the main axes about 1-1.3 times that of apical cells. Generally, each newly formed subapical or intercalary cell producing one lateral at its distal pole. Apical cells frequently dividing simultaneously into 3 to 6 cells, followed by cell elongation and formation of more or less equally developing branches (Figs 12A, B, arrows). Occasionally opposite pairs of laterals simultaneously initiated from one cell (Fig. 12C, arrow). Older cells sometimes producing a second (mostly opposite) (Fig. 12D, arrow) and even a third lateral. Cross walls at the base of the laterals only formed occasionally in older (basal) parts of the thallus; l/w ratio of laterals in open connection with the mother cell up to 60). Laterals occasionally displacing the main axes, especially in the basal parts of the thallus. Laterals unilateral or irregularly organized in the terminal branch systems, more irregular lower down. Thallus generally branching up to the 2nd (sometimes 3rd) order. Angle of ramification 40°-90°.

Thalli generally unattached; sometimes entangled with other macro-algae or seagrasses, or loosely attached by a small number of type-3 tenacular cells which are produced distally or laterally on terminal or intercalary cells. In average less than 1 % of the cells producing a tenacular cell.
Apical cells subcylindrical, straight or curved, 300-670 (-860) µm in diameter, 1.3-5.5 mm long, l/w ratio 3-40. Cells of the terminal branch systems subcylindrical, straight or slightly curved, 300-550 (-600) µm in diameter, 1-7 mm long, l/w ratio 3-30. Basal cells subcylindrical, straight, 430-750 (-1300) µm in diameter, l/w ratio 5-10. Cell walls 2-5 µm thick in the cells of the terminal branch systems, up to 20 µm thick in the basal cells.
Chloroplasts polygonal, elongated to star-shaped, 3-8 µm in diameter with strands spanning up to 14 µm long, forming an open parietal reticulum (Fig. 5F). Each chloroplast containing a single pyrenoid, 1.4-2.5 µm in diameter.
Large, elongate hexagonal or trapeziform prismatic calcium oxalate crystals present in most cells of the thallus (Fig. 3N-Q), up to 55 crystals per cell, 2-25 µm broad, up to 170 µm long, l/w ratio 5-40. Star-shaped clusters of fine needle-shaped crystals (possibly composed of silica) present in most cells, 20-35 µm in diameter; up to 8 clusters per cell.

Ecology: *C. philippinensis* grows in sheltered localities, on sandy substratum, often associated with seagrass beds in the infralittoral fringe to shallow subtidal (down to -5 m depth).

Geographical distribution: *C. philippinensis* possibly has a disjunct Indo-Pacific distribution. Up to now *C. philippinensis* was only known from the Zamboanga and Basilan Island area (see Silva *et al.* 1987). The Kenyan and Tanzanian specimens are the first records outside the Philippines.

Specimens examined: **Indian Ocean: Kenya**. Iwatine Bay, Mombasa: lower intertidal, epizoid on sponges between *Thalassia hemprichii*, (leg. Coppejans *et al.*, 11.ix.1992, HEC 9398); Kanamai, (leg. Coppejans, 9.vii.1985, HEC 5624); Malindi, Silversands, (leg. Coppejans, 22.iii.1988, HEC 7431); Mwamba Beach, Mombasa: mid to lower intertidal rock pools, epilithic, (leg. Coppejans, 5.ix.1991, HEC 8669b); **Tanzania**. Chole Bay, Utende Beach, Mafia Island: infralittoral fringe, epilithic between seagrasses, (leg. Coppejans, 31.vii.1993, HEC 9788); seaward side of Juani Island, Mafia Island: high intertidal, shallow rock pool, (leg. Coppejans & De Clerck, 11.i.1996, HEC 11204); **Pacific Ocean: The Philippines**. Malibago Bluewater Resort, Mactan Island: intertidal sandy reef flat with dead coral boulders, unattached, (leg. Leliaert *et al.*, 27.viii.1998, PH 567); Marigondon, Lapu Lapu City, Maktan Island: intertidal, loosely attached to rocky substratum, (leg. Leliaert *et al.*, 12.viii.1998, PH 172); Little Santa Cruz Island, opposite Zamboanga: sandy coral reef, 1-2 m depth, (leg. Bartlett A-195, i-ii.1941, MICH).

Notes:
C. philippinensis somewhat resembles two other coarse *Cladophoropsis* species, *C. macromeres* and *C. magna*. It differs from *C. magna* in the crystal morphology and from *C. macromeres* by its much broader filaments (Table 3).

One Philippine specimen (PH 172) was found to have much smaller cell dimensions, somewhat intermediate between *C. philippinensis* and *C. membranacea* (apical cells 200-320, main filaments up to 520 µm). This possibly indicates that the range of cell dimensions in *C. philippinensis* is more extensive than previously considered, or ultimately that *C. philippinensis* represents a growth form of *C. membranacea*.

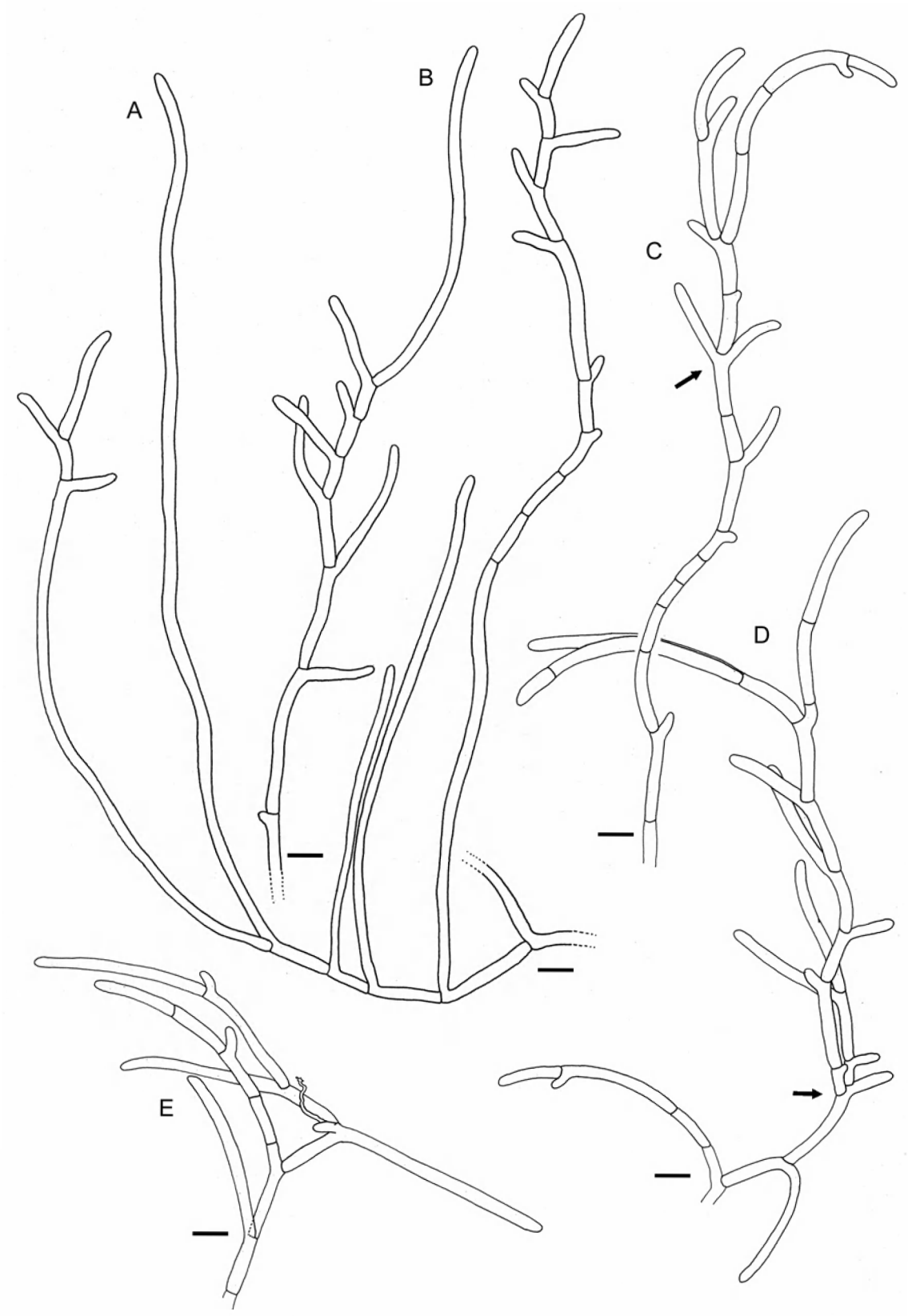


Fig. 12. *Cladophoropsis philippinensis*. **A-E.** Irregularly organized branch systems. (A-B: holotype, MICH; C-E: PH 567). Scale bars = 2 mm.

Cladophoropsis sundanensis Reinbold Figs 3L-M, 13, 14

Cladophoropsis sundanensis Reinbold, 1905: 147 [Lectotype: Kangean, Indonesia, leg. Weber-van Bosse, Siboga Expedition s.n., L! 937.279.372. Several locations were indicated in the original prologue (Timor, Labuan, etc.); only a single specimen from the Siboga Expedition, identified by Reinbold and labeled in his hand was found in L and is indicated as lectotype].

Siphonocladus sundanensis (Reinbold) Reinbold, *in* Weber-van Bosse, 1913: 83, 84, expl. fig. 18 on p. 77.

Siphonocladus fasciculatus Kjellman, 1897: 36, pl. 7: figs 10-17 [Holotype: Yokohama, Japan, leg. F.R. Kjellman, Vega-expedition, 18.ix.1879, UPS! A-000356-251828].

Cladophoropsis fasciculatus (Kjellman) Wille, *in* Engler & Prantl, 1910: 116.

Cladophoropsis carolinensis Trono, 1972: 48, pl. 3 [Holotype: reef flat near Utwa Village, Kusaie Island, Caroline Islands, leg. E.G. Meñez, Doty no. D23616, 7.vii.1960, BISH! 586970].

Description:

Thallus light to medium green, forming compact spongy cushions or moss-like mats, firmly attached to the substratum, often sand or sediment-trapping, generally 2-7 cm across, occasionally reaching a diameter of up to 15 cm, 1-1.5 cm thick, composed of strongly entangled branch systems. Attachment to the substratum by branched, multicellular rhizoids arising from the proximal pole of the basal cells and other cells in the basal region (type-1 rhizoids, Figs 13E, 14I), and by type-3 hapteroidal rhizoids (Fig. 14D) or type-3 tenacular cells (Fig. 13D, 14F-G) produced at the cell apices in any part of the thallus.

Cell division generally by centripetal invagination of the cell walls and occasionally by segregative cell division (Fig. 14H). Growth by apical and intercalary cell division, followed by cell elongation and limited cell enlargement. Diameter of the thickest part of the main axes about 1.3-3.5 times that of apical cells. Apical cells generally dividing more or less simultaneously into 3 to 7 cells followed by the development of laterals (Figs 13A-C, 14A-D). Generally, each newly formed cell producing a single branch at its distal pole; occasionally an opposite pair of laterals is initiated simultaneously (Fig. 13E, 14C, arrows); older (basal) cells also sometimes producing a second lateral. Laterals not displacing the main axes. Cross wall formation at the base of the laterals is usually delayed (Fig. 52B, C) but in some terminal branch systems steeply inclined cross walls may be formed almost immediately after formation of laterals (Fig. 53A, C, D); l/w ratio of laterals in open connection with the mother cell up to 40. Branches mostly unilaterally arranged in the terminal branch systems, more irregular lower down. Thallus generally branching up to the 3rd (occasionally 4th) order. Angle of ramification 30°-90°.

Structural reinforcement of the thallus achieved by interweaving of the filaments, and by anastomosis of the cells by hapteroid rhizoids and tenacular cells (Fig. 52D, 53F, G). In average 1-4 % of the apical cells producing a tenacular cell.

Apical cells (sub)cylindrical to slightly tapering, with rounded tip, straight, slightly curved or sinuous, (40-) 60-120 (-140) µm in diameter, length up to 6 mm, l/w ratio ranging from 1.5 to 80. Cells of the terminal branch systems straight or slightly curved, 80-140 µm in diameter, l/w ratio 4-50. Basal filaments usually straight, (80-) 180-250 µm in diameter, l/w ratio 3-40. Cell walls 1-2 µm thick in the cells of the terminal branch systems, (2-) 5-8 µm thick in the main axes and basal cells.

Chloroplasts polygonal, elongated or star-shaped, (3-) 4-6 µm in diameter with strands spanning up to 15 µm, forming an open parietal reticulum. Each chloroplast containing a single (sporadically 2) pyrenoid(s), 1.4-2.5 µm in diameter.

Prismatic calcium oxalate crystals broad to elongate rectangular, often with curved faces (Fig. 3L-M), present in most cells of the thallus, up to 7 crystals per cell, 2-15 µm in diameter, 15-25 µm long, l/w ratio 1-6 (-12).

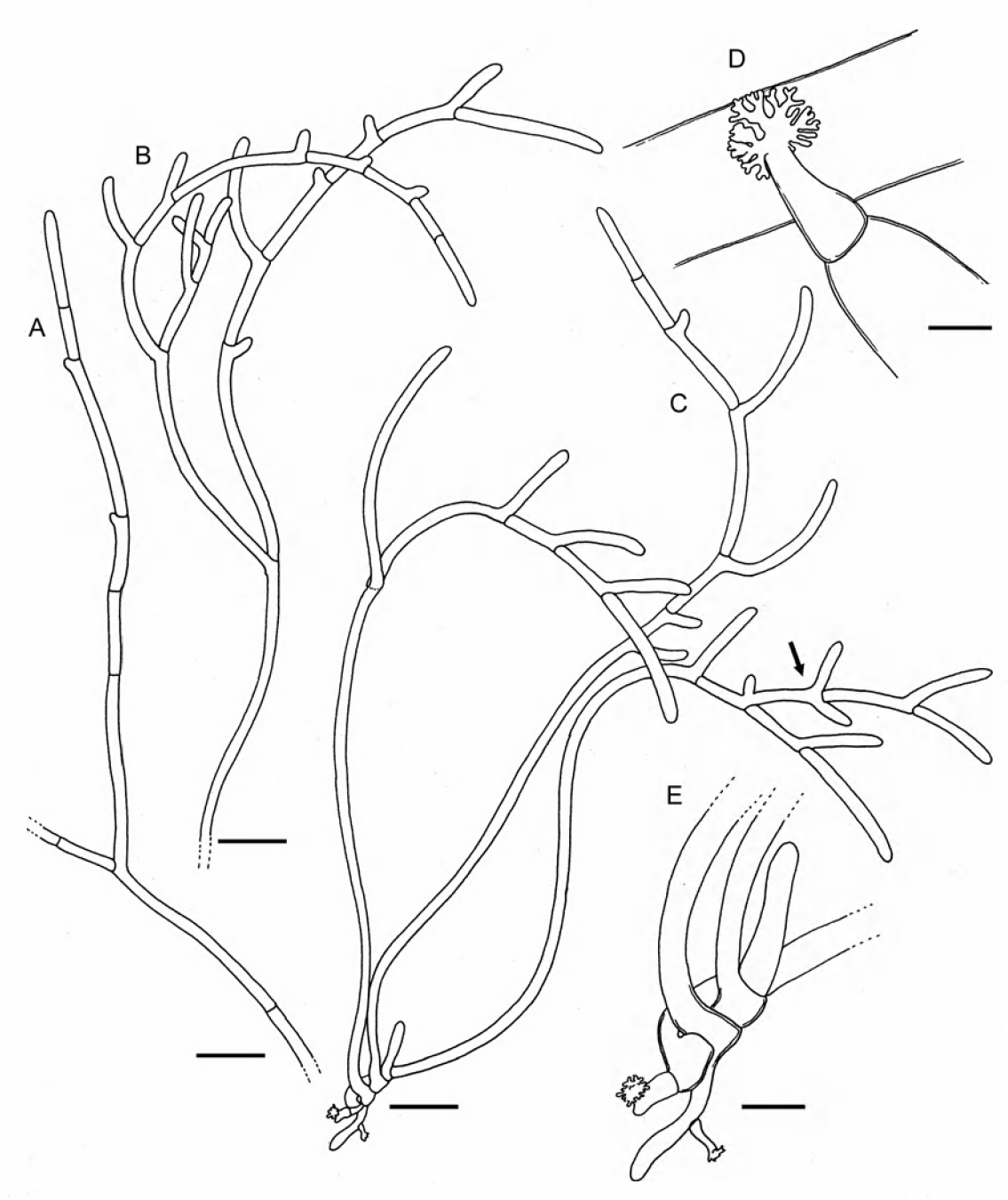


Fig. 13. *Cladophoropsis sundanensis* (lectotype, L). **A-C.** Thallus composed of unilaterally to irregularly organized terminal branch systems; occasionally cells producing a pair of opposite laterals (arrow); **D.** Type-3 tenacular cell; **E.** Detail of basal type-1 rhizoids. Scale bars: A-C = 500 µm; D = 50 µm; E = 500 µm.

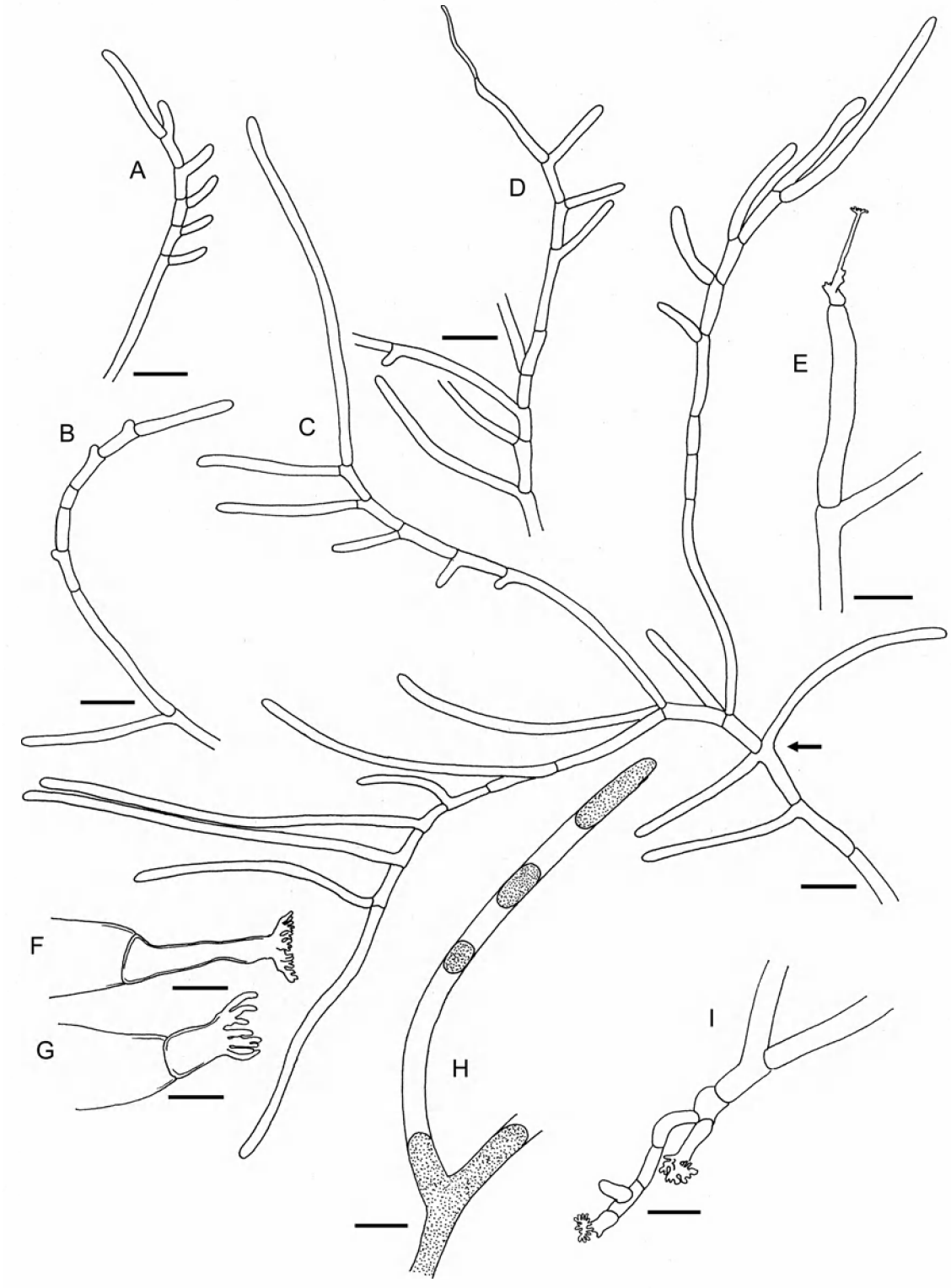


Fig. 14. *Cladophoropsis sundanensis* (FL 953). **A-D.** Terminal branch systems; **E.** Type-3 rhizoid; **F-G.** Type-3 tenacular cells; **H.** Lateral, undergoing segregative cell division; **I.** Basal type-1 rhizoids. Scale bars: A-D = 500 µm; E, H = 200 µm; F-G = 50 µm.

Ecology: *C. sundanensis* grows epilithic on horizontal to vertical surfaces, often on sand covered substrates, epiphytic on various algae, seagrasses and mangrove pneumatophores (e.g. *Sonneratia*), or epizoic on sponges, from the high intertidal to shallow subtidal (down to - 3 m depth) on exposed and semi-exposed shores, sometimes penetrating in mangrove creeks (Cribb 1960; Egerod 1974, 1975; this paper). *C. sundanensis* often grows intermixed with other filamentous Chlorophyta, e.g. *Boodleopsis pusilla*, *Cladophora* spp. and *Chaetomorpha* spp. The abundance of rhizoids varies greatly between plants. Those growing in the upper tide level produce less rhizoids throughout the thallus than those found at lower tide levels or exposed to surf.

Geographical distribution: *C. sundanensis* is a common and widely distributed species in the Indo-Pacific, Mediterranean Sea and Persian Gulf. The species has also been reported from the Atlantic Ocean (see Wynne 1998).

Specimens examined: **Indian Ocean: Kenya**. between English Point and Mc Kenzie Point, Mombasa, (leg. Coppejans, i.1986, HEC 5839); Gazi Bay: *Sonneratia* mangrove, (leg. Coppejans, 7.viii.1989, HEC 8275); Iwatine Bay, Mombasa: high intertidal rock pools, (leg. Coppejans *et al.*, 11.ix.1992, HEC 9401); Kanamai, Mombasa, (leg. Coppejans, vi.1985, HEC 5623); Tiwi, (leg. Coppejans, 13.vii.1987, HEC 6837); **Oman**. Mangroves of Shaghaf Island, Masirah Island: mid intertidal, (leg. Schils, MAS 463b); **Rodrigues**. Graviers: epilithic on horizontal sand-covered rock substratum, (leg. Coppejans, 19.ix.2001, HEC 14673); **Seychelles**. Bird Island, East coast: epilithic on coral boulders covered by *Thalassodendron ciliatum*, (leg. Coppejans *et al.*, 20.xii.1992, SEY 244); Ile Desnoeufs: steep sandy beach with large isolated flat rocks, epilithic on horizontal surface, (leg. Coppejans *et al.*, 2.i.1993, SEY 618); Ile du Sel, Poivre Atoll: lower intertidal, rocky substratum, (leg. Coppejans *et al.*, 1.i.1993, SEY 616); Le Corsaire, NW coast of Mahé Island: mid intertidal, rocky platform of an artificially built dike, (leg. Coppejans *et al.*, 12.xii.1992, SEY 61, 66); St. François Atoll, Bijoutier Island: subtidal coral slope, (leg. Coppejans *et al.*, 5.i.1993, SEY 732); **South Africa**. 1/4 Mile Reef, Sodwana Bay, KwaZulu-Natal: subtidal, - 9 m, (leg. De Clerck *et al.*, 11.ii.2001, KZN 2148); Isipingo Beach, KwaZulu-Natal: high intertidal pools, epilithic on vertical and overhanging rockwalls, (leg. Coppejans, 21.i.1995, HEC 10944); Island Rock, KwaZulu-Natal: intertidal rock pools, (leg. De Clerck & Cocquyt, 14.viii.2000, KZN 1693); Mabibi, KwaZulu-Natal: intertidal pools and infralittoral fringe, (leg. Coppejans *et al.*, 9.viii.1999, KZN 395); Treasure Beach, The Bluff, Durban, KwaZulu-Natal, (leg. Coppejans *et al.*, 3.viii.1999, KZN 0072a); **Sri Lanka**. Beruwela, intertidal rock platform, in front of Confifi Beach Hotel: sheltered and exposed side of the reef crest, epilithic on horizontal substratum, (leg. Coppejans, 25.i.1997, HEC 11813a); **Tanzania**. Kunduchi, in front of Bahari Beach Hotel: shallow subtidal, epiphytic on *Amansia dietrichiana*, (leg. Coppejans & De Clerck, 3.i.1996, HEC 11062); Kunduchi, Bahari Beach: mid to low intertidal, epilithic, (leg. Leliaert & Coppejans, 10.vii.2001, FL 901); Mbudya Island, west coast: supralittoral fringe, epilithic on vertical substratum, mixed with *Boodleopsis* sp., (leg. Leliaert & Coppejans, 11.vii.2001, FL 919); Chwaka Bay, Zanzibar: intertidal seagrass bed, on sponge, (leg. Leliaert & Coppejans, 18.vii.2001, FL 975); Fishermen's resort, Mbweni Cliffs, Zanzibar: epilithic on coral boulder, intertidal, (leg. Leliaert, 15.vii.1997, FL 606); Mana Hawanja Island close to Nangerera, Mnazi Bay, Mtwara area: high intertidal, epilithic on horizontal rock, under overhanging fossil coral cliff, (leg. Coppejans *et al.*, 29.vii.2000, HEC 12976); Matemwe, in front of Matemwe Beach Village, Zanzibar: mid intertidal reef flat, epiphytic on *Gelidiella acerosa* and *Turbinaria* sp., (leg. Leliaert & Coppejans, 16.vii.2001, FL 949 and FL 953); Nungwi, Zanzibar: drift, (leg. Leliaert & Coppejans, 21.vii.2001, FL 1000); Nungwi, Zanzibar: supralittoral fringe, epilithic on vertical fossil reef substratum, (leg. Leliaert & Coppejans, 21.vii.2001, FL 995); Uroa, Zanzibar: high intertidal, epilithic, sand trapping, (leg. Coppejans, 2.viii.1993, HEC 9833); Chwaka, Zanzibar: high intertidal mangrove creek, epilithic, (leg. Coppejans & De Clerck, 27.viii.1994, HEC 10714); Kizinkazi, Zanzibar: epiphytic on *Cystoseira myrica*, (leg. Coppejans & De Clerck, 26.viii.1994, HEC 10669); in front of Mafia Island Lodge, Mafia Island: mid intertidal, epiphytic on *Sonneratia*-pneumatophores, (leg. Coppejans & De Clerck, 12.i.1996, HEC 11224a); seaward side of Juani Island, Mafia Island: lower intertidal, epilithic on horizontal rock, (leg. Coppejans & De Clerck, 11.i.1996, HEC 11211); **Yemen**. Ra's Hammadara, NE-coast of Socotra: shallow subtidal, - 3 m, epilithic on dead coral, (leg. Leliaert, 23.ii.1999, SOC 152); **Mediterranean Sea: Greece**. Saron Gulf, Attika, (leg. Schiffner 965, 6.xii.1928, NY); **Pacific Ocean: Caroline Islands**. reef flat near Utwa Village, Kusaie Island, (leg. E.G. Meñez, Doty no. D23616, 7.vii.1960, BISH 586970: holotype of *Cladophoropsis carolinensis*); **Japan**. Yokohama, (leg. F.R. Kjellman, Vega-expedition, 18.ix.1879, UPS: holotype of *Siphonocladus fasciculatus*); **Indonesia**. Kangean, (leg. Weber-van Bosse, Siboga Expedition s.n., L 937.279.372: lectotype of *Cladophoropsis sundanensis*); **Papua New Guinea**. Medibur, Madang Province, (leg. Coppejans & Prud'homme van Reine, 23.vii.1990, Copp & PvR 13365a); **Tahiti**. Arue Reef, (leg. Setchell & Parks 5048, 23.v.1922, UC 261237); Reef at Tahara Mountain, (leg. Setchell & Parks 5155 and 5160, 17.vii.1922, UC 261238 and 261303); **The Philippines**. Bantayan Island: epilithic, (leg. Dargent & Bel, 5.viii.1999, HOD PH 99-30); Lumangcapan, Enrique Villanueva, Siquijor: high intertidal sandy reef flat, epiphytic on seagrasses, (leg. Leliaert *et al.*, 7.viii.1998, PH 42); Punta Engano, Mactan Island: high intertidal reef flat, epiphytic, (leg. Leliaert *et al.*, 5.viii.1998, PH 628); **Persian Gulf: Saudi Arabia**. Abu Ali Island, N of Jubail: infralittoral fringe, epilithic on beach rock, salinity 44 pm, temperature 31 °C, (leg. Coppejans, 1.viii.1992, HEC 9291); Abu Ali Island, N of Jubail: intertidal, shallow rock

pools, epiphytic on *Digenea*, (leg. De Clerck, 2.xi.1992, ODC 40); Abu Ali Island, N of Jubail: mid intertidal, in rock crevices, (leg. De Clerck, 1.xi.1992, ODC 21); close to Bomb Crater Bay, N of Jubail: lower intertidal rock pool, epiphytic or epizoic on sponges, (leg. Coppejans, 23.i.1992, HEC 8929); Fisherman's bay, Abu Ali Island, N of Jubail: lower intertidal, in crevices of the coastal beach rock exposed to surf, salinity 44 pm, seawater temperature 30 °C, (leg. Coppejans, 20.vii.1992, HEC 9190); N of Jubail: infralittoral fringe between *Digenea*, unattached, (leg. De Clerck, 11.xi.1992, ODC 125); Ras Al Bukhara, N of Jubail: mid intertidal, epiphytic on *Digenea* sp., salinity 44 pm, seawater temperature 27 °C, (leg. Coppejans, 27.vii.1992, HEC 9256); Ras Al-Zawr, N of Jubail: epilithic in crevices of the infralittoral fringe, salinity 44 pm, seawater temperature 28 °C, (leg. Coppejans, 24.vii.1992, HEC 9220).

Notes:

The original diagnosis of *C. sundanensis* was rather cryptic and the species became better known as *Siphonocladus sundanensis* through the description and illustration of Weber-van Bosse (1913: 83, 84, fig. 18).

C. sundanensis can be most easily confused with *C. membranacea* from which it mainly differs by its smaller cell diameter (Table 2).

Siphonocladus fasciculatus was treated as a taxonomic synonym of *Cladophoropsis zollingeri* by Yoshida *et al.* (1990: 272). The holotype of *S. fasciculatus* however, is very different from the latter. The type is characterized by slender filaments (apical cells 65-130 µm in diameter), thin cell walls (up to 4 µm in basal cells); branches are generally unilateral, sometimes opposite; rhizoids occasionally develop from the proximal pole of the cells and tenacular cells are sometimes present at the tips of the apical cells; tetrahedral protein cell inclusions are absent but each cell contains several elongate prismatic calcium oxalate crystals. Based on these characters we consider *C. fasciculatus* as a synonym of *C. sundanensis*.

Trono (1972) distinguished his new species *C. carolinensis* from *C. sundanensis* on the shape of the apical cells [tapering in *C. carolinensis* versus clavate in *C. sundanensis*, based on the illustrations of Børgesen (1935) and Dawson (1956)] and the longer filaments. Apical cells in the specimens examined (including the type) are found to be subcylindrical, more rarely slightly tapering or slightly swollen in the middle. Cell length in *C. sundanensis* (even within a single specimen) is found to be extremely variable with l/w ratios ranging between 1.5 and 80; the values found in *C. carolinensis* fall within those values. Neither the shape of the apical cells nor the length of the filaments seem to be suitable characters for distinguishing both species and we therefore consider *C. carolinensis* to be conspecific with *C. sundanensis*.

General references. As *C. sundanensis*: Weber-van Bosse (1913: 77-79, fig. 18); Børgesen (1935: 10-11, fig. 1); Yamada (1944: 11); Cribb (1960: 10); Dawson (1961: 404, pl. 1, figs 9-10); Egerod (1974: 141, figs 32-36; 1975: 46, figs 8-10); Jaasund (1976: 11, fig. 24); Sartoni (1976: 118, fig. 4; 1986: 365, fig. 6B; 1992: 313); Tseng (1984: 274, pl. 136, fig. 1); De Clerck & Coppejans (1996: 215, fig. 22); Leliaert *et al.* (2001: 452, figs 6-8); as *C. carolinensis*: Kraft (2000: 573, fig. 25A-D); Skelton & South (2002: Plate VII, figs 52–54).

Cladophoropsis composita complex

Phyllodictyon anastomosans and *Boodlea composita*, two of the most abundant and wide-spread tropical Cladophorophyceae taxa, have had a long history of confusing circumscriptions and several authors have commented on the vague boundaries between the two taxa (Egerod 1975, Kooistra *et al.* 1993, Leliaert *et al.* 1998, Wysor 2002). Both species were described by Harvey from both sides of the Indian Ocean: *Conferva composita* was based on a cushion-like specimen from Mauritius (Harvey 1834), *Cladophora anastomosans* was described from Western Australia as stipitate blades with branch systems confined to a single plan (Harvey 1859) (as will be discussed later, the original description only partly corresponds with the authentic material). In the discussion of *C. anastomosans*, Harvey (l.c.) already stressed the similarity in branching pattern with *C. composita*.

Numerous *Boodlea* and *Phyllodictyon* (as *Struvea*) species and varieties have been distinguished from *P. anastomosans* and *B. composita* based on small, often trifling differences in branching patterns, cell dimensions and blade sizes [*B. coacta*, *B. kaenana* (which is here regarded as a synonym of *C. membranacea*), *B. siamensis*, *S. delicatula*, *S. multipartita* and *S. tenuis*). Most of these taxa were later reduced to synonyms of either *P. anastomosans* or *B. composita*, depending on their thallus morphology: stipitate, unistratose blades, or cushion-like thalli composed of three-dimensional branch systems respectively (Murray & Boodle 1888b; Børgesen 1946; Egerod 1952; Cribb 1960; Steentoft 1967). This distinction in growth form has to date been widely adopted to distinguish both taxa (Womersley & Bailey 1970; Tseng 1984; Abbott 1989; Sartoni 1992; Wynne 1993, 1995; Leliaert *et al.* 1998; Littler & Littler 2000, 2003; Coppejans *et al.* 2001).

Egerod (1975) however, commented on the extreme variability of both species and the resulting vague boundaries between the two taxa. She noticed that the early developmental stages of *B. composita* and *P. anastomosans* are nearly identical, and hypothesized that both taxa might represent growth forms of the same species. Strangely enough, Egerod (l.c.) described a new genus and species in the same paper, *Pseudostruvea siamensis*, based on two characters which she previously recognized to be variable (presence of annular constrictions and the absence of tenacular cells). Moreover, she stated that *P. siamensis* also is indistinguishable from *B. composita* or *P. anastomosans* in the initial stages of thallus development.

The ambiguous distinction between *P. anastomosans* and *B. composita* can, paradoxically enough, be demonstrated by the authentic material of *P. anastomosans*, consisting of four cushion-like specimens with branch systems growing in three directions. One of the specimens (hereby designated as lectotype) partially consists of stipitate blades, and it is presumably on this fragment that Harvey (1859) based the original description.

Several molecular studies confirm the indistinct species boundaries and suggest a species complex. Partial LSU rRNA sequences of *B. composita*, *B. siamensis*, *P. anastomosans* and *Struveopsis siamensis* are nearly identical (maximum pairwise sequence divergence of 1%), indicating that they might represent growth forms of a single species. Phylogenetic studies based on ITS sequence analysis have demonstrated that thallus morphology, distinguishing *P. anastomosans* and *B. composita*, is incongruous with the evolutionary history (Wysor 2002). The ITS tree shows three well supported clades with a strong phylogeographic signal, containing a mixture of *P. anastomosans* and *B. composita* forms. This could indicate that the different thallus morphologies have evolved several times independently, or alternatively, the different architectural types are ecologically determined, or represent different developmental stages of the same species.

Table 4. Survey of characters in the six phenodemes within the *C. composita* complex.

Phenodeme	Thallus morphology	Branching systems	Apical cell division	Tenacular cells	Apical cell diameter (a) and diameter main filaments (m) (µm)
anastomosans Figs 15-20	Young thalli forming stipitate blades. Mature thalli composed of stipitate, flattened blades clustering into cushion-like thalli. Annular constrictions absent.	Ultimate branch systems composed of opposite or pseudodichotomously branching filaments; branching initially in a single plane, later becoming 3-dimensional. Branching in main axes opposite, essentially in a single plane.	division into 2 (sometimes 3) cells	type-1 and -3, abundant	a: (60-) 80-180 (-240) m: (150-) 200-750 (-875)
composita Figs 21-24	Cushion-like, composed of loosely entangled filaments. Often sand-trapping. Stipe absent.	Ultimate branch systems composed of regularly, opposite branching filaments, generally with a 3rd (and 4th) lateral produced perpendicular to the branching plane. Branching in main axes opposite, not strictly in a single plane.	division into 2, or simultaneously 3-8 cells	type-1 and -3, uncommon	a: (40-) 50-90 (-125) m: (140-) 180-250 (-400)
delicatula Figs 25-26	Stipitate blades, single or clustered. Annular constrictions absent.	Ultimate branch systems composed of regularly opposite branching filaments. Branching in main axes opposite. All branches strictly in a single plane.	division into 2 (3) cells	type-3 abundant; type-1 rare.	a: (70-) 90-180 (-280) m: (120-) 350-540 (-620)
montagnei Figs 27-28	Astipitate, reticulate blades.	Ultimate branch systems composed of pseudodichotomously branching filaments. Branching in main axes opposite. All branches strictly in a single plane.	division into 2 (rarely 3) cells	type-3 abundant; type-1 rare.	a: (50-) 70-140 (-180) m: (180-) 200-650 (-700)
siamensis Figs 29-35	Cushion-like, composed of tightly interwoven filaments. Stipes only present in juvenile thalli.	Ultimate branch systems composed of unilaterally or pseudodichotomously branching, often incurved filaments, generally with a 2nd (and 3rd) lateral produced perpendicular or opposite to the first lateral. Branching in main axes opposite or irregular.	division into 2 (sometimes 3) cells	type-1 and -3, abundant	a: (40-) 60-140 (-250) m: (120-) 160-380 (-875)
struveopsis Figs 36-37	Stipitate thalli, single or grouped into cushion-like thalli. Stipe and basal branches generally with annular constrictions.	Ultimate branch systems composed of opposite branching filaments, branches not strictly in a single plane. Braching in main axes opposite.	division into 2, or simultaneously 3-8 cells	generally absent	a: (85-) 100-220 (-260) m: (140-) 260-570 (-930)

Morphological examination of a large number of specimens worldwide of *P. anastomosans*, *B. composita* and morphological allied taxa, demonstrates a wide variety in thallus morphology, architecture, branching systems, cell dimensions and tenacular cell types. Based on the morphological characters listed in Table 4, six more or less distinct morphological entities can be recognized. As mentioned above, this morphological variety might be attributed to ecological or developmental plasticity, or the different morphological entities may be evolutionary determined. An unambiguous answer is still pending but field observations indicate that, despite the observed morphological plasticity and the presence of intermediate forms, often distinct morphological types can be observed in certain area's without the presence of intermediate or transitional forms. It is not unlikely that a number of semi-cryptic species exist, each with a considerable morphological plasticity, resulting in overlapping morphologies.

For now, we recognize a single species, ***Cladophoropsis composita*** (Harvey) Leliaert & Coppejans, comb. nov. prov. (= *Conferva composita* Harvey). Awaiting the true nature of the morphological entities in the *C. composita* complex (different species or growth forms of the same species), we choose to refer the different morphological types to **phenodemes**. The term "deme" was first introduced by Gilmour & Gregor (1939) and later refined by Gilmour & Heslop-Harrison (1954) and relates to "any assemblage of taxonomically closely related individuals". It makes no assumptions as to what level of relatedness the group in question is subject to. It can be prefixed with e.g. "pheno-", "geno-", "gamo-", to denote at what level the relationship between individuals occurs. Thus, a phenodeme is a group of morphologically allied individuals. The deme-terminology has until now only been adopted in diatom taxonomy (Mann 1999). We prefer the term "phenodeme" over "ecad" because in the latter the assumption is made that different morphological forms are ecologically induced within a single "species" (Coppejans & Prud'homme van Reine 1992; Silva *et al.* 1996).

A detailed study, based on extensive collections of *P. anastomosans* plants, was carried out in Chwaka Bay, Zanzibar (Tanzania). This collection is a good example for demonstrating the morphological transformations during thallus development. Initially the thallus consists of a cylindrical stipe initiating a small reticulate blade at its apical pole. The lamina is formed by a repetitive process of cell division (CI), opposite lateral formation and cell elongation. Growth in the initial stages of blade formation takes place by apical cells dividing more or less simultaneously into 3-5 cells, followed by the formation of opposite laterals (Fig. 19A-B). Later, apical cells generally divide into 2 (rarely 3) cells, and intercalary cell division occurs at regular intervals, resulting in a regular sequence of young laterals and more developed branch systems. In these young blades, referable to the *delicatula* phenodeme, all laterals are formed strictly in a single plane (Fig. 19C-D). In older blades, most of the newly formed, subapical cells produce a single lateral (instead of an opposite pair of laterals), resulting in unilateral or pseudodichotomous ultimate branch systems (Fig. 19G, 20C). Older cells generally produce a second lateral, opposite or perpendicular to the first one, resulting in 3-dimensional branch systems (Figs 19G-I). These stipitate blades, referable to the *anastomosans* phenodeme, remain flattened as a result of the main filaments, branching oppositely in a single plane (Figs 19E). At a later stage adjacent blades may attach to one another (Fig. 19F) and form irregular cushion-like thalli with the stipes becoming masked. At this stage the internal blade-like structure of the cushion-like thallus is still apparent. Mature thalli may detach from the substratum and continue to grow as loose lying masses in intertidal pools and tidal channels. The blade-like structure remains apparent in the peripheral parts of the thallus (Fig. 20A-F), but is completely lost in the centre where filaments are thinner, more elongate and three dimensionally branched (Fig. 20G-L). In attached cushion-like thalli the internal blade-like structure may become vague and will eventually be completely lost, referable to the *siamensis* phenodeme. Under certain environmental conditions (e.g. shaded rock pools), branching remains confined to a single plane

and stipe cells are lost, resulting in unistratose, astipitate blade-like thalli, referable to the *montagnei* phenodeme (Fig. 20M-O).

In older plants, portions of the thallus can easily dislodge, re-attach and go on growing as irregular cushions. In the field, this stage can easily be recognized by the thalli which fall apart when squeezed in the hand (young cushion- or sponge-like thalli are firm and resilient and do not easily fall apart). This mode of vegetative reproduction is probably very common and might be the reason that in certain area's only cushion-like thalli are found. Stipitate blade-like thalli most likely develop only from settling spores or zygotes as demonstrated by Chihara (1955 for "*Boodlea coacta*"). A similar mode of vegetative reproduction has also been observed in the *composita* phenodeme.

The ***anastomosans*** phenodeme

Figs 15-20

Corresponding taxa:

Cladophora ? *anastomosans* Harvey, 1859: pl. CI [Lectotype: Fremantle, Western Australia, leg. Harvey, Australian algae exsiccatae no. 582a, BM!; isolectotypes in BM!, S! and MEL!].

Pterodicyton anastomosans (Harvey) J.E. Gray, 1866: 70.

Struvea anastomosans (Harvey) Piccone & Grunow ex Piccone, 1884b: 20. [The authorship of this binomial is ambiguous; none indicated, but in footnote Piccone mentions that he thought it might be the type of a new genus, *Cormodictyon*, but that Grunow disagreed, wishing to place it in *Struvea* (Index Nominum Algarum)].

Phyllodictyon anastomosans (Harvey) Kraft & Wynne, 1996: 139, pls 16-25.

Struvea multipartita Pilger, 1920: 2-4, figs 1-8 [Holotype: Annobon Island, Equatorial Guinea, West Africa, leg. J. Mildbraed, 1911, 6659-A141, B!].

Boodlea struveoides Howe, *in* Britton, 1918: 496 [Holotype: Harrington Sound, Bermuda, leg. Howe 131, NY!].

Description:

Thalli forming either stipitate, reticulate blades, composed of densely branched filaments, up to 13 cm high (Figs 15A, 17B, 19A-F), or astipitate blade-like structures (Fig. 20M-O) or cushion-like plants with an internal blade like-structure (Figs 16, 18, 20A-L), lacking stipe cells, up to 35 cm across. Stipes generally clustered, unbranched or branched, without basal annular constrictions, attached to the substratum by branching, multicellular rhizoids arising from the proximal pole (Figs 15A, 17A, 19C-E). Cushion-like thalli attached by type-1 tenacular cells produced in any part of the thallus (Figs 15G-I, 18C-D), or loose-lying.

Young stipe cell cylindrical; when reaching a length of 5-10 mm, the distal end of the stipe cell dividing into two to several cells. Blade formation by a repetitive process of apical and intercalary cell division (CI), formation of laterals and cell elongation and enlargement. Ultimate branch systems strictly opposite in the initial stages of blade formation, later becoming pseudodichotomous by cells producing a single lateral and displacing the apical cell. Older cells generally producing a 2nd (to 4th) lateral, opposite or perpendicular to the first lateral, resulting in three-dimensional branch systems; branching of the perpendicular laterals mostly restricted to the first or second order. Ultimate branch systems mostly curved (Fig. 20C). Branching in the main axes generally opposite with all branches essentially in a single plane, resulting in

flattened blades (Figs 16, 18A-B, 20A-F, M-O). Intercalary cell divisions in the main axes occurring at regular intervals (Fig 20N-O). Formation of cross walls at the proximal pole of newly formed laterals somewhat delayed; laterals in open connection with the mother cell up to 420 µm long (l/w ratio: 4.5). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching up to the 7th order. The diameter of the stipe cells or cells of the main axes 1.6-8 times that of the apical cells. Angle of ramification 45-90°.

Mature blades plane, irregular in outline, either single or clustered and coalescent by type-3 tenacular cells. Clustered blades eventually forming cushion-like thalli in which the internal blade-like structure remains. Reinforcement of the lamina by interweaving of the filaments, and attachment of adjacent cells mostly by type-3 tenacular cells, less frequently by type-1 tenacular cells. The first type borne singly, terminal or subterminal on apical cells or laterals in open connection with the mother cell. In mature blades, in average18-47 % of the apical cells form a type-3 tenacular cell.

Apical cells cylindrical to slightly tapering with rounded tip, straight or slightly curved, (60-) 80-180 (-240) µm in diameter, l/w ratio 1.5-10. Cells of the main axes (150-) 200-750 (-875) µm in diameter, l/w ratio 2.3-9. Stipe cells subcylindrical, 350-800 (-1000) µm in diameter, tapering towards the base, up to 16 (-34) mm long.

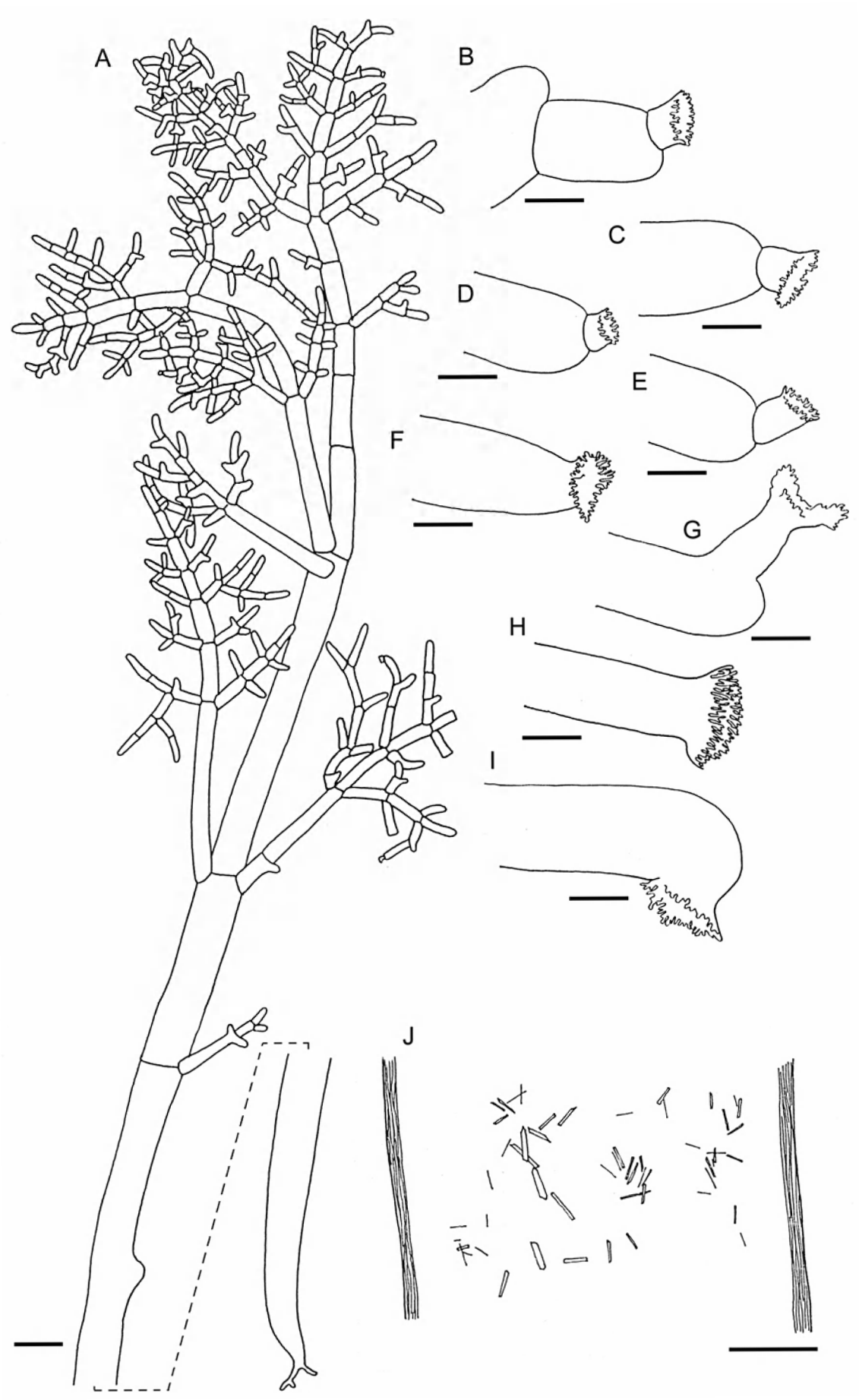
Thickness of the cell wall ca. 2 µm in the ultimate branches, up to 10 µm in the main axes (Fig. 15J).

Chloroplasts polygonal to star-shaped, 2.5-7 µm in diameter with strands spanning up to 18 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

Prismatic calcium oxalate crystals present in all cells of the thallus (except for the type-3 tenacular cells), elongate hexagonal to needle-shaped, up to 5 µm in diameter and 30 µm long (Figs 15J, 17E).

Specimens examined: **Atlantic Ocean: Bermuda.** Harrington Sound, epilithic, (leg. Howe 130, 18.vi.1900, NY; leg. Howe 131, 18.vi.1900, NY: holotype of *Boodlea struveoides*); **Equatorial Guinea.** Annobon Island, infralittoral fringe, (leg. Milbraed 6659, x.1911, B A141: holotype of *Struvea multipartita*); **Carribean Sea: Barbados.** Rocky Bay, (leg. Vickers s.n., 23.ii.1899, BR); **Colombia.** Santa Marta, Ensenada de Concha, intertidal, epilithic, (leg. Schnetter A 1281, 30.vii.1970, L 366235); **Curaçao.** Boca Ascension, (leg. Vroman Cu 109-4, 23.iv.1958, L 8168); **Puerto Rico.** W of mouth of Guanica Harbor, low intertidal, on *Rhizophora* stilt roots, (leg. Howe 7277, 30.vi.1915, L 938 303 961); **Indian Ocean: Australia.** Fremantle, Western Australia, (leg. Harvey 21, 1853, AK 26743; leg. Harvey 582a, BM: lectotype and isolectotypes of *Cladophora anastomosans*; same number, MEL 666891 and S: isolectotypes); **Kenya.** Gazi, (leg. Coppejans *et al.*, 15.ix.1992, HEC 9479a); Kanamai, Mombasa, (leg. Coppejans, i.1986, HEC 6063); Kanamai, Mombasa, (leg. Coppejans, ii.1986, HEC 6108); Mc Kenzie Point, Mombasa, (leg. Coppejans, i.1986, HEC 6018); Mwamba Beach, Mombasa, epiphytic on *Laurencia papillosa*, (leg. Coppejans, 5.ix.1991, HEC 8690); Nyali Beach reef, Mombasa, intertidal reef pool, (leg. Coppejans, 12.vii.1987, HEC 6760); Shimoni, (leg. Coppejans, 10.iii.1988, HEC 7318); Tiwi, (leg. Coppejans, 13.vii.1987, HEC 6784); Vipingo, 35 km N of Mombasa, (leg. Coppejans, 29.vii.1989, HEC 8155); **Seychelles.** L'Islette, Mahé, intertidal rock pools, (leg. Coppejans, Kooistra & Audiffred, 10.i.1993, SEY 811); Pointe du Sel, Ile Sourie, Mahé, reef pools, (leg. Coppejans, Kooistra & Audiffred, 10.xii.1992, SEY 5); **Tanzania.** Ras Ruvula, Mnazi Bay, Mtwara area, mid to low intertidal, shallow rock pools, epilithic, (leg. Coppejans, Dargent & Bel, 21.vii.2000, HEC 12772); Tandooni, Verani, Pemba Island, mid intertidal, (leg. Coppejans & De Clerck, 24.i.1996, HEC 11472); **Zanzibar (Tanzania).** Chwaka, intertidal reef flat, epilithic, (leg. Leliaert, 18.vii.1997, FL 612); Chwaka, drift, (leg. Leliaert, 18.vii.1997, FL 610; leg. Leliaert, 30.vii.1997, FL 712; leg. Leliaert & Coppejans, 16.vii.2001, FL 958b); Chwaka, intertidal reef flat, epilithic or epiphytic on *Laurencia* sp. (leg. Leliaert, 31.vii.1997, FL 713, FL 715, FL 730; leg. Leliaert & Coppejans, 20.vii.2001, FL 994); Chwaka, intertidal seagrass bed, loose lying on sandy substratum, (leg. Leliaert & Coppejans, 18.vii.2001, FL 980); Chwaka, mid intertidal reef flat, loosely attached to the rocky substratum, (leg. Leliaert &

→ **Fig. 15.** *Cladophoropsis composita* complex: *anastomosans* phenodeme (lectotype of *Cladophora anastomosans*, BM). **A.** Stipitate lamina composed of opposite branches; **B-E.** Type-3 tenacular cells; **F-I.** Type-1 tenacular cells; **J.** Detail of a cell showing the lamellate cell walls and crystalline cell inclusions. Scale bars: A = 1 mm; B-J = 100 µm.


A
B
C
D
E
F
G
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I
J

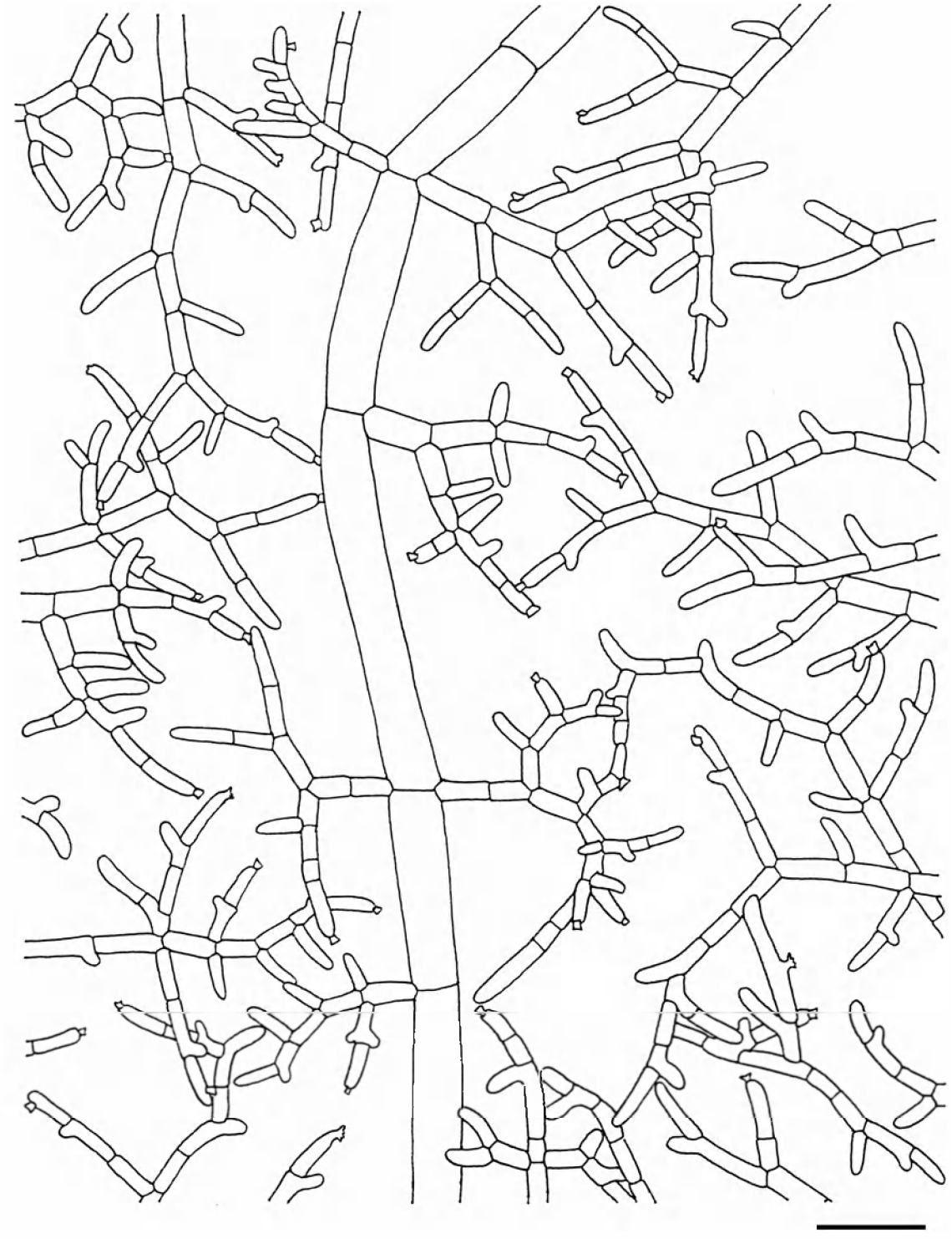

Fig. 16. *Cladophoropsis composita* complex: *anastomosans* phenodeme (isolectotype of *Cladophora anastomosans*, BM). Branch-systems of an older, cushion-like thallus. Scale bar = 1 mm.

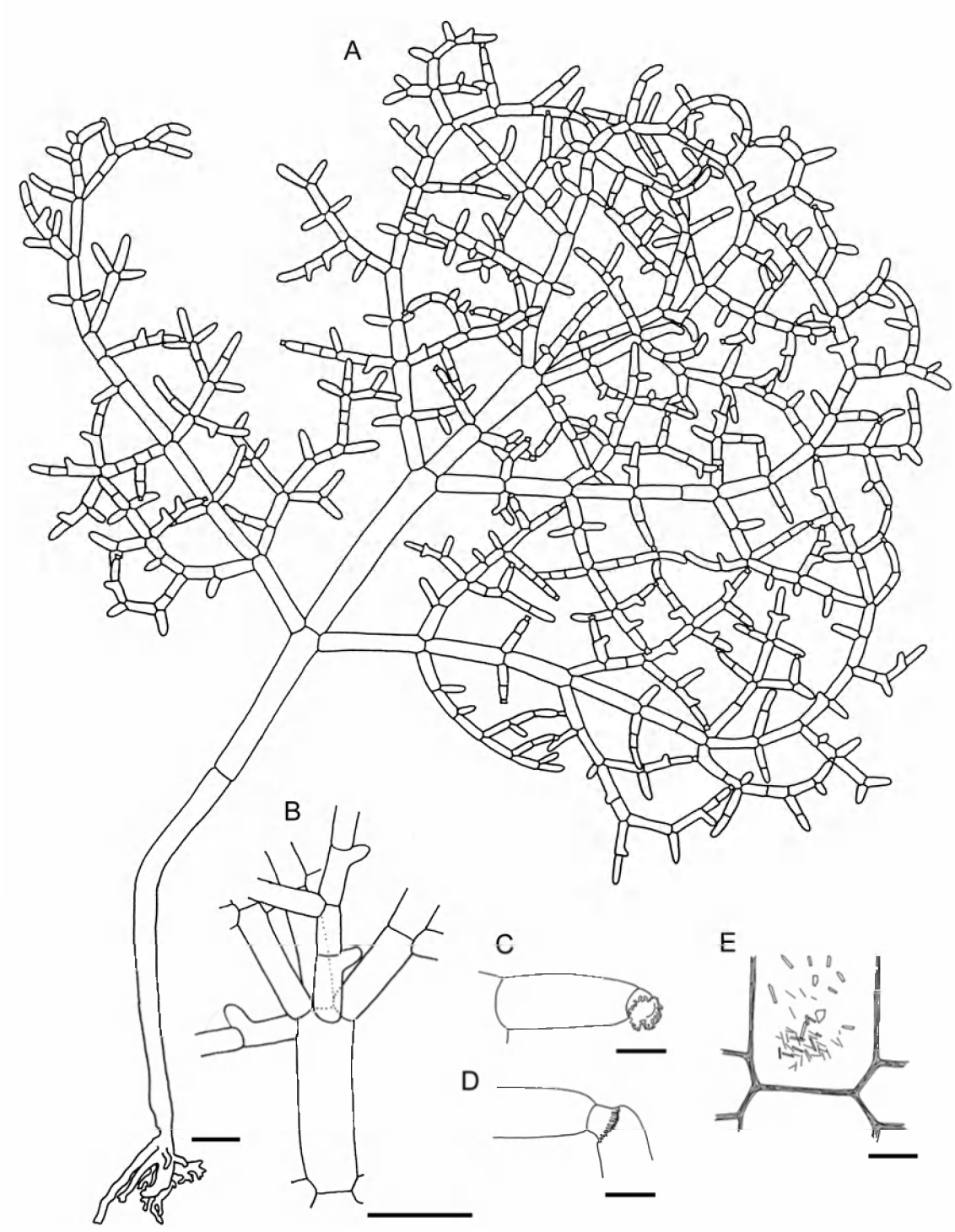

Fig. 17. *Cladophoropsis composita* complex: *anastomosans* phenodeme (holotype of *Boodlea struveoides*, NY). **A.** Stipitate blade composed of opposite branches; **B.** Cell of the central axis producing laterals in all directions; **C-D.** Type-3 tenacular cells; **E.** Portion of the proximal pole of a cell and laterals, showing the lamellate cell walls and crystalline cell inclusions. Scale bars: A-B = 500 µm; C-E = 100 µm.

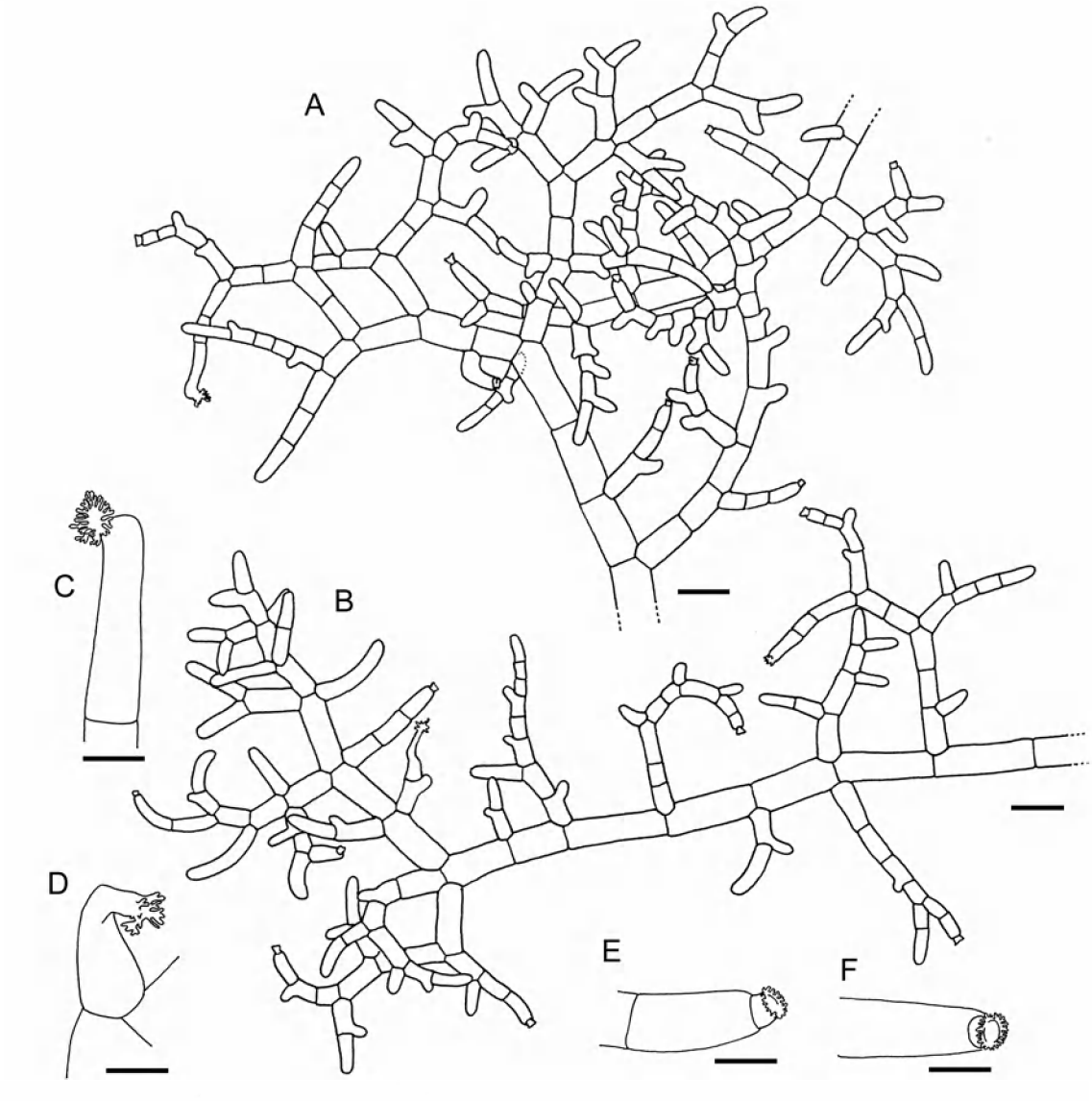

Fig. 18. *Cladophoropsis composita* complex: *anastomosans* phenodeme (Howe 130, NY as *Boodlea struveoides*). **A-B.** Pseudodichotomous and opposite terminal branches of a cushion-like thallus; some laterals producing secondary, perpendicular laterals; **C-D.** Type-1 tenacular cells; **E-F.** Type-3 tenacular cells. Scale bars: A-B = 500 μm; C-F = 100 μm.

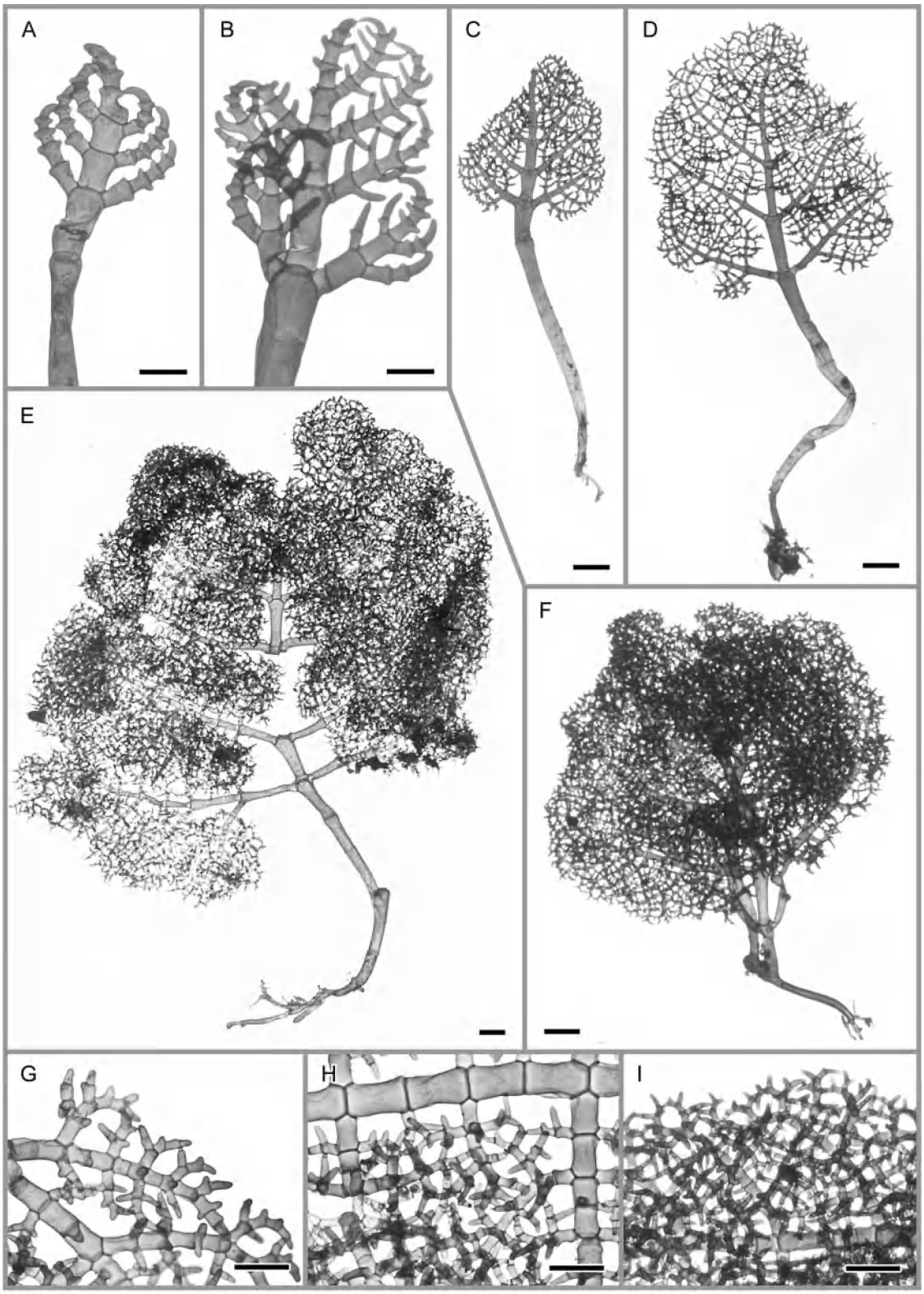

Fig. 19. *Cladophoropsis composita* complex: *anastomosans* phenodeme (FL 713, Chwaka Bay, Zanzibar). **A-B.** Initial stages of blade development: cells dividing simultaneously into 3-5 cells followed by the production of opposite pairs of laterals; **C-D.** Young blades with all branches lying in a single plane; **E.** Older blade with branches becoming three-dimensional; **F.** Clustered blades with stipes still conspicuous; **G.** Branches in the peripheral part of a lamina; **H-I.** Laterals in the central part and peripheral part of an older lamina with laterals becoming three-dimensional. Scale bars: A-B, G-I: 500 µm; C-F = 1 mm.

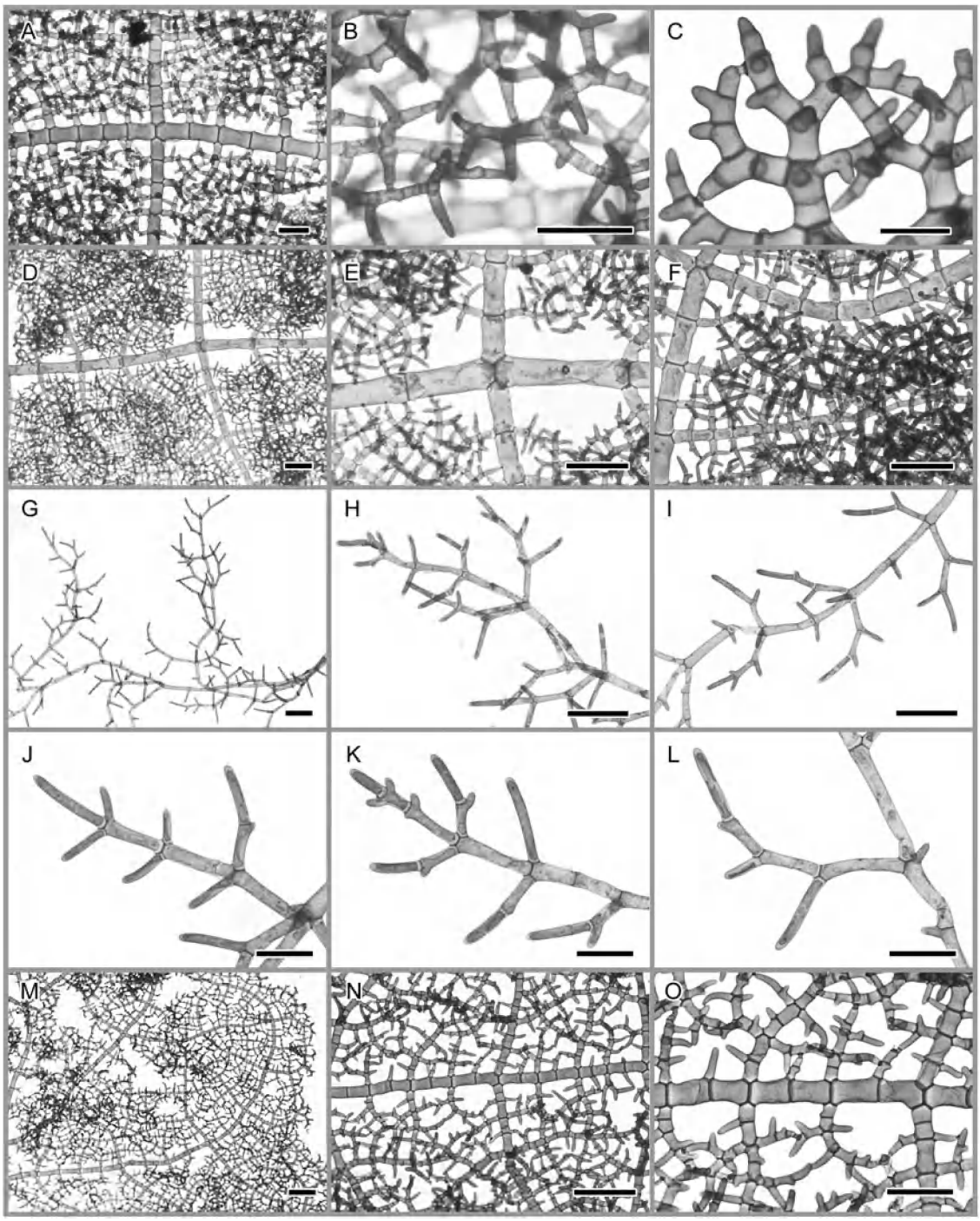

Fig. 20. *Cladophoropsis composita* complex: *anastomosans* phenodeme (Chwaka Bay, Zanzibar). **A-F.** Branch-systems in the peripheral parts of a loose-lying cushion-like thallus (FL 958); **G-H.** Branch-systems in the central part of the same loose-lying cushion: elongate, three-dimensionally branched filaments (FL 958); **M-O.** Lamina with branches essentially in a single plane (FL 958b, attached, astipitate blade-like thalli). Scale bars: A-B, J-K, O = 500 µm; C = 250 µm; D-I, M-N = 1 mm.

Coppejans, 17.vii.2001, FL 967b); Chwaka, mid intertidal seagrass beds, on coral rubble and shell fragments, (leg. Leliaert & Coppejans, 17.vii.2001, FL 959); Chwaka, mid intertidal, shallow pools, epilithic, (leg. Coppejans & Dargent, 30.vii.1997, HEC 12159; 27.viii.1994, HEC 10713); Chwaka, shallow subtidal, on coral rubble, (leg. Leliaert & Coppejans, 17.vii.2001, FL 966); Matemwe, back-reef coral pools, close to the fringing reef, epiphytic on *Gelidiella acerosa*, (leg. Coppejans & Dargent, 25.vii.1997, HEC 12042); Matemwe, intertidal reef flat, epilithic in pools, (leg. Leliaert, 21.vii.1997, FL 652); Nungwi, intertidal reef flat, epilithic, (leg. Leliaert, 20.vii.1997, FL 641, FL 642; leg. Leliaert & Coppejans, 21.vii.2001, FL 1010); Nungwi, intertidal rock pools, epilithic on horizontal surface, (leg. Leliaert, 25.vii.1997, FL 695); Nungwi, low intertidal, epilithic, (leg. Coppejans & De Clerck, 23.viii.1994, HEC 10583a, b, c); Paje, reef pools behind fringing reef, (leg. Leliaert, 23.vii.1997, FL 684); Pongwe, infralittoral fringe, shallow rock pool, epilithic, (leg. Coppejans & Schils, 26.vi.1999, HEC 12594); Pongwe, intertidal reef flat, epilithic, (leg. Leliaert, 19.vii.1997, FL 618 and HEC 11892); Pongwe, intertidal reef flat, epiphytic on various macro-algae or epilithic on coral boulders, (leg. Leliaert, 19.vii.1997, FL 617); Uroa, infralittoral fringe, shallow pool, epilithic, (leg. Coppejans, 2.viii.1993, HEC 9819); Uroa, mid intertidal reef flat, (leg. Leliaert & Coppejans, 19.vii.2001, FL 987, FL 985); **Pacific Ocean: Australia.** Cooktown, Queensland, (unknown collector s.n., 1879, MEL 666892); **Indonesia.** harbour of Taipabu, NW coast Binongko, Tukang Besi Islands, Banda Sea, (leg. Coppejans & Prud'homme van Reine, 10.ix.1984, Snellius-II 10329); Selat Linta, E of Komodo Island, (leg. Coppejans & Prud'homme van Reine, 18.ix.1984, Snellius-II 10843); **Papua New Guinea.** between Sinub and Wongat Island, Madang Province, (leg. Coppejans & Prud'homme van Reine, 18.vii.1990, Copp & PvR 13237); NW point of Christmas Bay, Bagabag, Madang Province, (leg. Coppejans & Prud'homme van Reine, 2.viii.1990, Copp & PvR 13508); **The Philippines.** Mactan Island, (leg. Leliaert & Liao, 6.viii.1998, PH 620b); Santa Cruz-Island (large), Zamboanga City, Mindanao, intertidal, epiphytic on seagrass stems, (leg. Leliaert & Liao, 23.viii.1998, PH 467).

Notes:

The *anastomosans* phenodeme has been encountered pantropically and is commonly found from high intertidal to shallow subtidal (down to 2 m depth), epilithic, epiphytic on macro-algae, seagrasses and mangroves, or loose lying.

Four herbarium specimens, consisting of cushion-like thalli (all numbered Harvey, Australian algae 582a), are present in BM. One of these specimens (presumably the one on which Harvey based the original description) partly consists of stipitate, blade-like thalli and is here indicated as lectotype (Fig. 15). Although the type material clearly illustrates that mature *P. anastomosans* thalli form irregular cushion-like plants, the general conception of the species until today has been that of thalli forming stipitate, reticulate blades with branching essentially in a single plane (see the numerous descriptions and illustrations in the general references below).

Struvea multipartita was described from the tropical West African coast, as cushion-like plants, composed of branched stipes bearing reticulate blades. It was treated as a taxonomic synonym of *S. anastomosans* by Steentoft (1967) and Lawson & John (1982). Examination of the holotype confirms that this taxon is similar to the *anastomosans* phenodeme.

Boodlea struveoides has been described as forming stipitate blades. The holotype indeed consists of three stipitate blades with branch systems more or less in one plane (fig. 17). Another specimen, however, also identified as *B. struveoides* by Howe (Howe 130, collected on the same date, from the same location and habitat as the holotype) consists of a cushion-like thallus, composed of three-dimensional branch systems. Both specimens correspond to the *anastomosans* phenodeme.

General references. As *Cladophora anastomosans*: Harvey (1859: pl. CI). As *Struvea anastomosans*: Børgesen (1912: 268, fig. 15; 1913: 54-56, fig. 39; 1952: 7-8, fig. 3); Taylor (1928: 73, pl. 3, fig. 10; 1960: 122, pl. 9, fig. 2); Egerod (1952: 359-361, fig. 4, pl. 31; 1971: 123-125, figs 10-16; 1975: 50, fig. 15); Isaac & Chamberlain (1958: 135, 137, figs 1, 10); Pham-Hoang (1969: 452, fig. 4.58); Chang *et al.* (1975: 41, 59, fig. 13); Schnetter & Bula-Meyer (1982: 29-30, pl. 7G-H); Tseng (1984: 276, pl. 137, fig. 2); Lawson & John (1987: 100, pl. 10, figs 1, 2); Sartoni (1992: 317-319, fig. 12B, C); Wynne (1995: 292, 332, fig. 86). As *Phyllodictyon anastomosans*: Kraft & Wynne (1996: 139, pls 16-25); Littler & Littler (2000: 328, fig. on p. 329).

The ***composita*** phenodeme Figs 21-24

Corresponding taxa:

Conferva composita Harvey, 1834: 157 [*non Conferva composita* (Vaucher) Chevalier, 1836, Fl. Paris. ed. 2, 1: 26] [Lectotype: Cap Malheureux, N-coast of Mauritius, leg. C. Telfair s.n., Herb. Hooker, BM!].

Cladophora composita (Harvey) Kützing, 1849: 415 ("*Cladophora Aegagropila composita*").

Aegagropila composita (Harvey) Kützing, 1854: 14, pl. 67.

Boodlea composita (Harvey) Brand, 1904: 187-190.

Boodlea composita forma *contracta* Brand, 1904: 190, pl. VI: fig. 28 [Lectotype: Waianae, Oahu, Hawaii, leg. Tilden, American Algae s.n., M!, "as *Cladophora* (*Aegagropila*) *composita* var. *contracta* F. Brand"; syntypes[1]: same locality, leg. Tilden, American Algae no. 539, MIN, NY! and PC!].

Boodlea composita forma *elongata* Brand, 1904: 190, pl. VI: fig. 30 [Type: Hawaii, leg. Tilden; the location of the type material could not be retrieved].

Description:

Thallus forming astipitate cushions or mats, up to 20 cm across and 3.5 cm thick, composed of densely branched, loosely entangled filaments, generally with small *Struvea*-like plumules in the peripheral parts (Figs 21A, 23A, 24A). Cushions often sand-trapping, loosely attached to the substratum by type-1 tenacular or rhizoidal cells (Figs 22E-J, 23F, 24H-J).

Growth by apical and intercalary cell divisions (CI). Apical cells dividing into two, or simultaneously into 3-8 cells, followed by the formation of opposite pairs of laterals (Fig. 24A-D). Older cells generally producing a 3rd (sometimes a 4th) lateral, perpendicular to the first pair, resulting in three-dimensional branch systems (Fig. 21A-B, 22A, 23A-E). Intercalary cell divisions may appear below the 7th primary cross wall, but are most common in the main axes (Fig. 21A-B, arrows). Branching in the main axes generally opposite (Figs 21B, 22A). Formation of cross walls at the proximal pole of newly formed laterals somewhat delayed; laterals in open connection with the mother cell up to 300 µm long (l/w ratio: 4). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching up to the 5th order. The diameter of the main axes 1.4-5 (-8) times that of the apical cells. Angle of ramification generally 50°-90°.

Limited reinforcement of the thallus by loose interweaving of the filaments, infrequently by attachment of adjacent cells by type-3 tenacular cells (Fig. 22B-D). The latter borne singly, terminally or subterminally on apical cells. In mature thalli, in average 0-6 % of the apical cells producing a type 3 tenacular cell.

Apical cells cylindrical with blunt tips, straight to strongly curved, (40-) 50-90 (-125) µm in diameter, l/w ratio 1.5-8 (-18). Cells of the main axes (140-) 180-250 (-400) µm in diameter, l/w ratio 2-13.

Thickness of the cell wall ca. 2 µm in the ultimate branches, up to 5 µm in the main axes.

Chloroplasts polygonal to star-shaped, 3-7 µm in diameter with strands spanning up to 16 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

Prismatic calcium oxalate crystals present in all cells of the thallus, except for the tenacular cells, very abundant in cells of the main axes, elongate hexagonal to needle-shaped, up to 6 µm in diameter and 45 µm long (Fig. 21C).

[1] In the International Code of Zoological Nomenclature (ICZN) any one of the original syntypes remaining after the selection of a lectotype is referred to as a **paralectotype**, in the ICBN such specimens remain "syntypes".

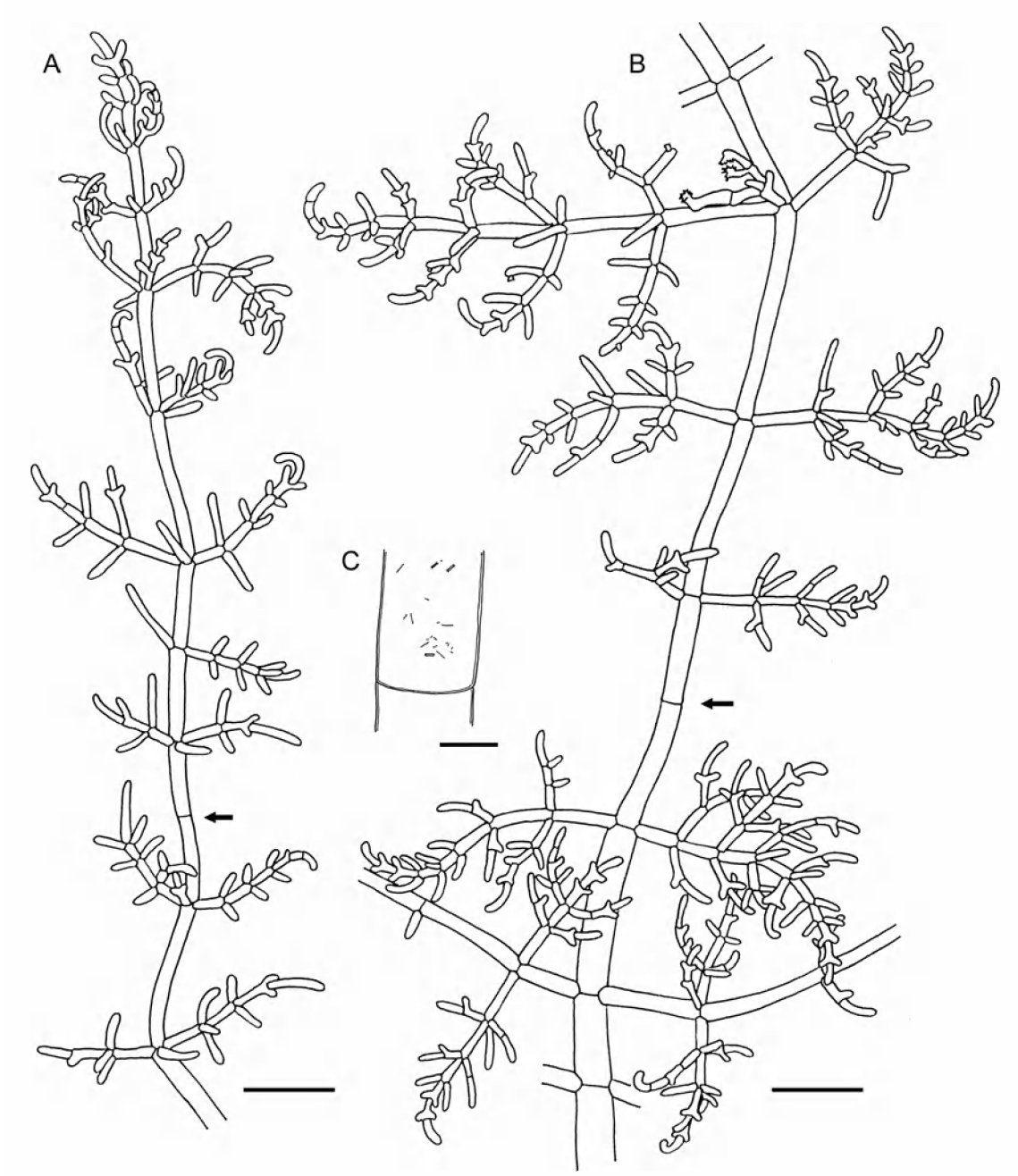

Fig. 21. *Cladophoropsis composita* complex: *composita* phenodeme (lectotype of *Conferva composita*, BM). **A.** Terminal, opposite branches and older cells producing perpendicular laterals; **B.** Main axis with opposite branches, producing terminal branch-systems; arrows indicating intercalary cell divisions; **C.** Base of a cell with prismatic calcium oxalate crystals. Scale bars: A-B = 1 mm; C = 250 µm.

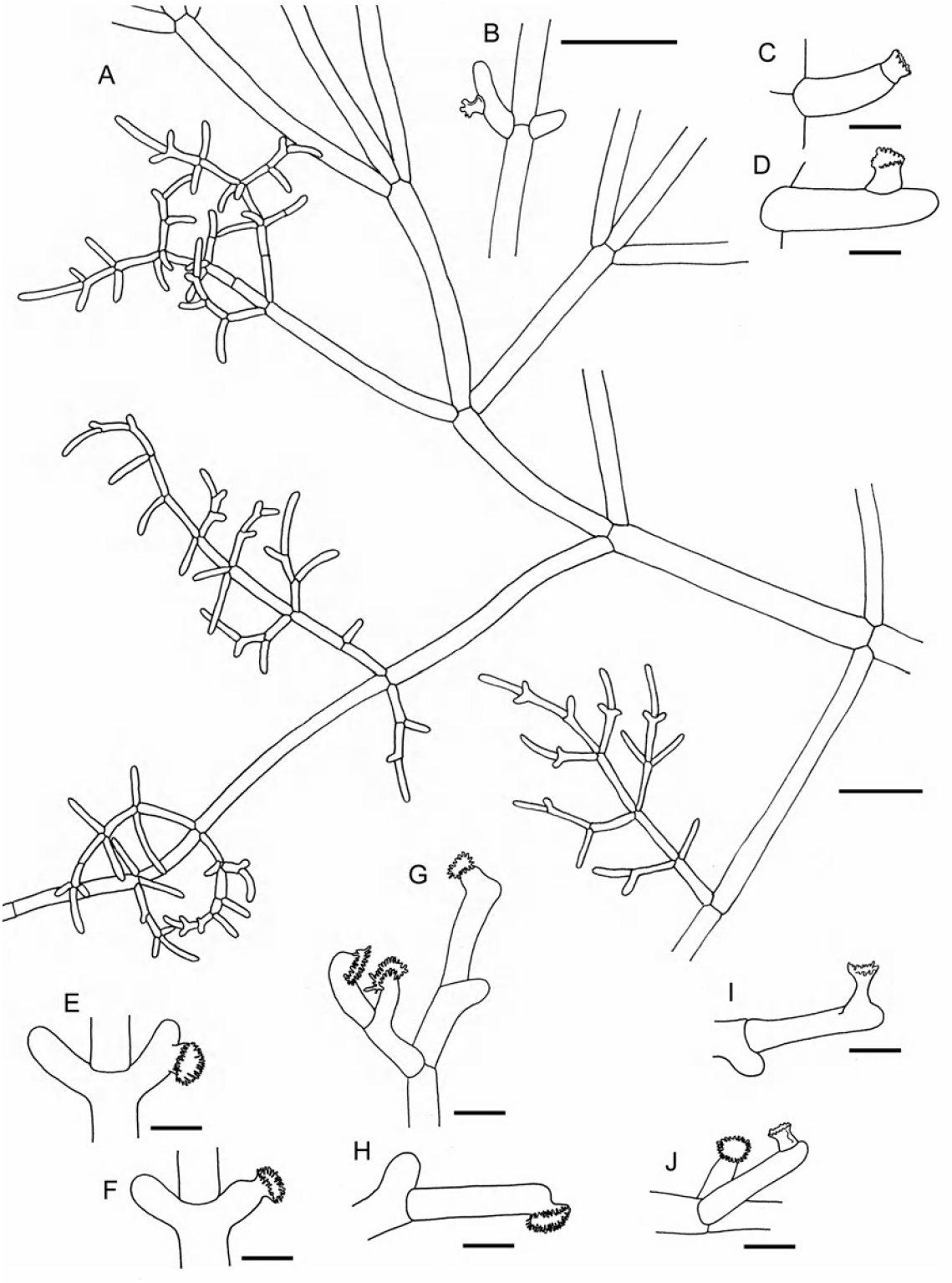

Fig. 22. *Cladophoropsis composita* complex: *composita* phenodeme (lectotype of *Conferva composita*, BM). **A.** Main axis with opposite branches, producing terminal branch-systems; **B-D.** Type-3 tenacular cells; **E-J.** Type-1 tenacular cells. Scale bars: A = 1 mm; B-J = 100 µm.

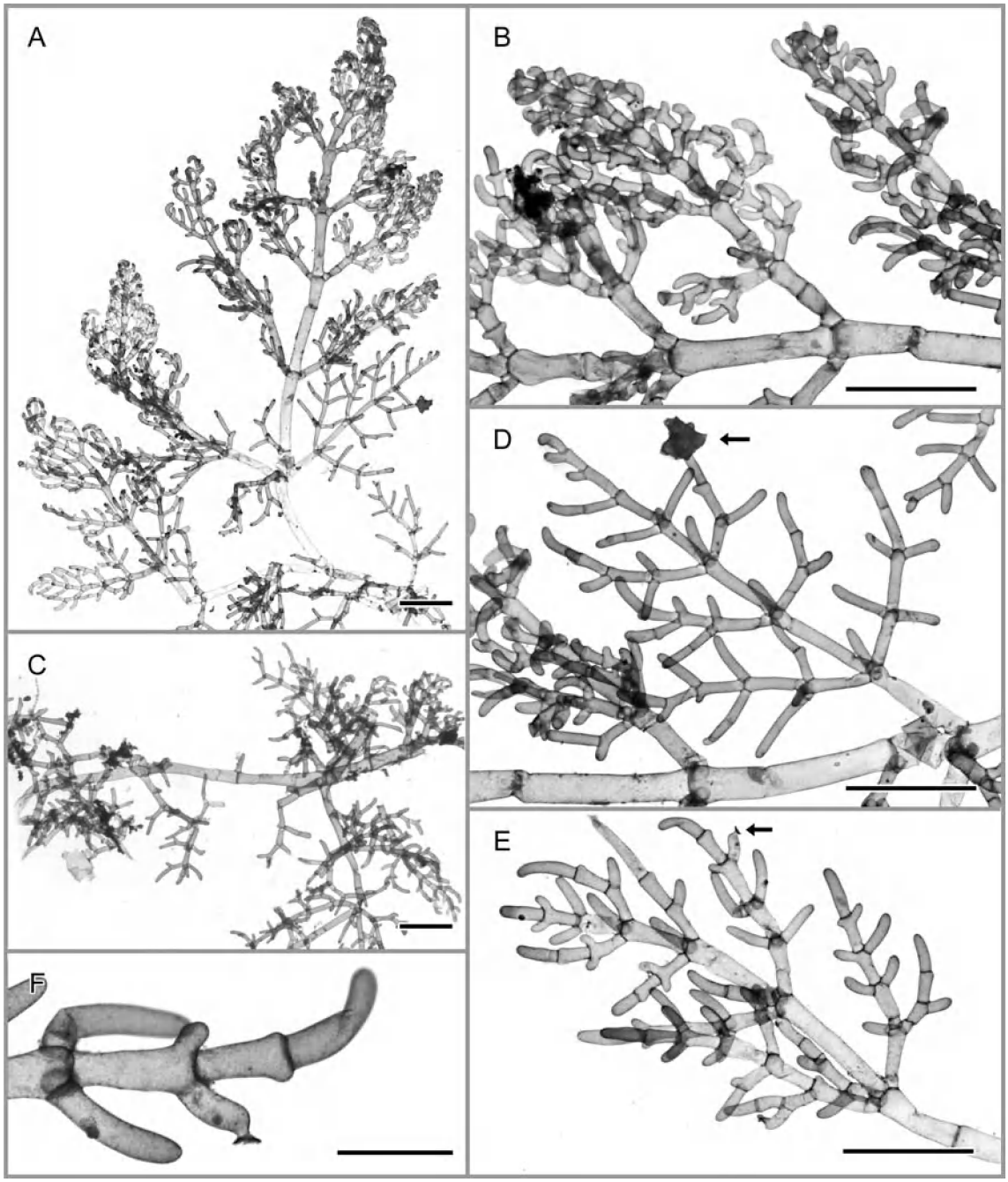

Fig. 23. *Cladophoropsis composita* complex: *composita* phenodeme (FL 694, Chwaka Bay, Zanzibar). **A.** Terminal branch-systems forming a "*Struvea*"-like plumule, sticking out of the cushion-like thallus; **B.** Detail of densely branched and incurved, short celled filaments; **C.** Branch-systems in the central part of the cushion-like thallus. **D-E.** Detail of branch-systems composed of longer, straight cells; attachment to corral rubble by type-1 tenacular cells (arrows); **F.** Terminal branches with a type-1 tenacular cell. Scale bars: A-E = 1 mm; F = 250 µm.

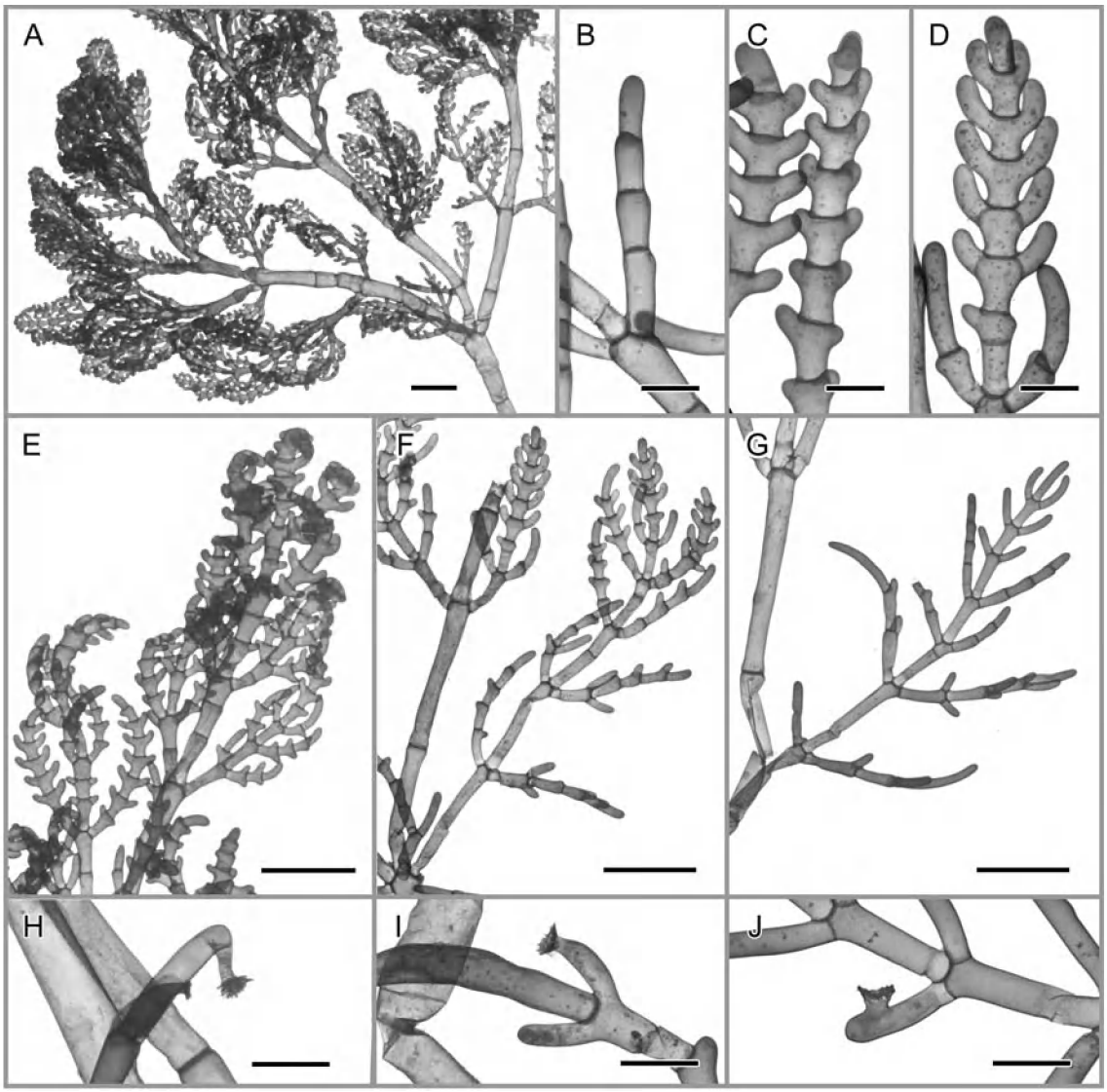

Fig. 24. *Cladophoropsis composita* complex: *composita* phenodeme (FL 662, Chwaka Bay, Zanzibar). **A.** Regular opposite terminal branches and main axes; **B-D.** Apical cells dividing simultaneously into 3-8 cells, followed by the formation of opposite pairs of laterals; **E.** Detail of densely branched and incurved, short celled filaments in the peripheral part of the thallus; **F-G.** Detail of branch-systems in the central part of the cushion-like thallus, composed of longer, straight cells; **H-J.** Type-1 tenacular cells. Scale bars: A, E-G = 1 mm; B-D, H-J = 250 µm.

Specimens examined: **Indian Ocean: Kenya.** Bamburi Bay, Mombasa, (leg. Coppejans, 17.ix.1990, HEC 8604); Casuarina Point, Malindi, (leg. Coppejans, 21.iii.1988, HEC 7422); Chale Island, Gazi, mid intertidal, on sand covered, horizontal substratum, (leg. Coppejans *et al.*, 14.ix.1992, HEC 9472); Mc Kenzie Point, Mombasa, (leg. Coppejans, vi.1985, HEC 5687); Nyali Beach reef, Mombasa, infralittoral fringe, (leg. Coppejans, 12.vii.1987, HEC 6766); Tiwi, (leg. Coppejans, 13.vii.1987, HEC 6785, HEC 6823); **Madagascar.** Grand Récif, Tuléar, reef platform and pools; partly emerged at good low tide; rather rare, (leg. Coppejans *et al.*, 14.viii.2002, HEC 14965); Plage de Monseigneur, Fort Dauphin, horizontal rock substratum of shallow pool (5-10 cm) low intertidal, (leg. Coppejans *et al.*, 31.viii.2002, HEC 15225); **Mauritius.** unknown locality, (leg. Telfair s.n., BM: lectotype and isolectotypes of *Conferva composita*); **Réunion.** St. Gilles les Bains, (leg. Dargent, 17.iv.1998, HOD RUN 98-17); **Tanzania.** Dar es Salaam, (leg. Danke s.n., B 09452); Mbudiya Island, Kunduchi, mid intertidal pools, epilithic on vertical walls, (leg. De Clerck, 11.vii.1997, ODC 665); Misali Island, W of Pemba Island, on horizontal rock substratum, mid intertidal, locally very abundant, (leg. Coppejans & De Clerck, 21.i.1996, HEC 11358); **Zanzibar (Tanzania).** Chwaka, high intertidal, epilithic on sand covered substratum, (leg. Leliaert, 31.vii.1997, FL 722); Matemwe, high intertidal reef flat, on wooden poles, (leg. Leliaert & Coppejans, 16.vii.2001, FL 950); Matemwe, intertidal pools, epilithic, (leg. Leliaert, 21.vii.1997, FL 662); Matemwe, intertidal reef flat, epiphytic on *Laurencia* sp., (leg. Leliaert & Coppejans, 14.vii.2001, FL 926, FL 927); Matemwe, mid to high intertidal reef flat, epilithic on shell-fragments and coral rubble, very loosely attached, (leg. Leliaert & Coppejans, 14.vii.2001, FL 923); Nungwi, fringing reef, epilithic or epiphytic, (leg. Leliaert, 25.vii.1997, FL 694); Nungwi, high intertidal reef pools, epilithic or epiphytic, (leg. Leliaert, 26.vii.1997, FL 702); Nungwi, infralittoral fringe, seaward side of fringing reef, epilithic or epiphytic, (leg. Leliaert & Coppejans, 21.vii.2001, FL 1007); Paje, fringing reef, epilithic, loosely attached, (leg. Leliaert, 23.vii.1997, FL 679); Pongwe, intertidal reef flat, loose lying, (leg. Leliaert, 19.vii.1997, FL 621); Pongwe, very loosely attached on sand covered substratum, (leg. Leliaert, 19.vii.1997, FL 622); Uroa, mid intertidal reef flat, loosely attached to coral rubble, (leg. Leliaert & Coppejans, 19.vii.2001, FL 986); **Pacific Ocean: Hawaii.** Waianae, Oahu, (leg. Tilden, American Algae s.n., M: lectotype of *Boodlea composita* forma *contracta*; leg. Tilden 539, 17.iii.1900, NY and PC: syntypes of *B. composita* forma *contracta*); **The Philippines.** Punta Engano, Mactan Island, Cebu, high intertidal reef flat, epilithic, (leg. Leliaert & Liao, 5.viii.1998, PH 625); **Vietnam.** Vicinity of the "Institut Oceanographique de Nhatrang", on coral rubble, (leg. Dawson 11119, 27.i.1953, B 09439).

Notes:

The *composita* phenodeme has been encountered in the Indo-Pacific but most probably also occurs in the tropical Atlantic Ocean. The phenodeme has been observed in high to low intertidal, mostly in sheltered habitats, epilithic (often on sand covered substrates) or epiphytic on macro-algae or seagrasses.

Three specimens of *Conferva composita*, collected in Mauritius by Mrs. C. Telfair, are present in BM; the largest one is here designated as lectotype (Fig. 21, 22). The type material corresponds with Kützing's drawings (1854: pl. 67), illustrating the characteristic opposite ultimate branch systems. The species was first moved to the genera *Cladophora* and *Aegagropila* by Kützing (1849 and 1854), and was later placed in *Boodlea* by Brand (1904: 187) based on the presence of tenacular cells.

Brand (1904: 190) distinguished *B. composita* forma *contracta* and forma *elongata* on the basis of differences in length/width ratio's of the cells. Both forma's fall within the limits of the *composita* phenodeme.

General references: Børgesen (1940: 21-25, fig. 6); Jaasund (1976: 11, fig. 23); Sartoni (1992: 306-307, fig. 7C).

The ***delicatula*** phenodeme Figs 25-26

Corresponding taxa:

Struvea delicatula Kützing, 1866: 1, pl. 2: figs e-g [Holotype: New Caledonia (Wagap), leg. Vieillard, s.n., L! 937 183 109].

Struvea delicatula var. *caracasana* Grunow ex Murray & Boodle, *in* Murray & Boodle, 1888b: 281, pl. XVI: fig. 7 [Type: Caracas, Cabo Blanco, Venezuela, leg. "Gollma" (probably Julius Gollmer); the location of the type material could not be retrieved].

Struvea anastomosans var. *caracasana* (Grunow ex Murray and Boodle) Collins, 1909: 376.

Struvea tenuis Zanardini, 1878: 39 [Holotype: Sorong, Iryan Jaya, Indonesia ("Soron, Novam Guineam"), leg. Beccari, FI, MB or MCVE?].

Description:

Thallus forming stipitate blades, up to 3 (-5) cm high, composed of densely branched filaments forming a reticulum in a single plane, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe (Fig. 25B). Stipes single or clustered, unbranched (unicellular) or branched (multicellular), without basal annular constrictions.

Young stipe cell cylindrical; when reaching a length of 4-9 mm, the distal end of the stipe cell dividing into two to several cells. Blade formation by a repetitive process of cell division, formation of laterals and cell elongation and enlargement. Cell division by centripetal invagination of the cell walls. Growth by apical and intercalary cell divisions; apical cells dividing into 2 or simultaneous 3 cells; newly formed cells producing a pair of opposite laterals; all branches lying strictly in a single plane. Intercalary cell divisions occurring at regular intervals in the main axes (Figs 25A, 26A). Formation of cross walls at the proximal pole of newly formed laterals somewhat delayed; laterals in open connection with the mother cell up to 320 µm long (l/w ratio 3). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching up to the 4th order; 1st order branches curved towards the blade apex. The diameter of the stipe 2-7 times that of the apical cells. Angle of ramification 45°-90°.

Mature blades elliptical in outline; reinforcement by anastomosis of adjacent cells by type-3 tenacular cells, borne singly on the tips of apical cells or laterals in open connection with the mother cell (Figs 25D-I, 26B). In mature blades, in average 34-65 % of the apical cells producing a type-3 tenacular cell.

Apical cells cylindrical to slightly tapering with rounded tips, straight or curved, (70-) 90-180 (-280) µm in diameter, l/w ratio 1-3.6. Cells of the main axes (120-) 350-540 (-620) µm in diameter, l/w ratio 1-3.5. Stipe cells subcylindrical 400-725 µm in diameter, 4-9 mm long.

Thickness of the cell wall ca. 2 µm in the ultimate branches, up to 7 µm in the main axes (Fig. 25C).

Chloroplasts polygonal to star-shaped, 3-7 µm in diameter with strands spanning up to 14 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

Prismatic calcium oxalate crystals present in all cells of the thallus (except for the tenacular cells), especially abundant in the stipe cell and cells of the main axes, elongate hexagonal to needle-shaped, up to 4 µm in diameter and 25 µm long (Fig. 25C).

Specimens examined: **Atlantic Ocean: Cameroon.** unknown locality, (leg. Ledermann 262, B A79, A80, A81); **Carribean Sea: Aruba.** Lago, shallow subtidal, epilithic, (leg. Vroman Ar 20-10, L 8150); Savaneta, (leg. Vroman Ar 5-2, 5.iv.1958, L 8175); **Bonaire.** lagoon, infralittoral fringe, mangrove, (leg. Vroman Bo 22-3, 26.iii.1958, L 8170); **Puerto Rico.** W coast of Punta Arenas, Mayaguez, (leg. Diaz-Piferrer s.n., 21.iii.1967, L 989 079 201); **Indian Ocean: Kenya.** Gazi, tide channel, (leg. Coppejans, 9.viii.1989, HEC 8302a, b); Msambweni, ca. 55 km S of Mombasa, infralittoral fringe, reef pool, epilithic on the horizontal substratum, (leg. Coppejans *et al.*, 16.ix.1992, HEC 9493); **Pacific Ocean: Indonesia.** Bari Flores, (leg. Weber-van Bosse 1009, xii.1888, L 937 279 460); Borneo bank, (leg. Weber-van Bosse, Siboga expedition s.n., vi.1899, L 937 279 470); Java, (leg. Weber-van Bosse s.n., M); Kambaragi Bay, Tanah Djampeah, subtidal, 30 m depth, (leg. Weber-van Bosse, Siboga expedition s.n., 4.v.1899, L 937 279 320); Sailoes-besar, (leg. Weber-van Bosse, Siboga expedition s.n., L 937 279 306); SE side of Pearl bank, Sulu Archipelago, (leg. Weber-van Bosse, Siboga expedition 371, 27.vi.1999, L 937 279 315); Sunda Island, (leg. Weber-van Bosse s.n., M); unknown locality, (leg. Weber-van Bosse s.n., 1888, L 937 279 298); **New Caledonia.** Wagap, (unknown collector 2111, 1863, L 937 183 109: holotype of *Struvea delicatula*); **Papua New Guinea.** Boisa, Madang Province, (leg. Coppejans, 7.vii.1988, HEC 7748); **The Philippines.** Lumangcapan, Enrique Villanueva, Siquijor, shallow subtidal coral boulders, epiphytic on *Caulerpa racemosa*, (leg. Leliaert & Liao, 7.viii.1998, PH 21); Pitogo, Zamboanga City, Mindanao, shallow subtidal, epiphytic on *Hypnea* sp., (leg. Leliaert & Liao, 22.viii.1998, PH 451).

Notes:

The *delicatula* phenodeme has been encountered pantropically and has been collected from the lower intertidal to subtidal (down to 40 m depth), epilithic or epiphytic on macro-algae or seagrasses.

S. delicatula was originally described and illustrated as a plant with a branched stipe bearing tripinnate blades (Kützing 1866: 1, pl. 2: figs e-g). The conspecificity of *S. delicatula* and *S. anastomosans* was proposed by Murray & Boodle (1888b: 281), who, however, erroneously adopted the younger name (Silva *et al.* 1996). Børgesen (1913) at first followed Murray & Boodle (l.c.) but, after having examined both types he revised his opinion and considered *S. delicatula* distinct, based on its smaller thallus and more dense branching (Børgesen 1933). Nevertheless, *S. delicatula* has later been generally regarded as a synonym of *S. anastomosans* (Cribb 1960, Egerod 1952, 1975). Murray & Boodle (1888b: 278, 281, fig. 7) distinguished *S. delicatula* var. *caracasana* by the small bipinnate blades and the scarce tenacular cells. The name has since then only been used sporadically (e.g. Taylor 1960: 122, pl. 5, fig. 1). Based on the original illustrations we consider this taxon similar to the *delicatula* phenodeme.

Murray & Boodle (1888b: 281, fig. 5) described and illustrated the type of *S. tenuis* as a small stipitate blade composed of strictly opposite branching filaments up to the 2nd order. Egerod (1952) followed Murray & Boodle (1888b) in distinguishing *S. tenuis* from *S. anastomosans* by its smaller size and the bipinnate branching in contrast to the tri- or quadripinnate branching in *S. anastomosans*. Okamura (1908) and Yamada (1934) however already suggested that *S. delicatula* might represent a juvenile thallus of *S. anastomosans*, but it was Cribb (1960) who formally considered both species conspecific, based on Børgesen's (1913) observations.

We are aware that young thalli of the *anastomosans* phenodeme are similar or indistinguishable from the *delicatula* phenodeme. However we choose to recognize this separate phenodeme based on the fact that in certain geographical area's (e.g. Indonesia and Papua New Guinea) thalli apparently stop development at this stage.

General references. As *Struvea delicatula*: Murray & Boodle (1888b: 281, figs 6, 8); Okamura (1908: 201, pl. 40, figs 9-12); Okamura (1908: 203, pl. 40, figs 9-12); Børgesen (1933: 3); Yamada (1934: 46, fig. 10); Segawa (1938: 135-136, fig. 3). As *S. tenuis*: Murray & Boodle (1888b: 281, fig. 5); Okamura (1908: 201, pl. 40, figs 7-8); Yamada (1934: 45-46, fig. 9). As *Phyllodictyon anastomosans*: Littler & Littler (2003: 200, fig. on p. 201).

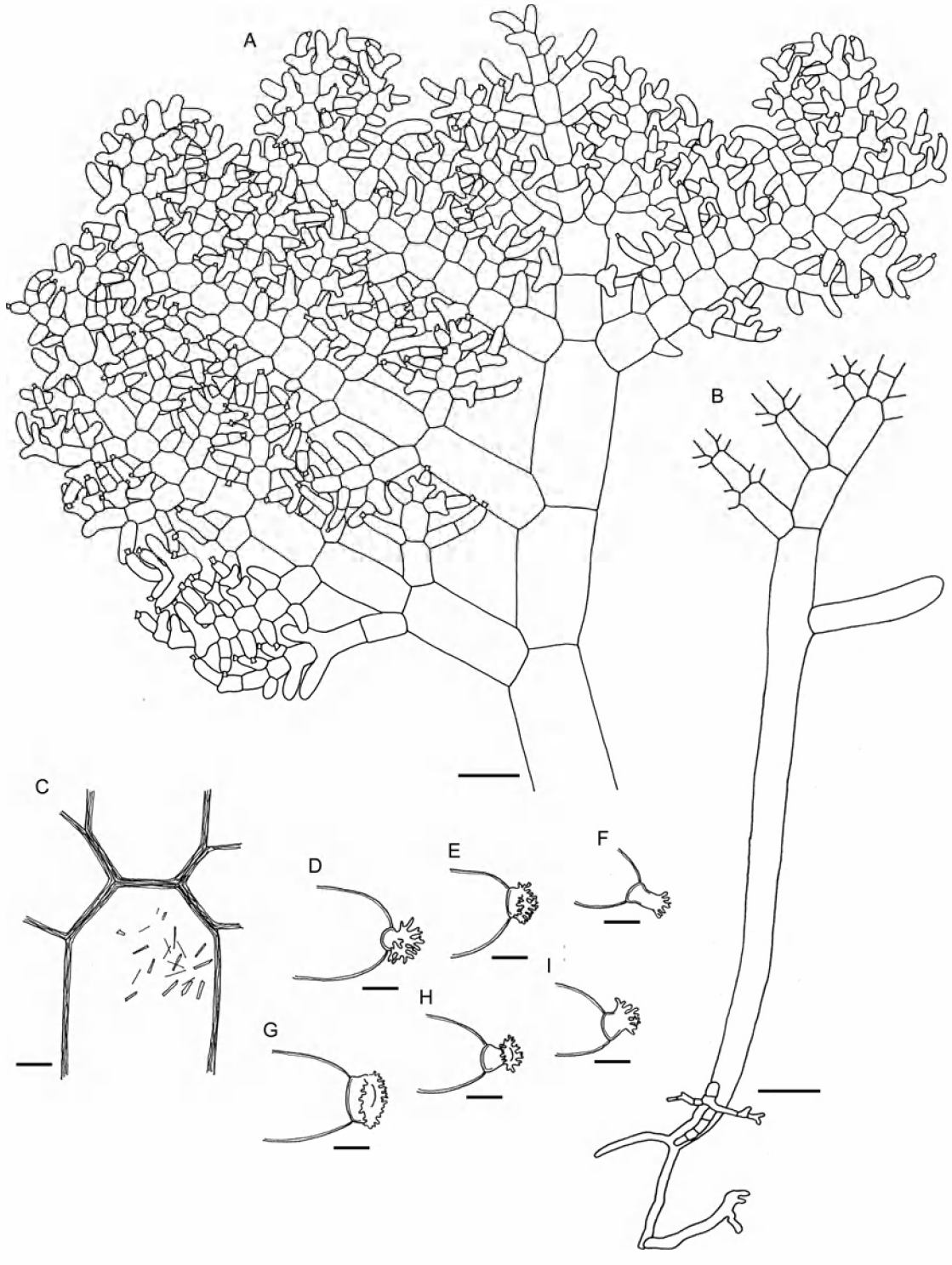

Fig. 25. *Cladophoropsis composita* complex: *delicatula* phenodeme (holotype of *Struvea delicatula*, L). **A.** Lamina composed of regular opposite branches lying in a single plane; **B.** Stipe cell, attached by type-1 rhizoids; **C.** Detail of cell walls, cross-walls at the base of the laterals, and prismatic calcium oxalate crystals; **D-I.** Type-3 tenacular cells. Scale bars: A = 500 µm; B = 1 mm; C = 50 µm; D-I = 50 µm.

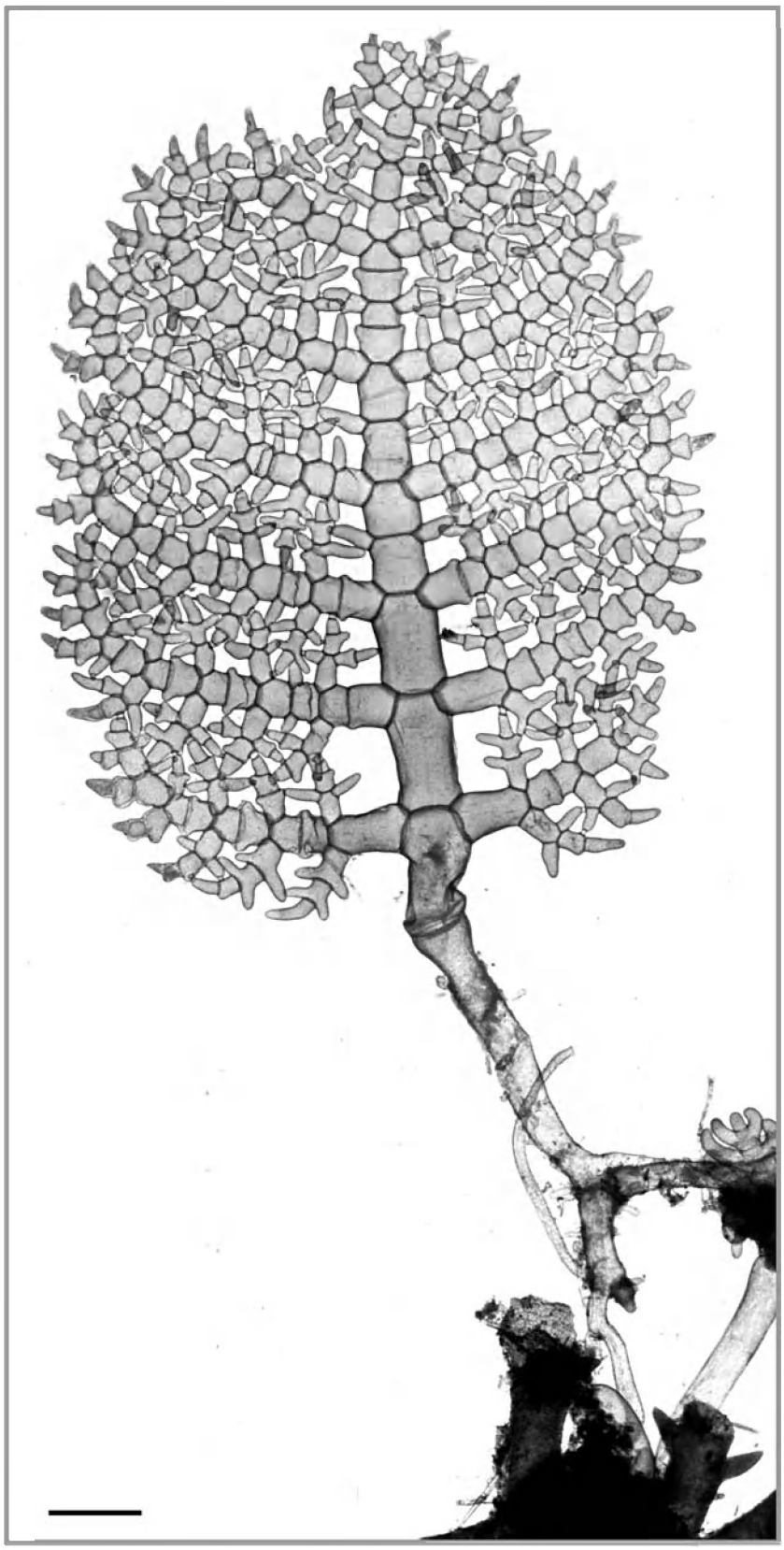

Fig. 26. *Cladophoropsis composita* complex: *delicatula* phenodeme (PH 451, Philippines). Stipitate lamina composed of regular opposite branches lying in a single plane. Scale bar = 500 μm.

The ***montagnei*** phenodeme Figs 27-28

Corresponding taxon:

Microdictyon montagnei Harvey ex J.E. Gray, 1866: 69 [Holotype: Lifuka, Ha'apai group, Tonga, leg. Harvey, Friendly Island Algae no. 89, Herbarium Dickie, BM!, isotype in PC!].

Boodlea montagnei (Harvey ex J.E. Gray) Egerod, 1952: 332, footnote.

Description:

Thallus forming astipitate, reticulate blades, composed of densely branched filaments (Fig. 27A, 28A), attached to the substratum by type-1 tenacular cells or rhizoidal cells.

Blade formation by a repetitive process of apical and intercalary cell division (CI), formation of laterals, cell elongation and enlargement. Division of apical cells into 2 (rarely 3) cells. Newly formed cells either producing a single lateral (eventually displacing the apical cell resulting in pseudodichotomous branch systems, Fig. 28E) or an opposite pair of laterals (Fig. 28D). Axes branching regularly opposite with intercalary cell divisions occurring at regular intervals (Fig. 27B, 28C). Formation of cross walls at the proximal pole of newly formed laterals somewhat delayed; laterals in open connection with the mother cell up to 250 µm long (l/w ratio 2.6). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching up to the 7th order; branches lying strictly in a single plane (in some parts of the lamina, a few laterals may develop perpendicular to the main branching plane). The diameter of the main axes 2.2-10 times that of the apical cells. Angle of ramification (60-) 75-90°.

Reinforcement of the lamina by attachment of adjacent cells by type-3 tenacular cells, borne singly on the tips of apical cells or laterals in open connection with the mother cell (Figs 27D-E, 28D). In mature blades, in average 30-55 % of the apical cells producing a type-3 tenacular cell.

Apical cells cylindrical to slightly tapering with rounded tips, straight or curved, (50-) 70-140 (-180) µm in diameter, l/w ratio 1-5. Cells of the main axes (180-) 200-650 (-700) µm in diameter, l/w ratio 1-5.5.

Thickness of the cell wall ca. 2 µm in the ultimate branches, up to 12 µm in the main axes.

Chloroplasts polygonal to star-shaped, 3-7 µm in diameter with strands spanning up to 18 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

Prismatic calcium oxalate crystals present in all cells of the thallus (except for the tenacular cells), especially abundant in the cells of the main axes, elongate hexagonal to needle-shaped, up to 6 µm in diameter and 45 µm long (Fig. 27F).

Specimens examined: **Indian Ocean: Zanzibar (Tanzania).** Chwaka Bay, intertidal flat, loose lying, (leg. Leliaert, 18.vii.1997, FL 611, FL 614); Chwaka, intertidal seagrass bed, epizoic on sponge, (leg. Leliaert & Coppejans, 18.vii.2001, FL 978); Chwaka, intertidal seagrass beds, loosely attached to rocky substratum, (leg. Leliaert & Coppejans, 17.vii.2001, FL 961); Chwaka, mangrove channel and intertidal flat, loose-lying, (leg. Coppejans & Schils, 27.vi.1999, HEC 12610); Kiwengwa, drift, (leg. Leliaert, 22.vii.1997, FL 663); Matemwe, mid intertidal reef flat, epilithic on shaded wall of a small rock pool, (leg. Leliaert & Coppejans, 16.vii.2001, FL 958a); **Pacific Ocean: Indonesia.** unknown locality, (leg. Weber-van Bosse, Siboga expedition s.n., 1899, L 938 046 399); E Tarupa Kecil, NE Taka Bone Rate, (leg. Coppejans & Prud'homme van Reine, 26.ix.1984, Snellius-II 11278); Selat Linta, E of Komodo Island, (leg. Coppejans & Prud'homme van Reine, 18.ix.1984, Snellius-II 10842); **Papua New Guinea.** Boisa, Madang Province, (leg. Coppejans, 7.vii.1988, HEC 7735); Durangit reef, Hansa Bay, Madang Province, (leg. Coppejans, 17.vii.1988, HEC 7847); Gumbi Bay, Madang Province, (leg. Coppejans, 25.vii.1988, HEC 7943); Kranket Island, Madang Province, (leg. Coppejans, 7.viii.1988, HEC 8078; leg. Coppejans & Prud'homme van Reine, 13.vii.1990, Copp & PvR 13133, Copp & PvR 13134); Laing Island (Bogia), Hansa Bay, Madang Province, (leg. Coppejans, vi.1980, HEC 4431; viii.1986, HEC 6451; 22.viii.1986, HEC 6581; 29.vi.1988, HEC 7638; 5.vii.1988, HEC 7690); Megiar Harbour, Madang Province, (leg. Coppejans, 18.viii.1986, HEC 6535); Motupore Island, Port Moresby area, (leg. Coppejans, vi.1986, HEC 6347); N of Pig (Tab) Island, Madang Province, (leg. Coppejans & Prud'homme van Reine, 5.viii.1990, Copp & PvR 13588); NW point of Christmas Bay, Bagabag, Madang Province, (leg. Coppejans & Prud'homme van Reine, 2.viii.1990, Copp & PvR 13509b); Sarang Harbour, Madang Province, (leg. Coppejans & Prud'homme van Reine, 23.vii.1990, Copp & PvR 13351); **Solomon Islands.** Guadalcanal, Komimbo, (leg. Womersley & Bailey 239, 14.viii.1965, L 211504); **The Philippines.** Mactan Island, Cebu Province, intertidal, epilithic, (leg. Leliaert & Liao, 6.viii.1998, PH 646); Mactan Island, Cebu Province, (leg. Coppejans,

19.iv.1998, HEC 12262); Malibago Bluewater Resort, Mactan Island, Cebu, intertidal reef flat, epilithic or loose lying on coral rubble, (leg. Leliaert & Liao, 27.viii.1998, PH 565, PH 572); Santa Cruz Island (small), Zamboanga City, Mindanao, intertidal, epilithic, (leg. Leliaert & Liao, 24.viii.1998, PH 517); Simunu, Tawi, (leg. Dargent & Bel, 19.viii.1999, HOD PH 99-156); **Tonga.** unknown locality, (leg. Harvey s.n., BM); Lifuka, Ha'apai group, (leg. Harvey, Australian Algae 89, 1857, BM: holotype of *Microdictyon montagnei*; PC: isotype).

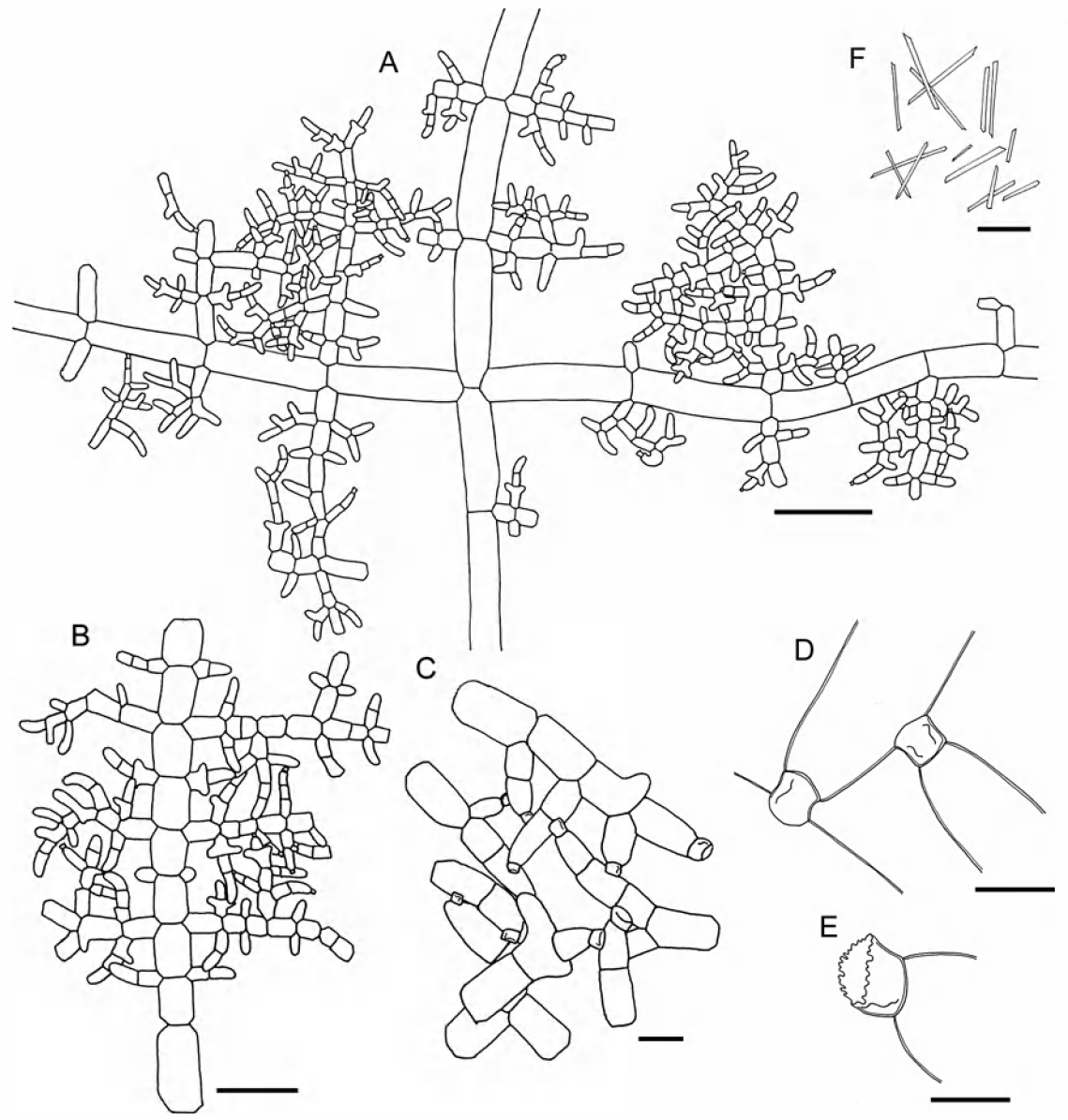

Fig. 27. *Cladophoropsis composita* complex: *montagnei* phenodeme (holotype of *Microdictyon montagnei*, BM). **A-B.** Part of a reticulate lamina composed of opposite branching main axes; terminal branch-systems unilateral, pseudodichotomous or opposite; **C-E.** Type-3 tenacular cells. **F.** Elongate trapeziform to needle shaped prismatic calcium oxalate crystals. Scale bars: A = 1 mm; B = 500 µm; C-E = 100 µm; E = 50 µm.

Notes:

We have only seen specimens of the *montagnei* phenodeme from the tropical Indo-West Pacific where it grows on intertidal reef flats, epilithic on rocks or coral rubble, epiphytic on various macro-algae, epizoic on sponges, or loose-lying.

The holotype of *Microdictyon montagnei* consists of a delicate, yellow-green reticulate blade, composed of oppositely branched main filaments interspersed among a dense meshwork of narrower filaments representing the higher branch orders; ultimate branch systems are opposite or pseudodichotomous (maximum two laterals per cell) with all branches essentially in a single plane. The diagnosis supplied by Gray (1866) was very elementary and the species only became better known through the work of Setchell (1929: 573-580, figs 97-105). Setchell (l.c.) discussed the close resemblance between the *Microdictyon* section *Boodleoides* (consisting of a single species, *M montagnei*) and *Boodlea* but stresses that all *Microdictyon* species can be distinguished from *Boodlea* by the branching being strictly in a single plane. The transfer of *M. montagnei* to *Boodlea* based on the presence of type-3 tenacular cells was already suggested by Murray (1889) but it was Egerod (1952) who made the new combination.

As discussed above, the *B. montagnei*-type morphology is indistinguishable from certain developmental stages of the *anastomosans* phenodeme. We recognize a separate *montagnei* phenodeme based on the fact that in certain area's (e.g. Indonesia and the Philippines) this morphological form is found by itself without the presence of stipitate plants. As already described by Setchell (1929: 573) branching in the *montagnei* phenodeme may become three-dimensional in certain parts of the thallus, and consequently the distinction with the *siamensis* and *anastomosans* phenodeme becomes vague.

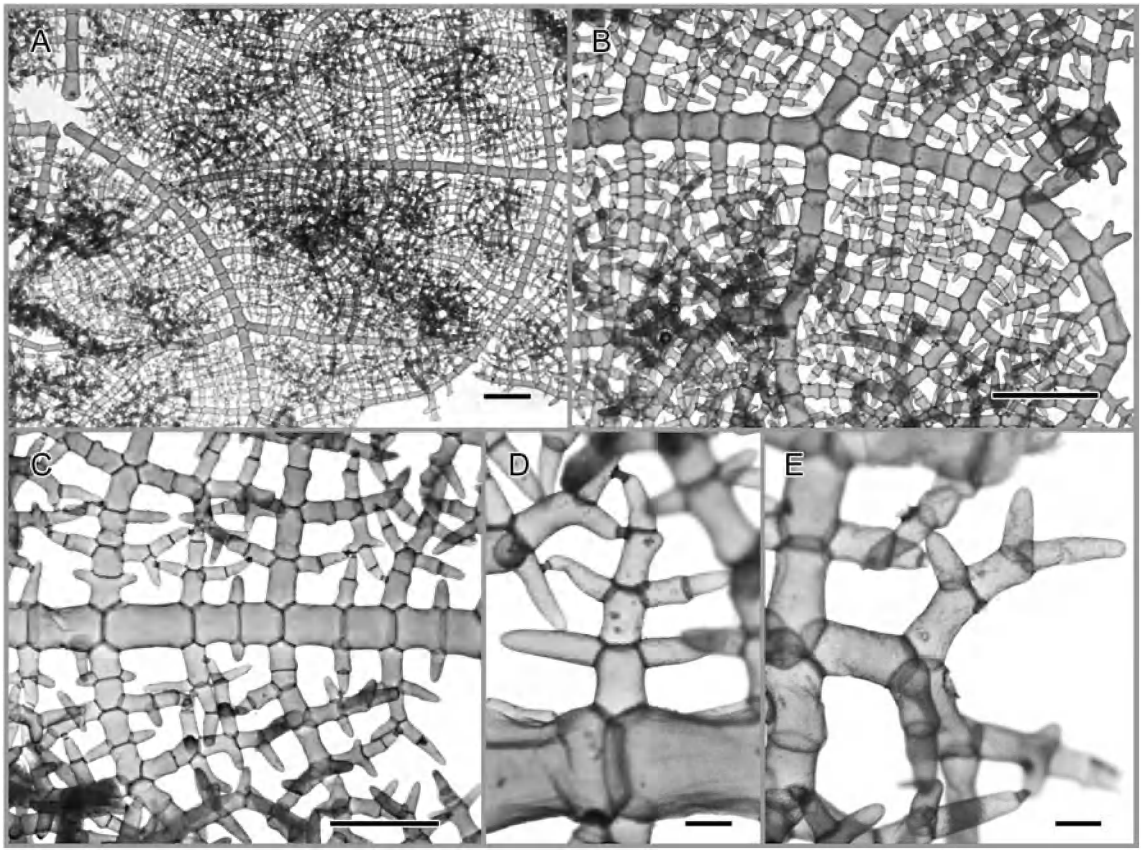

Fig. 28. *Cladophoropsis composita* complex: *montagnei* phenodeme (PH 572, Philippines). **A-B.** Reticulate lamina composed of oppositely branched main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders; **C.** Main axes with intercalary cell divisions at regular intervals; **D.** Ultimate, opposite branches; anastomosis by type-3 tenacular cells; **E.** Ultimate, unilateral to pseudodichotomous branches. Scale bars: A-B = 1 mm; C = 500 μm; D-E = 100 μm.

The ***siamensis*** phenodeme Figs 29-35

Corresponding taxa:

Boodlea siamensis Reinbold, 1901: 191-192 ["*B.* (*coacta* var?) *Siamensis*"] [Holotype: Ko Kahdat, Ko Chang Archipelago, Thailand, leg. Reinbold s.n., The Danish Expedition to Siam (1899-1900), Herb. Reinbold, M!].

Cladophora coacta Dickie, 1876: 451 [Holotype: O-shima, Wakayama Prefecture, S-coast of Japan, H.N. Moseley s.n., Challenger Expedition, Herb. Dickie, BM!].

Boodlea coacta (Dickie) Murray & De Toni in Murray, 1889: 245, pl. 49.

Boodlea composita forma *irregularis* Brand, 1911: 145 [Lectotype: Tahiti ("Tautira insulae Tahiti ad scopulos"), leg. J.E. Tilden 105, x.1909, B!; isolectotypes: M! and MIN].

Boodlea siamensis forma *robusta* Børgesen, 1930: 153-155, fig. 2 [Lectotype: Dwarka, Gujarat, India, leg. Børgesen 5426 (incl. slide), C!; syntypes (see footnote on p. 144): Dwarka, Børgesen 5412 & 5457; Port Okha, Børgesen 5541 (slide) & 5561, C!].

Boodlea composita forma *robusta* (Børgesen) Børgesen, 1934: 9-10.

Boodlea paradoxa Reinbold, 1905: 148-149 [Lectotype: Buru Island, Moluccas, Indonesia, leg. Weber-van Bosse, Siboga Expedition, Herbarium Reinbold, M!].

Nereodictyon imitans Gerloff, 1960: 614-618, fig. 2 [Holotype: Malindi, Kenya, leg. Makerer College s.n. EA G1].

Description:

Thallus forming firm cushions, composed of densely branched, tightly interwoven filaments, forming a three-dimensional reticulum. Young thalli attached to the substratum by type-1 rhizoids sprouting from the base of the stipe cell (Fig. 30A); mature plants attached by type-1 tenacular cells and type-3 rhizoids, produced in any part of the thallus (Fig. 30B, 32F-G).

Young thalli stipitate with opposite or unilateral branch systems (Fig. 30A). Older plants soon forming cushions, with the stipe cell becoming obscured and eventually lost. Growth by a repetitive process of apical and intercalary cell division (CI), formation of laterals, cell elongation and enlargement. Division of apical cells into 2 (sometimes 3) cells. Newly formed (sub-apical) cells producing a single lateral, eventually displacing the apical cell, resulting in pseudodichotomies (Figs 29A, 31C, 32A, 33A, 35A). Older cells often producing a second lateral, perpendicular or opposite to the first one (Figs 32A, 34A). Main branch systems regularly opposite to irregularly organized with frequent intercalary cell divisions (Figs 29A, 31E, 32A, 33A). Formation of cross walls at the proximal pole of newly formed laterals somewhat delayed; laterals in open connection with the mother cell up to 320 (-500) µm long (l/w ratio 3-6). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching three-dimensional, up to the 5^{th} (-6^{th}) order. The diameter of the main axes 1.2-8 times that of the apical cells. Angle of ramification 40-90°.

Reinforcement of the lamina by tightly interweaving of the, often curved, branch systems and attachment of adjacent cells by type-3 tenacular cells, borne singly on the tips (occasionally laterally) of apical cells or laterals in open connection with the mother cell (Figs 29C-D, 32B-E, 33C-I, 34 E-G, 35B-C). In mature blades, in average 10-55 % of the apical cells producing a type-3 tenacular cell.

Apical cells cylindrical to slightly tapering with rounded tips, straight or curved, (40-) 60-140 (-250) µm in diameter, l/w ratio 1-10 (-15). Cells of the main axes (120-) 160-380 (-875) µm in diameter, l/w ratio 1.5-10 (-26).

Thickness of the cell wall ca. 2 µm in the ultimate branches, up to 7 µm in the main axes.

Chloroplasts polygonal to star-shaped, 3-7 µm in diameter with strands spanning up to 20 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

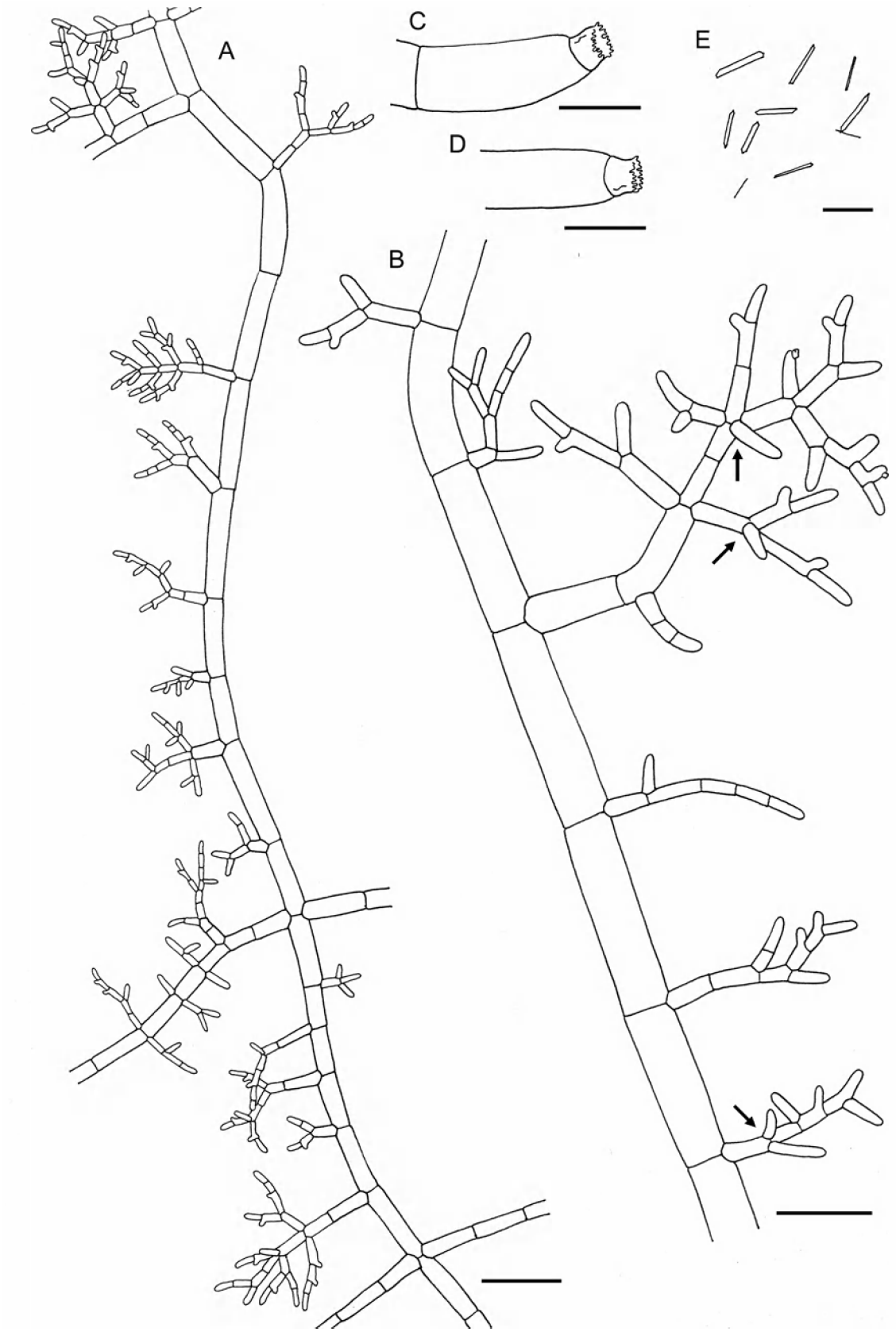

Fig. 29. *Cladophoropsis composita* complex: *siamensis* phenodeme (holotype of *Boodlea siamensis*, M). **A-B.** Oppositely or unilaterally branched main axes; opposite or pseudodichotomous terminal branch-systems, some cells producing laterals perpendicular on the original branching plane (arrows); **C-D.** Type-3 tenacular cells; **E.** Elongate hexagonal or trapeziform calcium oxalate crystals. Scale bars: A = 1 mm; B = 500 µm; C-D = 100 µm; E = 50 µm.

Prismatic calcium oxalate crystals present in all cells of the thallus (except for the tenacular cells), especially abundant in the cells of the main axes, elongate hexagonal to needle-shaped, up to 6 μm in diameter and 40 μm long (Fig. 29E).

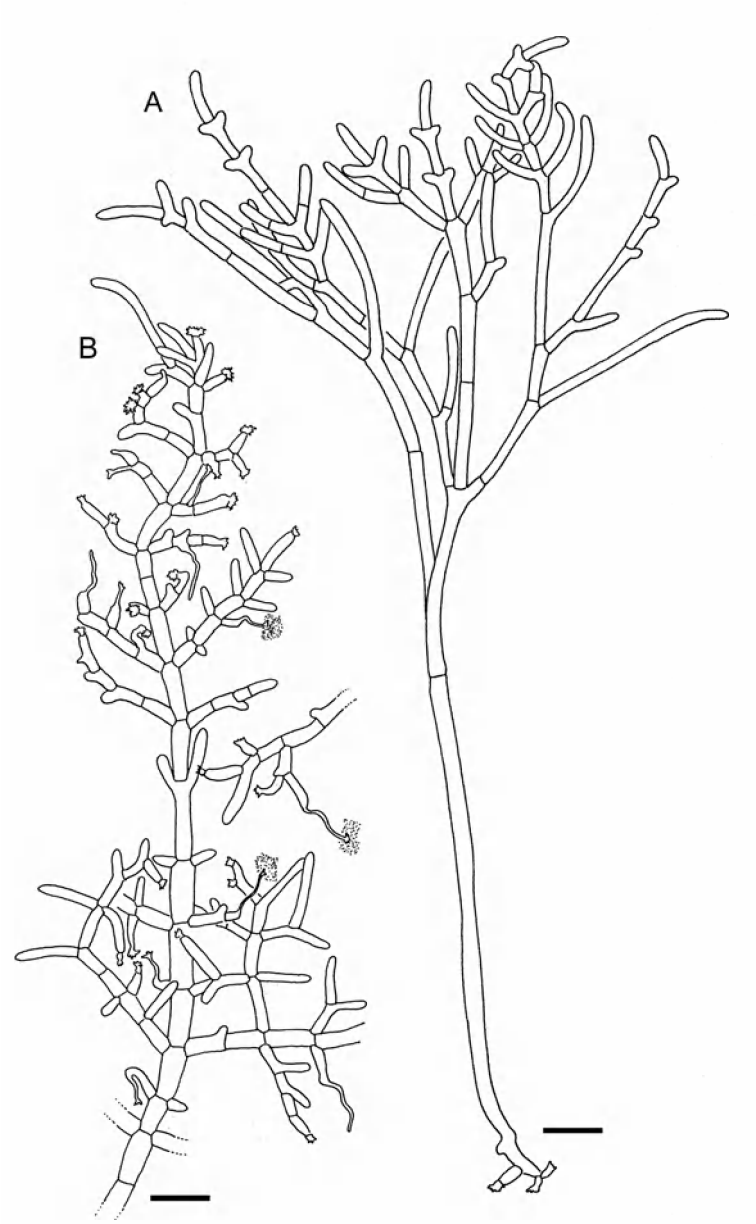

Fig. 30. *Cladophoropsis composita* complex: *siamensis* phenodeme. **A.** Young, stipitate thallus with opposite or unilateral terminal branch-systems (L 936.181.459); **B.** Thallus growing on sand-covered rock, producing numerous type-1 and -2 tenacular cells and type-3 rhizoids (FL 722). Scale bars = 500 μm.

Specimens examined: **Carribean Sea: St. Thomas.** unknown locality, (leg. Børgesen 1068, 1905-1906, L 936 181 459); **Indian Ocean: India.** Dwarka, (leg. Børgesen 5426, 1927-1928, C: lectotype of *Boodlea siamensis* forma *robusta*; Børgesen 5412, 5457 & 5561: syntypes); Port Okha, (leg. Børgesen 5561, 1927-1928, C: syntype of *B. siamensis* forma *robusta*); **Kenya.** between English Point & Mc Kenzie Point, Mombasa, (leg. Coppejans, i.1986, HEC 5836); Chale Island, Gazi, (leg. Coppejans, 9.viii.1989, HEC 8316); Gazi, mangrove creek, (leg. Coppejans, i.1986, HEC 6075; 8.vii.1987, HEC 6736); Iwatine Bay, Mombasa, high intertidal, (leg. Coppejans *et al.*, 11.ix.1992, HEC 9397); Kanamai, Mombasa, (leg. Coppejans, vi.1985, HEC 5625); Kikambala, (leg. Napper 439, 5.i.1956, B 09440); Kikari, SE end of Manda Island, (leg. Greenway & Rawlins 8884, 12.ii.1956, B 09444); Kiu Island lagoon, Lamu District, on dead coral, (leg. Greenway & Rawlins 9379, 23.x.1957, B 33891); Mwamba Beach, Mombasa, mid intertidal, on sand covered coral, (leg. Coppejans, 5.ix.1991, HEC 8693); Nyali Beach, Mombasa, (leg. Coppejans, vi.1985, HEC 5659); Osine, Lamu District, shallow bay, wave exposed, (leg. Greenway & Rawlins 9321,

9.x.1957, B 09441); Ras Wasin, Shimoni, (leg. Coppejans, 8.iii.1988, HEC 7266); Silversands, Malindi, (leg. van Someren E.A.H. 10.485, i.1956, B 09443); Vipingo, 35 km N of Mombasa, (leg. Coppejans, 29.vii.1989, HEC 8189); **Madagascar.** Tamatave Reef, (leg. Voeltzkow s.n., 1904, B A449); **Mauritius.** unknown locality, (leg. Vaughan 290, B 09448); unknown locality, (leg. Voeltzkow s.n., xii.1904, B A469); **Oman.** Daynayah, Ashai, (leg. Jupp, 13.i.1994, FL 875, FL 876, FL 877, FL 878); **Réunion.** St. Gilles les Bains, (leg. Dargent, 19.iv.1998, HOD RUN 98-35); Trois Bassins, (leg. Dargent, 22.iv.1998, HOD RUN 98-45); **Seychelles.** Alphonse Atoll, drifting outside the atoll, (leg. Coppejans, Kooistra & Audiffred, 4.i.1993, SEY 729); Anse Forbans, Mahé, lagoon section, sandy reef flat, (leg. Coppejans, Kooistra & Audiffred, 10.xii.1992, SEY 1); Mare Anglaise, Mahé, rock pool, (leg. Coppejans, Kooistra & Audiffred, 12.xii.1992, SEY 52); **South Africa.** Sodwana Bay, KwaZulu-Natal, (leg. Coppejans *et al.*, 8.viii.1999, KZN 237, leg. De Clerck & Cocquyt, KZN 1737); **Tanzania.** Ras Ruvula, Mnazi Bay, Mtwara area, low intertidal, (leg. Coppejans, Dargent & Bel, 21.vii.2000, HEC 12771); Ras Ruvula, Mnazi Bay, Mtwara area, subtidal, 15 m depth, loosely attached on coral, (leg. Coppejans, Dargent & Bel, 28.vii.2000, HEC 12938); Fungu Achungu, Mnazi Bay, Mtwara area, subtidal reef slope, 6 m depth, on coral rubble on sand, (leg. Coppejans, Dargent & Bel, 11.viii.2000, HEC 14222); Chole Bay in front of Mafia Island Lodge, Mafia Island, low intertidal, epilithic in seagrass bed, (leg. Coppejans & De Clerck, 8.i.1996, HEC 11124); Shangani Reef, N of Chole Bay, Mafia Island, subtidal, 25 m depth, on coral fragments on sand, (leg. Coppejans & De Clerck, 14.i.1996, HEC 11256); **Zanzibar (Tanzania)**; Chwaka, intertidal reef flat, epilithic or loosely attached to the substratum, (leg. Leliaert, 18.vii.1997, FL 613; 31.vii.1997, FL 714); Chwaka, intertidal seagrass bed, epilithic on coral rubble, (leg. Leliaert & Coppejans, 18.vii.2001, FL 977); Chwaka, intertidal seagrass bed, epiphytic on *Laurencia* sp., (leg. Leliaert & Coppejans, 18.vii.2001, FL 979); Chwaka, mid intertidal reef flat, loosely attached to the rocky substratum, (leg. Leliaert & Coppejans, 17.vii.2001, FL 968); Chwaka, shallow subtidal seagrass beds, 1-2 m depth, epilithic, loosely attached, (leg. Leliaert & Coppejans, 17.vii.2001, FL 964); Matemwe, sandy reef pools, epilithic, (leg. Leliaert, 21.vii.1997, FL 649, FL 651); Nungwi, intertidal reef flat, epilithic on sand covered substratum, (leg. Leliaert, 20.vii.1997, FL 643; leg. Leliaert & Coppejans, 21.vii.2001, FL 1008); Nungwi, mid intertidal reef flat, epilithic, loosely attached to the substratum, (leg. Leliaert & Coppejans, 21.vii.2001, FL 999); Nungwi, mid intertidal, epilithic or epiphytic, (leg. Leliaert, 25.vii.1997, FL 696); Uroa, infralittoral fringe, epiphytic on *Amphiroa* sp. and *Halimeda opuntia*, (leg. Coppejans, 24.vii.1993, HEC 9677); **Yemen.** Dihamd-Qadeb, N-coast of Socotra, shallow subtidal, 2 m depth, epilithic on sand covered rock, (leg. Leliaert, 26.ii.1999, SOC 226); E of Rhiy di Howlaf, N Socotra, shallow subtidal, 3 m depth, on coral rubble, (leg. Leliaert, 19.ii.1999, SOC 112); Rhiy di-Adhoh, NE Socotra, (leg. Leliaert, 24.ii.1999, SOC 204); Siqirah, NE Socotra, shallow subtidal, 3 m depth, epilithic on dead coral, (leg. Leliaert, 24.ii.1999, SOC 201); Socotra, (leg. Leliaert, SOC 254); **Pacific Ocean: Cook Island.** Mangaia, (leg. Gill s.n., BM); **Hawaii.** Nanakuli, (leg. Papenfuss 10787, 23.xi.1941, S); **Indonesia.** Ambon, (leg. Weber-van Bosse, Siboga expedition s.n., 16.xi.1899, L 936 181 314); Bira, (leg. Weber-van Bosse, Siboga expedition s.n., L 936 181 328); Buru Island, Moluccas, (leg. Weber-van Bosse, Siboga Expedition, Herbarium Reinbold, M: lectotype of *Boodlea paradoxa*); E Tarupa Kecil, NE Taka Bone Rate, (leg. Coppejans & Prud'homme van Reine, 26.ix.1984, Snellius-II 11279); Elat, Groot-Key rif (stat. 261), (leg. Weber-van Bosse, Siboga expedition s.n., 16.xii.1899, L 936 181 326); harbour of Taipabu, NW coast Binongko, Tukang Besi Islands, Banda Sea, (leg. Coppejans & Prud'homme van Reine, 10.ix.1984, Snellius-II 10330, Snellius-II 10351); Insula Edam, Java, (leg. Möller s.n., 4.ix.1897, B 09456); Moearas reef, (leg. Weber-van Bosse, Siboga expedition s.n., 22.vi.1899, L 936 181 313); Pulu-Karang, S Aru, (leg. Arnoldi s.n., 2.v.1909, L 940 118 146); S Tomea, Tukang Besi Islands, Banda Sea, (leg. Coppejans & Prud'homme van Reine, 7.ix.1984, Snellius-II 11165); Sikka, Flores, (leg. Weber-van Bosse 1091, xii.1888, L 936 181 397); unknown locality, (leg. Weber-van Bosse, Siboga expedition s.n., M); unknown locality, (leg. Weber-van Bosse, Siboga expedition s.n., xi.1899, L 936 181 332); W Kudingareng Keke Island, SW Sulawesi, shallow subtidal, 1 m depth, (leg. Verheij 0907, 20.xii.1989, L 992 261 222); **Japan.** unknown locality, (leg. Moseley, Challenger expedition s.n., BM); Hachijyo Island, Sokodo, intertidal pools, epilithic, (leg. Tanaka 79, 12.v.1990, L 993 356 415); Hachijyo Island, Sokodo, intertidal pools, epilithic, (leg. Tanaka s.n., 12.v.1999, B 36273); Hoshizuna-no-hana, Iriomote Island, shallow subtidal, lagoon, (leg. Coppejans, 15.ix.1993, HEC 10075); O-shima, Wakayama Prefecture, S-coast of Japan, (leg. Moseley s.n., Challenger Expedition s.n., Herb. Dickie, BM: holotype of *Cladophora coacta*); Sesoko, Okinawa, subtidal, (leg. Coppejans, 7.ix.1993, HEC 9982); Sunosaki (Boshu), low intertidal, on sandy rocks, (leg. Okamura 99, vi.1899, BM); Sunosaki (Boshu), low intertidal, on sandy rocks, (leg. Okamura 99, vi.1899, L 937 072 241); Sunosaki, Boshu, low intertidal, on sandy rocks, (leg. Okamura s.n., vi.1899, M); Sunozaki, Boshu, (unknown collector s.n., M); Tateyama, (leg. Higashi s.n., viii.1932, B 09434); Tateyama, (leg. Higashi s.n., viii.1932, M); **Papua New Guinea.** Gumbi Bay, Madang Province, (leg. Coppejans, 25.vii.1988, HEC 7934); Hatzfeldthafen, Madang Province, (leg. Coppejans, 21.vii.1988, HEC 7903); Horse Shoe Reef, Port Moresby area, shallow subtidal reef platform, 2 m depth, (leg. Coppejans & De Clerck, 30.vii.1994, HEC 10340); island N of Demasa Island, Madang Province, (leg. Coppejans & Prud'homme van Reine, 15.vii.1990, Copp & PvR 13170); Laing Island, Madang Province, (leg. Coppejans, 10.vii.1986, HEC 6674); Loloata Island, Port Moresby area, shallow subtidal, 5 m depth, (leg. De Clerck & Coppejans, 28.vii.1994, ODC 250); Motupore Island, Port Moresby area, infralittoral fringe, lagoon, on horizontal substratum, (leg. Coppejans & De Clerck, 21.vii.1994, HEC 10203); Motupore Island, Port Moresby area, inner slope of the fringing reef, (leg. Coppejans, vi.1986, HEC 6339); NW point of Christmas Bay, Bagabag, Madang Province, (leg. Coppejans & Prud'homme van Reine, 2.viii.1990, Copp & PvR 13509a); Ruo Island, Madang Province, (leg. Coppejans & Prud'homme van Reine, 19.vii.1990, Copp & PvR 13262); SW of Wangat Island, Madang Province, (leg. Coppejans & Prud'homme van Reine, 14.vii.1990, Copp & PvR 13157); W of Malamal Island, Madang Province, (leg. Coppejans, 7.viii.1988, HEC 8067); **Philippines.** Philippines, (unknown collector s.n., M); **Samoa.** unknown locality, (leg. Reichinger s.n., B 09454, B 09455); **Tahiti.** unknown locality, (leg. Tilden 105, x.1909, M: lectotype of Boodlea composita f. irregularis; B 09435, B 09436, B 09437, B 09438: isolectotypes); Papeivi Pass, free floating, (leg. Setchell & Parks 5214, 24.vi.1922, UC 261241, L 936 073

147); **Thailand.** Ko Kahdat, Ko Chang Archipelago, (leg. Reinbold s.n., Danish Expedition to Siam, Herb. Reinbold, M: holotype of *Boodlea siamensis*); **The Philippines.** Cangalwang, Siquijor, intertidal reef flat, epiphytic on seagrasses and macro-algae, (leg. Leliaert & Liao, 8.viii.1998, PH 85); Caw-Oy, Olango Island, Cebu, intertidal, epilithic, (leg. Leliaert & Liao, 13.viii.1998, PH 219); Karagasan, Zamboanga City, Mindanao, infralittoral fringe, on *Kappaphycus monolines*, (leg. Leliaert & Liao, 25.viii.1998, PH 547); Lumangcapan, Enrique Villanueva Siquijor, high intertidal, sandy reef flat, epilithic, loosely attached to the substratum, (leg. Leliaert & Liao, 7.viii.1998, PH 7, PH 47); Mactan Island, intertidal, epilithic, (leg. Leliaert & Liao, 6.viii.1998, PH 648); Marigondon, Lapu Lapu City, Maktan Island, Cebu, intertidal, epiphytic on various macro-algae, (leg. Leliaert & Liao, 12.viii.1998, PH 175); Tolingon, Isabel, Leyte Island, epiphytic or epilithic, (leg. Leliaert & Liao, 20.viii.1998, PH 368); **Tonga.** Tongatapu, (leg. Graeffe 1717 & 1717b, S); **Vietnam.** Vicinity of the "Institut Oceanographique de Nhatrang", on coral rubble, (leg. Dawson 11119, 27.i.1953, L 961 176 478); **Red sea: Egypt.** Dahab, (leg. De Clerck, 24.v.1997, ODC 571).

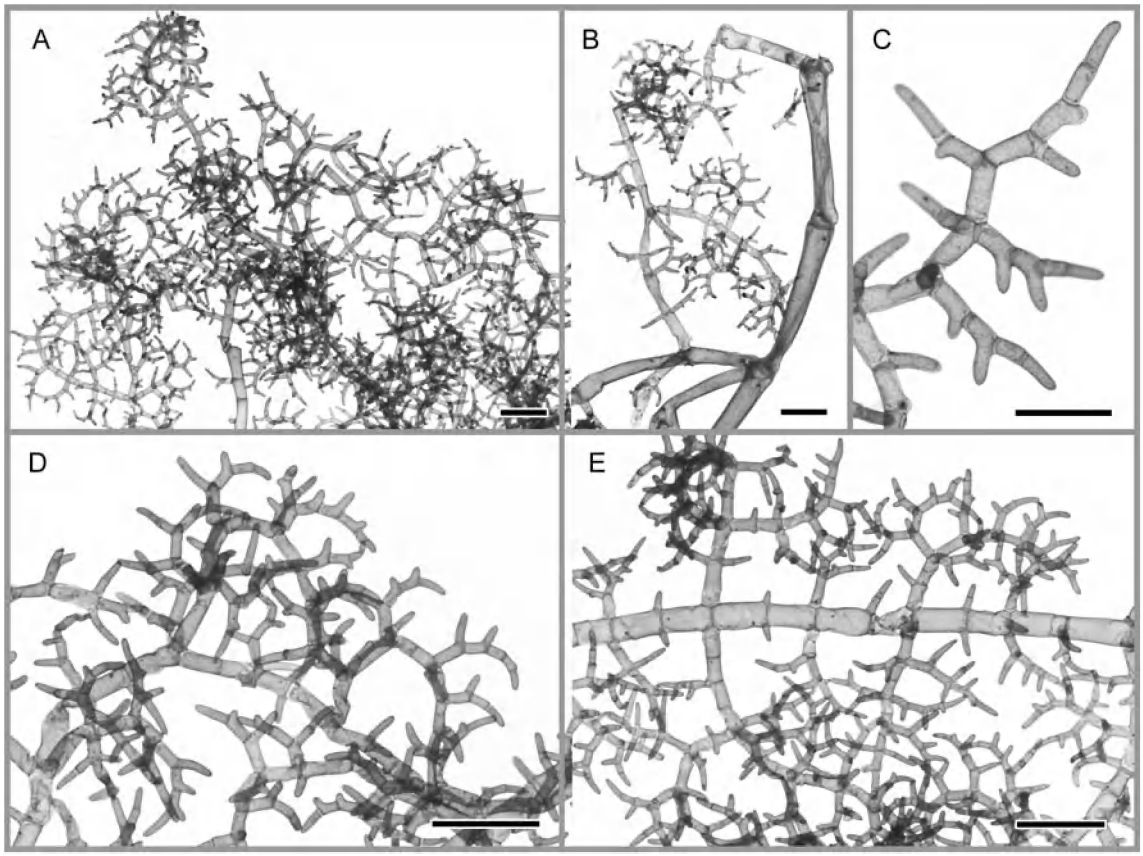

Fig. 31. *Cladophoropsis composita* complex: *siamensis* phenodeme (FL 714, Chwaka Bay, Zanzibar). **A-B.** Branching filaments forming a three-dimensional reticulum; **C.** Unilateral or pseudodichotomous terminal branches; **D.** Incurved terminal branch-systems; **E.** Main axes with intercalary cell divisions at regular intervals. Scale bars: A-B, D-E = 1 mm; C = 500 µm.

Notes:

The *siamensis* phenodeme has been encountere pantropically and is found commonly from the high intertidal to subtidal (down to 25 m depth), epilithic on rocky substratum or on dead coral, or epiphytic on macro-algae, seagrasses or mangroves.

The type material of *B. siamensis* consists of a cushion-like thallus composed of conspicuous, coarse main axes set with opposite or unilateral branches bearing the ultimate branch systems, composed of pseudodichotomous branching filaments; older cells generally producing a 2nd (and 3rd) lateral, perpendicular or opposite to the first one. Reinbold`s (1901) original description was rather cryptic and the species became better known by the work of Weber-van Bosse (1913: 68-70, fig. 11). Børgesen (1913: 49, fig. 34-36) described and illustrated (as *B. siamensis*) a Caribbean plant with an intermediate morphology between the *siamensis* and the *composita* phenodeme. Later, Børgesen (1946: 16) considered *B. siamensis* to fall within the variability of *B. composita*; the conspecificity of both taxa has since then been

widely accepted. Most *B. composita* references in the literature are referable to the *siamensis* phenodeme [e.g. Taylor (1945: 50, pl. 1, figs 1, 2); Egerod (1952: 362, fig. 6a); Chang *et al.* (1975: 37, 58, fig. 10); Egerod (1975: 50-52, fig. 19), Littler & Littler (2000: 326, fig. on p. 327; 2003: 200, fig. on p. 201)]. Two forma's of *B. siamensis* (*irregularis* and *robusta*) have been described. Examination of the type material of both taxa (Figs 33 and 34, respectively) demonstrates that they fall within the limits of the *siamensis* phenodeme.

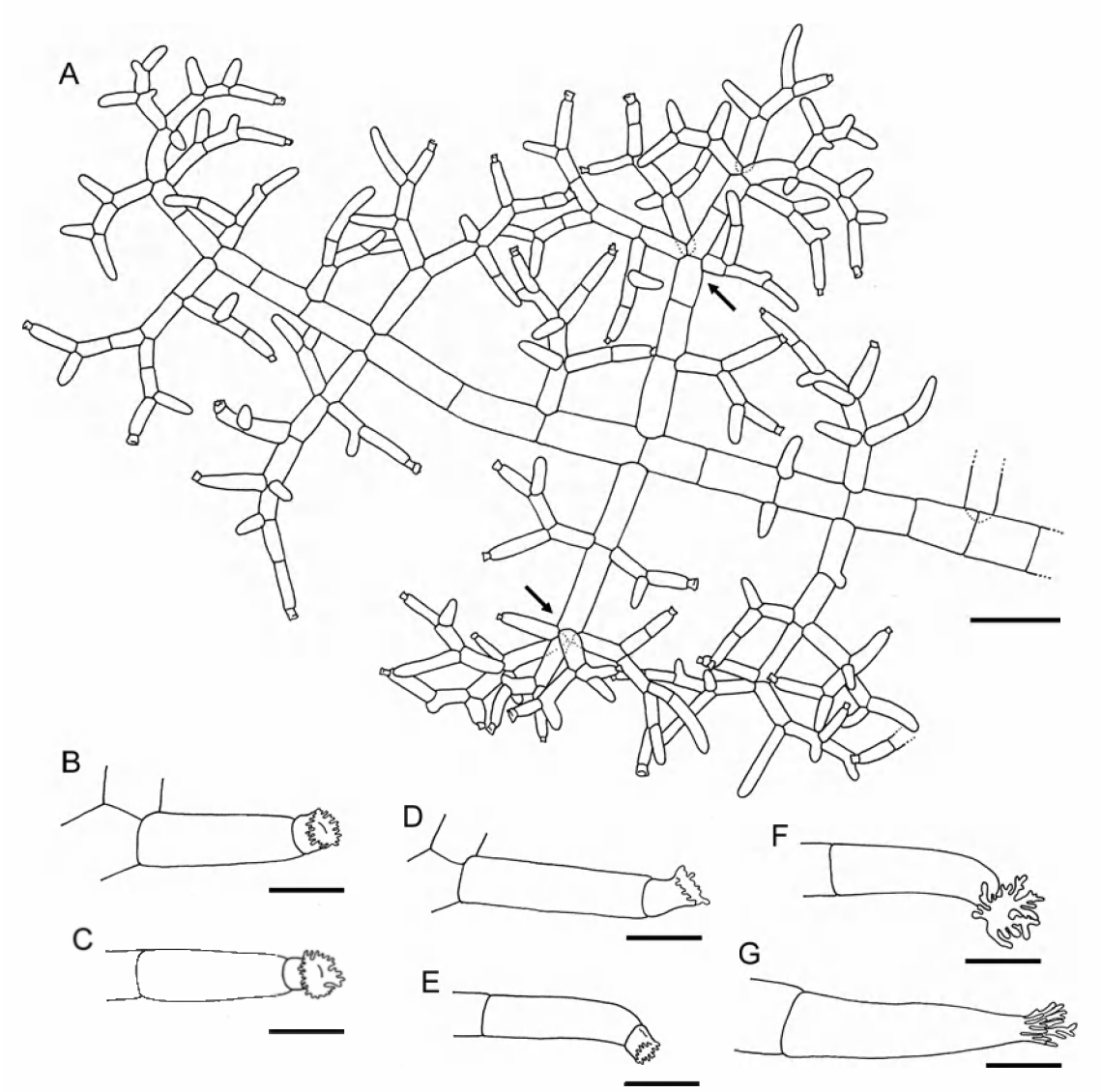

Fig. 32. *Cladophoropsis composita* complex: *siamensis* phenodeme (lectotype of *Boodlea paradoxa*, M). **A.** Oppositely branched main axis with numerous intercalary cell divisions; unilateral to pseudo-dichotomous or opposite terminal branch-systems, many cells producing branches perpendicular on the original branching plane (arrows), resulting in a three-dimensional reticulum; B-E. Type-3 tenacular cells; F-G. Type-1 tenacular cells. Scale bars: A = 500 µm; B-G = 100 µm.

Two specimens of *Cladophora coacta* Dickie, which match the prologue of the original description are present in BM; both specimens were collected by H.N. Moseley during the Challenger Expedition, and are labelled "*Cladophora coacta* n. sp. ?". Only one specimen is certainly from Japan and is considered as holotype (Fig. 33). The original description of *C. coacta* was very cryptic and the species became better known as *Boodlea coacta* through the descriptions and illustrations of Murray (1889: 245, pl. 49) and Okamura (1901: 41, pl. 15).

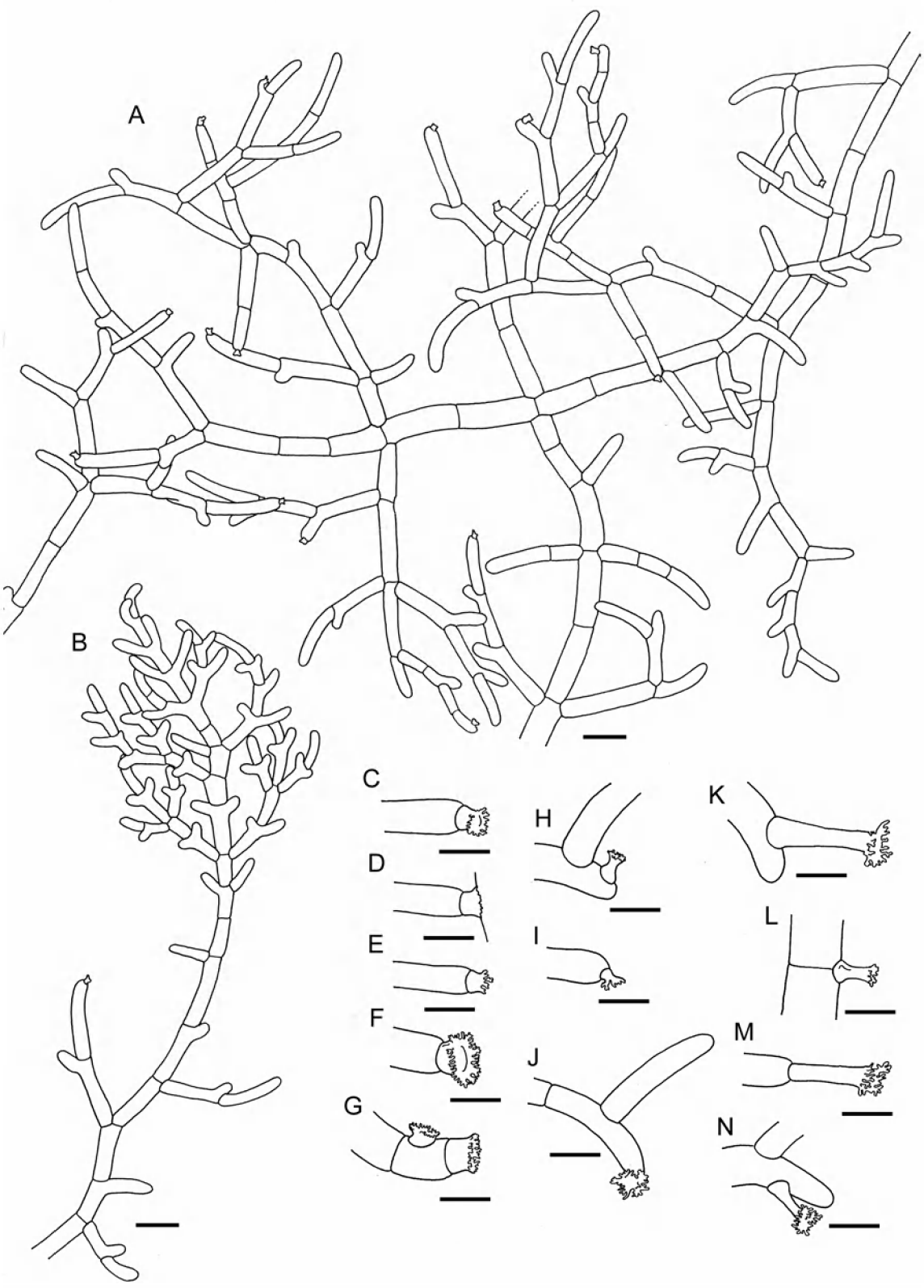

Fig. 33. *Cladophoropsis composita* complex: *siamensis* phenodeme (holotype of *Cladophora coacta*, BM). **A.** Oppositely branched main axis, unilateral to pseudodichotomous terminal branch systems; **B.** Terminal opposite branch systems forming a "*Struvea*"-like plumule; **C-I.** Type-3 tenacular cells; **J-K.** Type-1 tenacular cells; **L-N.** Intermediate forms between type-1 and -3 tenacular cells. Scale bars: A-B = 200 µm; D-N = 100 µm.

Dickie (1876: 451) commented on the similarities between *C. coacta* and *C. anastomosans*. The type of *C. coacta* is characterized by opposite terminal branch systems (Fig. 33B) in some parts of the thallus and unilateral or pseudodichotomous terminal branch systems (Fig. 33A) in other parts; the taxon can therefore be regarded as intermediate between the *composita* and the *siamensis* phenodeme.

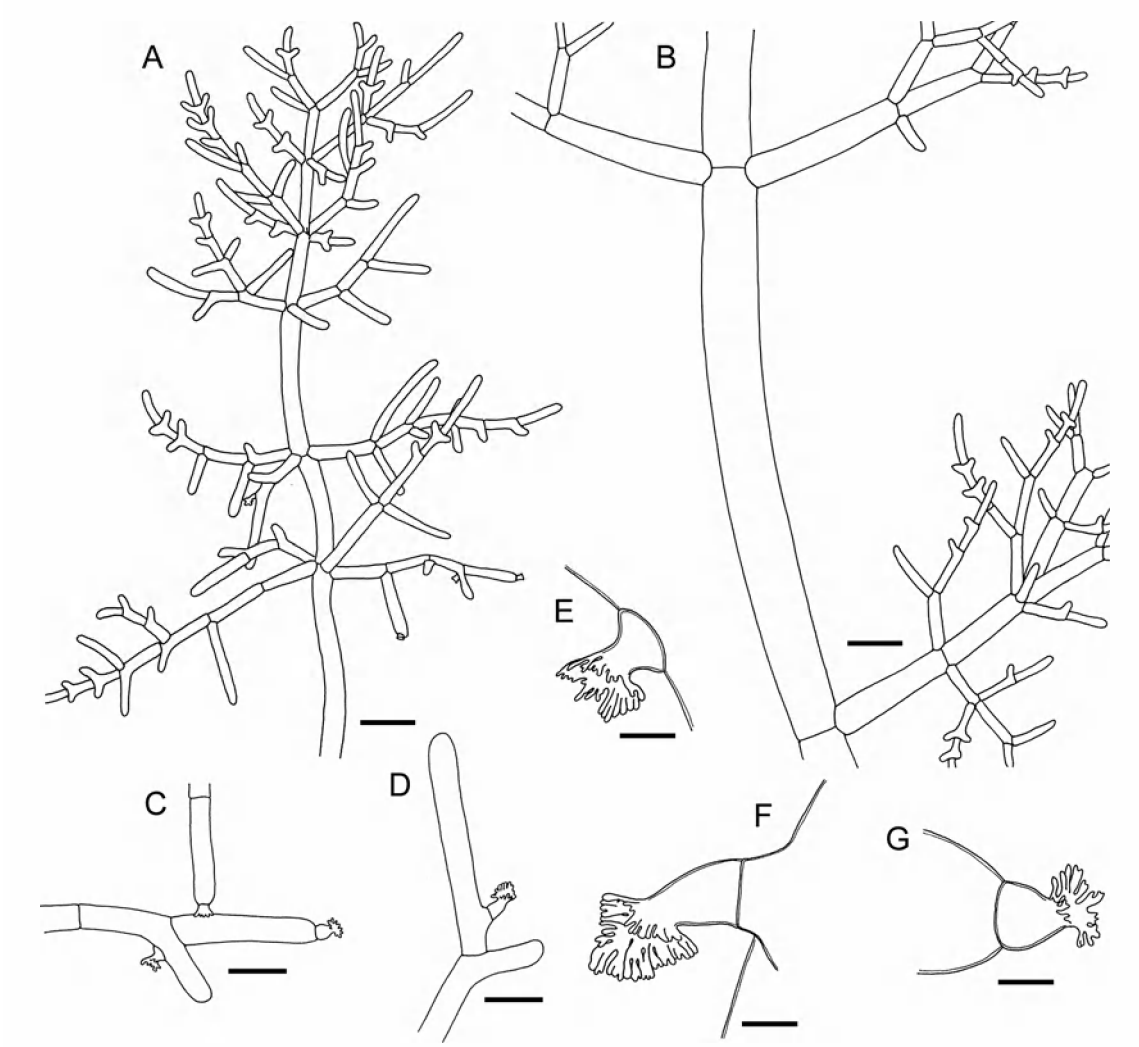

Fig. 34. *Cladophoropsis composita* complex: *siamensis* phenodeme (lectotype of *Boodlea composita* forma *irregularis*, B). **A.** Terminal branch-system with unilateral or opposite laterals and branches perpendicular on the original branching plane; **B.** Large cells of a main axis; side branches single or opposite; **C-G.** Type-3 tenacular cells. Scale bars: A-B = 500 µm; C-D = 200 µm; E-G = 50 µm.

The type specimen of *B. paradoxa* consists of a cushion-like thallus composed of coarse, oppositely branched main filaments with three-dimensional, irregular, pseudodichotomous terminal branch systems. Reinbold's (1905) original diagnosis was rather cryptic. A more thorough description and illustration was provided by Weber-van Bosse (1913: 72-73, fig. 13) who commented on the similarities between *B. paradoxa* and *B. montagnei* (as *Microdictyon montagnei*); the synonymy was later proposed by Papenfuss & Egerod (1957: 83-84). Since the branch systems in *B. paradoxa* are clearly three-dimensional (as opposed to the characteristic two-dimensional branch systems in the *montagnei* phenodeme), we consider this taxon equivalent to the *siamensis* phenodeme.

Gerloff (1960) based his new, monospecific genus, *Nereodictyon*, on a single specimen from Kenya, earlier identified as "*Struvea anastomosans*". Gerloff (l.c.) distinguishes *Nereodictyon*

from *Boodlea* and *Microdictyon* by the absence of tenacular cells. The original illustration, however, shows typical *B. siamensis*-like branch systems. Presence of tenacular cells is now known to be a variable character in this taxon, and we therefore consider it likely that *N. imitans* is referable to the *siamensis* phenodeme. Examination of the crystalline cell inclusions in the type material should give a decisive answer about the status of *Nereodictyon*. We were not able to get hold of the type material.

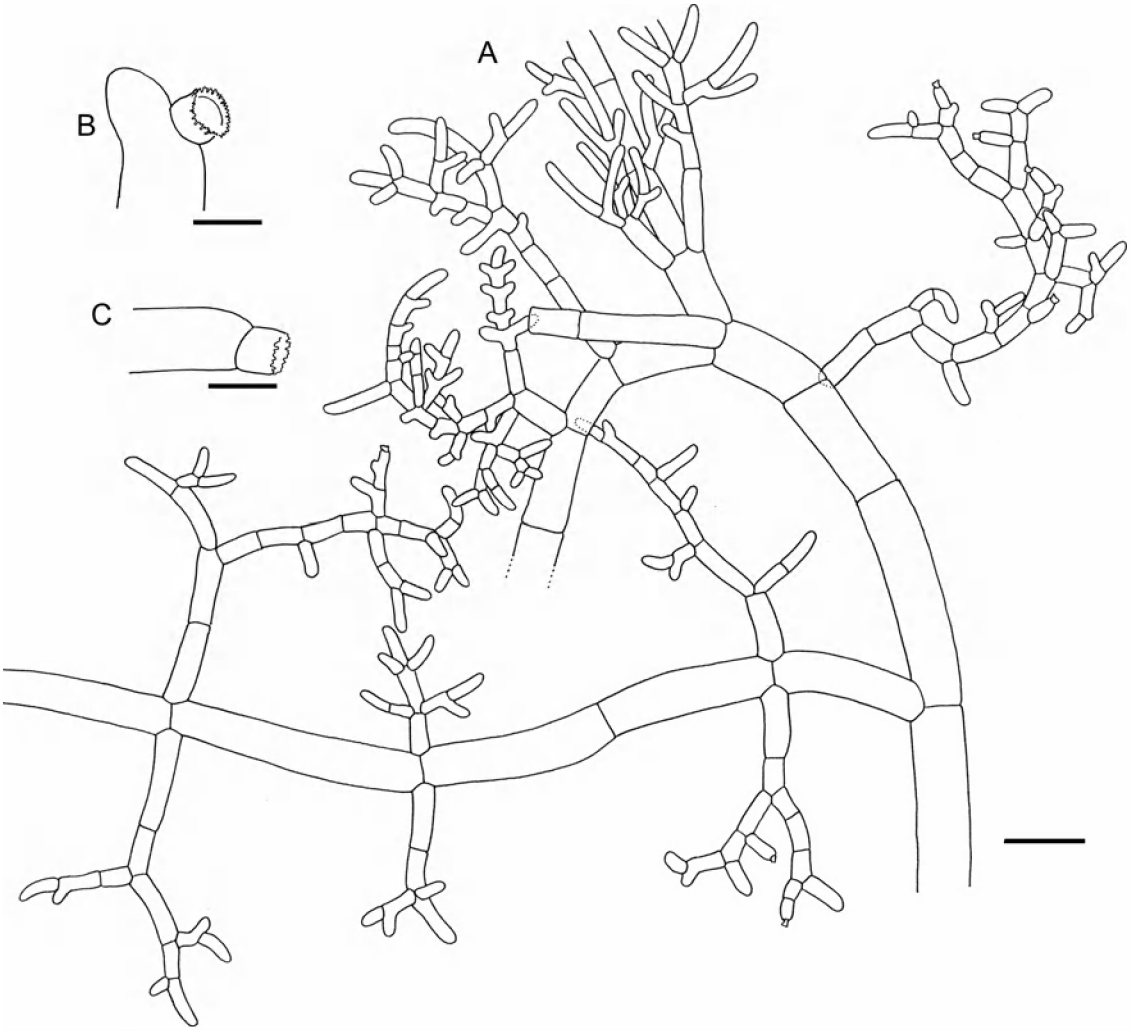

Fig. 35. *Cladophoropsis composita* complex: *siamensis* phenodeme (lectotype of *Boodlea siamensis* forma *robusta*, C). **A.** Main axes with opposite or single side branches; ultimate branches opposite, unilateral or pseudodichotomous, many cells producing laterals perpendicular on the original branching plane; **B-C.** Type-3 tenacular cells. Scale bars: A = 1 mm; B-C = 100 µm.

The cushion-like phenodemes, *composita* and *siamensis*, differ in branch pattern and the abundance of tenacular cells (type-1 and -3). The *composita* phenodeme is characterized by regular, opposite ultimate branch systems, often resulting in small *Struvea*-like plumules sticking out of a cushion-like thalli. Older cells generally produce a 3rd and 4th lateral, perpendicular to the first pair, resulting in three-dimensional branch systems. Tenacular cells in the *composita* type are relatively rare and the limited structural reinforcement of the thallus is merely achieved by loose interweaving of the filaments. In the *siamensis* phenodeme newly formed sub-apical cells generally produce a single lateral, resulting in unilateral or

pseudodichotomous, ultimate branch systems. Like in the *composita* form, secondary, perpendicular laterals are generally formed, resulting in three-dimensional branch systems. The thallus is strongly reinforced by numerous tenacular cells (mainly type-3), in combination with tight interweaving of the often curved branch systems. However, many intermediates between the *composita* and *siamensis* phenodemes have been observed in the field. These plants produce both types of branch systems; generally the internal structure of the thallus is *siamensis*-like, while some terminal branch systems in the peripheral parts are regularly opposite.

The life history of *B. coacta* was studied by Chihara (1955: 8-19). According to his experiments young individuals are present in early autumn, growth takes place from spring to summer of the following year after which formation of sporangia takes place. The whole cell is transformed into a sporangium; in its formation, the chloroplasts, nuclei and pyrenoids unite with each other and congregate to a network from which the swarmers are formed. About the same time one or more short conical projections are observed on the lateral side or summit of each sporangium. The swarmers escape through an aperture formed in the apex of the projections as described by Børgesen (1913) for *B. siamensis*. Every swarmer is long pear-shaped, about 16-22.5 μm long, 9-12.5 μm wide, and has four flagella, one eye-spot and numerous chloroplasts. They show a tendency of positive phototaxis. Conjugation was never observed. After swimming for some time, they settle down and immediately germinate. The early sporelings have an upright part and a rhizoid. The fact that bi-flagellate gametes were never observed suggests that *B. coacta* only reproduces asexually.

General references. As *Boodlea coacta*: Okamura (1901: 41, pl. 15); Chihara: (1955: 9-18, figs 1-5).

The ***struveopsis*** phenodeme Figs 36, 37

Corresponding taxa:

Pseudostruvea siamensis Egerod, 1975: 48-50, figs 12-14 [Holotype: Ko Phuket, Nai Yang, Thailand, epiphytic on *Cladophora rugulosa* (misapplied name for *Cladophora prolifera*) growing on sandstone/limestone slabs of the intertidal, leg. V. Hansen, LE 72-7, x.1972, UC; isotype in C!; paratype: 15 km south of Takuapa in a mat of *Cladophoropsis sundanensis*, upper tide level, on rocky outgrop, leg. L. Egerod LE 71-2-26, 9.iv.1971, UC and C!].

Struveopsis siamensis (Egerod) P.C. Silva, *in* Silva *et al.*, 1996: 800.

Pseudostruvea covalamensis Iyengar, 1980: 59-64, figs 1-27. [Holotype: Kovalam, near Madras, India, leg. Iyengar 103, 22.iii.1962, Herbarium Iyengar, Centre of Advanced Study in Botany, University of Madras; paratypes: Mahabalipuram, leg. Iyengar & Ramanathan, 12.viii.1941 and Kovalam, 18.iv.1962].

Struveopsis covalamensis (Iyengar) P.C. Silva, *in* Silva *et al.*, 1996: 800 [Iyengar (ms.) intended to name this species *Struveopsis covalamensis* gen. et sp. nov. but in the meantime *Struveopsis* was described independently by Rhyne & Robinson (1968). Apparently unaware of this publication, Iyengar (1980, edited and completed by T.V. Desikachary) placed the new species in Egerod's (1975) genus, *Pseudostruvea*].

Description:

Thallus forming 3-6 cm high clusters of erect stipitate blades; stipes unbranched (composed of a single cell) or branched, generally with basal annular constrictions (Figs 36A, 37B). Attachment to the substratum by multicellular rhizoids, arising from the lower pole of the stipe cells (Fig. 36B). Older plants may become cushion-like, with inconspicuous stipes.

Thallus initially consisting of a subcylindrical to clavate stipe initiating a small reticulate blade at its apical pole; initial division of the stipe cell possibly segregative (Fig. 37A, arrow). Growth of the lamina by a repetitive process of apical and intercalary cell division (CI), formation of laterals, cell elongation and enlargement. Apical cell dividing into two, or simultaneously into 3 to 7 cells, followed by the formation of opposite pairs of laterals (Fig. 37C-D). Intercalary cell division starting from the third to 15th cell under the apical cell. Older cells (mostly in the main axes) possibly producing a second, third and fourth lateral, in any direction (Fig. 37C). Cross wall formation at the proximal pole of laterals somewhat delayed; laterals in open connection with the mother cell up to 380 µm long (l/w ratio 3.5). Older branches laterally inserted with a steeply inclined wall cutting it off from the parent cell. Cells in basipetal direction becoming longer and often increasingly club-shaped, often with annular constrictions and a basal bulge (Figs 36C-D, 37E-F). The diameter of the thickest part of the main axes (not including stipe cells) about 2.5-5 that of the apical cells. Branching three-dimensional, up to the 5th (or 6th) order. Diameter of the stipe cells 4-11 times that of the apical cells. Angle of ramification 20°-75°.

Apical cells cylindrical with rounded tip, often curved, (85-) 100-220 (-260) µm in diameter, l/w ratio 1.2-8 (-12). Cell of the main axes subcylindrical to club-shaped, (140-) 260-570 (-930) µm in widest diameter, length/width ratio 2.2-10 (-20). Stipe cells subcylindrical to clavate, (190-) 340-1150 µm in diameter, up to 14 mm long.

Thickness of the cell walls of ultimate branches less than 1 µm, of the main axes and stipe 5-15 µm.

Chloroplasts polygonal to star-shaped, 2.5-8 µm in diameter with strands spanning up to 15 µm long, forming an open parietal reticulum; each chloroplast containing a single pyrenoid.

Prismatic calcium oxalate crystals present in most of the cells, especially abundant in the cells of the main axes and stipe, up to 4 µm in diameter and 70 µm long.

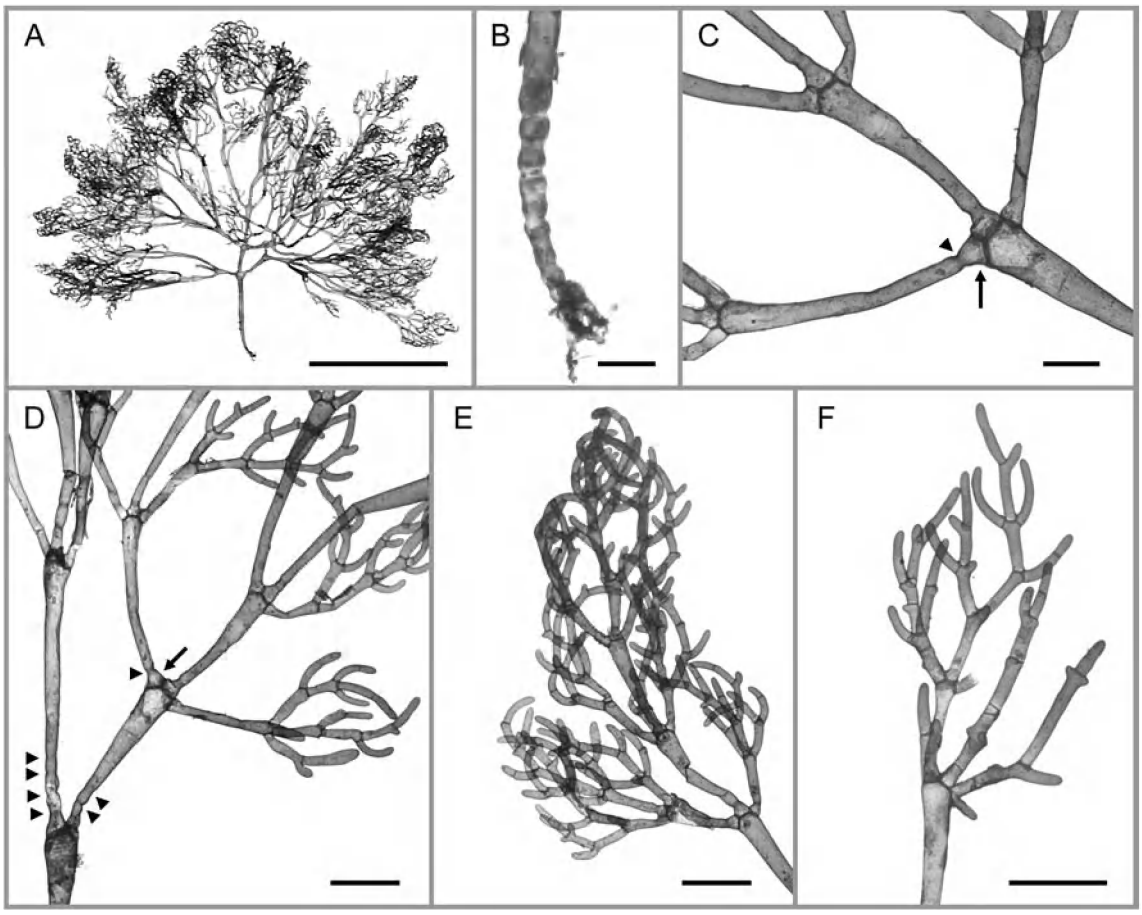

Fig. 36. *Cladophoropsis composita* complex: *struveopsis* phenodeme (FL 677, Kiwengwa, Zanzibar). **A.** Stipitate thallus; **B.** Base of stipe cell with annular constrictions; **C-D.** Opposite or pseudodichotomous main axes; clavate cells with a basal bulge (arrows) and a few annular constrictions (arrowheads); **E-F.** Opposite or pseudodichotomous terminal branch-systems. Scale bars: A = 1 cm; B-C = 500 µm; D-F = 1 mm.

Specimens examined: **Indian Ocean: Tanzania.** Kiwengwa, Zanzibar, fringing reef, epilithic, (leg. Leliaert, 22.vii.1997, FL 677); Mbudya Island, Kunduchi, low intertidal pools, on vertical walls, (leg. Coppejans & De Clerck, 18.i.1996, HEC 11334); Mbudya Island, west coast, High intertidal, shaded rock pool, epilithic on horizontal to vertical substratum, (leg. Leliaert & Coppejans, 11.vii.2001, FL 916); **Thailand.** Nai Yang, Koh Phuket, growing on sandstone/limestone slabs, mid-littoral, (leg. Hansen, Egerod no. LE 72-7, x.1972, C: isotype of *Pseudostruvea siamensis*); Takuapa, upper littoral, epilithic on rock, (leg. Egerod LE 71-2-26, 9.iv.1971, C: paratype of *P. siamensis*).

Notes:

The *struveopsis* phenodeme has only been encountered in the Indian Ocean and has been recorded from Thailand (type locality of *P. siamensis*), Somalia (Sartoni 1992: 314) and Tanzania (Coppejans *et al.* 2000: 65). The plants grow epilithic in the intertidal, often in shaded and sheltered rock pools.

We have not been able to examine the type material of *Struveopsis covalamensis*, but based on the original illustrations (Iyengar 1980: figs 6, 7) this species is considered equivalent to the *struveopsis* phenodeme.

The *struveopsis* phenodeme can be distinguished from the other morphological types by the presence of a conspicuous stipe, generally with basal annular constrictions, and the lack of tenacular cells. Specimens in sheltered and shaded rock pools are unmistakable by the very conspicuous, clavate stipe. However, in more exposed habitats, older thalli form cushions with inconspicuous stipe cells. Furthermore, under exposed conditions or in sand covered habitats,

type-1 and -3 tenacular cells may be produced, fading the boundary with the *composita* phenodeme.

General reference. As *Pseudostruvea siamensis*: Sartoni (1992: 314-315, fig. 11).

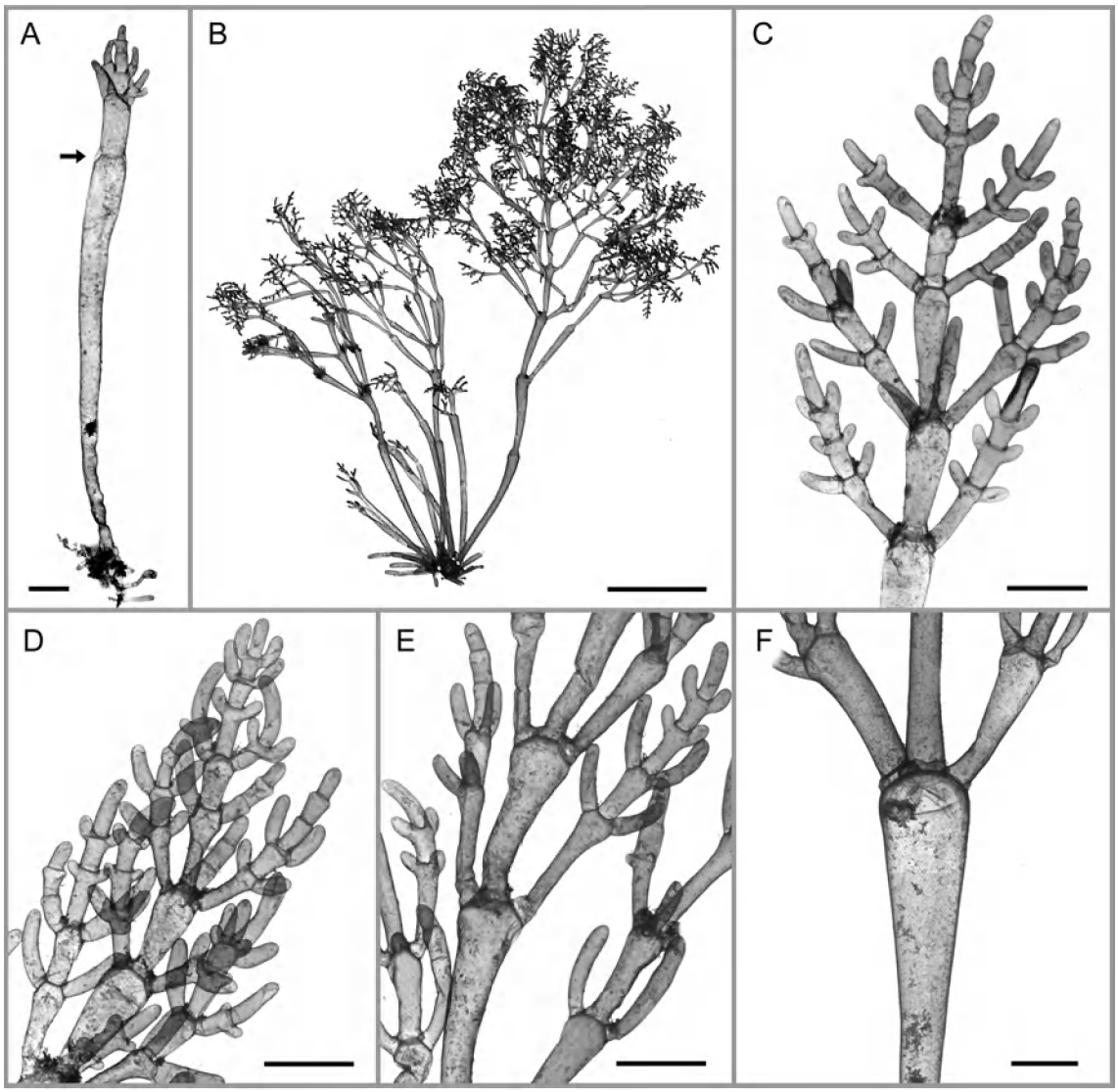

Fig. 37. *Cladophoropsis composita* complex: *struveopsis* phenodeme (FL 916, Mbudya Island, Tanzania). **A.** Young thallus consisting of a stipe with basal annular constrictions and terminal, opposite branches; initial division of the stipe cell segregative (arrow); **B.** Stipitate thalli; stipes composed of clavate cells; main axes oppositely or pseudodichotomously branched; **C-D.** Opposite terminal branch systems; older cells producing laterals perpendicular on the original branching plane; **E-F.** Clavate cells of the main axes. Scale bars: A = 1 mm; B = 1 cm; C-F = 1 mm.

Relations of the *C. composita* complex with *C. membranacea*

The branch systems in *C. membranacea* are typically unilateral and apparently seem completely different from those in the *C. composita* complex. Kooistra *et al.* (1993) and Wysor (2002) however, demonstrated a very close relationship between both taxa. Kooistra (pers. comm.) also suggested that both taxa might represent growth forms of the same species since under certain environmental conditions (e.g. high temperatures), the branches in *C. membranacea* may become opposite and *Boodlea*-like. Indeed, the Indo-Pacific representatives of *C. membranacea* (including *B. kaeneana* and *B. trukensis*), often develop opposite laterals and may be very similar to irregular growth forms in the *C. composita* complex. However, *C. membranacea* differs from the *C. composita* complex by the much longer cells, the greater delay of cross wall formation at the base of the laterals and the shape of the crystalline cell inclusions. The l/w ratio of the apical cells is generally 4-40 in *C. membranacea* versus 1-10 (-18) in the *B. composita* complex. The l/w ratio of laterals in open connection with the mother cell is generally more than 20 in *C. membranacea*, and less than 6 in the *B. composita* complex. Calcium oxalate crystals in the *B. composita* complex are elongate hexagonal or trapeziform (often needle-shaped) (Fig 3R-T), while in thalli of *C. membranacea* broad to elongate rectangular, and broad trapeziform crystals are also found (Fig 3G-K). The idea that *C. composita* and *C. membranacea* are distinct species or cryptic species groups is confirmed by differences in chromosome numbers (1 N = 12 and 16 respectively) and chromosome sizes (*C. composita* having significantly smaller chromosomes) (Kapraun & Nguyen 1994).

In conclusion, a wide morphological diversity is observed within the *C. composita* complex, which is, to some extent, attributable to ecological and developmental phenotypical plasticity. However, preliminary molecular results based in ITS sequences suggest the presence of a number of cryptic species. Four main questions remain (partly) unresolved. (1) How many species should be recognized in the complex? (2) What is the exact extent of the phenotypic plasticity? (3) Is morphology totally incongruent with the evolutionary history? (4) What is the relationship with the cryptic species complex *C. membranacea*, in particular the Indo-Pacific representatives?

Further investigation is needed. An integrated morphological (based on field observations and culture studies), molecular and ecological study on a wide geographical level is essential to assess the question of what drives the morphological variety in the group.

7.2. Section *Spongocladia* (Areschoug) Leliaert & Coppejans stat. nov. & comb. nov. prov.

This section contains a single species, *C. vaucheriiformis*.

Cladophoropsis vaucheriiformis (Areschoug) Papenfuss Figs 5G, 38-43

Spongocladia vaucheriiformis[1] Areschoug, 1854: 201, 202, pl. 2 ("*vaucheriaeformis*") [Lectotype: Mauritius, leg. Areschoug or Pike, S! A2572; syntypes[2]: Mauritius, S! A2569, A2570 & A2571. Several specimens from Mauritius are present in S; one of these, labeled "Spongocladia vaucheriaeformis Aresch. Ad litora insula Mauritius, dedit Areschoug" from the Areschoug herbarium is here indicated as lectotype].

Cladophoropsis vaucheriiformis[1] (Areschoug) Papenfuss, 1958: 104 ("*vaucheriaeformis*").

Spongodendron crassum Zanardini, 1878: 38 [Lectotype: Sorong, W Irian Jaya, Indonesia, leg. O. Beccari, v.1872, BM! In the original prologue, Aru-Vokan (Wokam Island, Kepulauan Aru, Indonesia) is indicated as type locality. However, only a single specimen labelled in Beccari's hand "*Spongodendron crassum* Zan., Nova-Guinea, Sorong (non Ins. Aru) v.1872" was found in BM and is here indicated as lectotype. The Beccari collections are normally housed in FI, but this specimen was sent to Murray & Boodle (BM) by Beccari (Murray and Boodle 1888a: 169) and apparently never sent back].

Spongodendron dichotomum Zanardini, 1878: 38 [Lectotype: Sorong, W Irian Jaya, Indonesia, leg. O. Beccari, v.1872, BM! No type locality was indicated in the original prologue ("ubi praecedens"). The single specimen (marked as type in BM) and labelled in Beccari's hand "Nova-Guinea, Sorong (non Ins. Aru) v.1872" is here indicated as lectotype. The Beccari collections are normally housed in FI, but the type of *S. dichotomum* was sent to Murray & Boodle (BM) by Beccari (Murray and Boodle 1888a: 169) and apparently never sent back].

Spongocladia dichotoma (Zanardini) Murray & Boodle, 1888a: 175.

Cladophoropsis dichotoma (Zanardini) Papenfuss, 1958: 104.

Spongocladia neocaledonica Grunow ex G. Murray & Boodle, *in* G. Murray & Boodle, 1888a: 175 [Holotype: Poro, New Caledonia, leg. Grunow 3558, 9.x.1884, W!; isotype in BM!].

Cladophoropsis neocaledonica (Grunow ex G. Murray & Boodle) Papenfuss, 1958: 104.

Description:

Thallus dull green, forming large tough clumps of variable morphology, up to 50 cm across and up to 15 (-20) cm high, consisting of numerous individual plants, each composed of much ramified and entangling filaments, living in symbiosis with a *Halichondria* species (Porifera) (R. van Soest, pers. comm.). Thallus morphology ranging from prostrate mats, with or without short, papillous protuberances (Fig. 38C), to upright forms with subcylindrical, finger-like, dichotomously branched, fastigiate processes, 2-10 (-20) mm in diameter and up to 9 cm long (Fig. 38A-B, F, G), irregularly branching processes, 2-5 mm in diameter, with pointed tips, up to 20 cm high (Fig. 38E), or thick blade-like outgrowths, up to 5 cm broad and 15 cm long (Fig. 38D). Adjacent cylindrical processes frequently anastomosing by type-3 tenacular cells or rhizoidal cells.

Cell division by centripetal invagination of the cell walls, or by segregative cell division (Fig. 40I). Growth mainly by elongation and branching of the filaments without cell division, resulting in siphonous branch systems (Figs 40A, C, D), also by apical and intercalary cell division, and subsequent cell elongation (Fig. 42G). The diameter of the thickest part of the main axes 0.4-1.2 times that of apical cells.

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[1] See ICBN, art. 60.8, ex. 13.

[2] See note on p. 144.

Branching of the filaments irregular and extremely variable, even within a single thallus. Newly formed subapical or intercalary cells possibly producing one lateral at their apical or subapical pole (39D, 41A). Apical or intercalary cells sometimes dividing by segregative cell division into 3-11 short cells, followed by the formation of more or less equally developing unilateral branches (Figs 39B, 42E). Cross walls at the base of the laterals absent; laterals not displacing the main axes. Branching generally up to the 2nd or 3rd order. Angle of ramification extremely variable 25-90°.

Attachment to the substratum by hapteroidal rhizoids or tenacular cells. Rhizoids septate or aseptate, most often produced at the proximal pole of the cells, with or without a basal cross wall separating it from the mother cell (Fig. 41D). Structural reinforcement of the thallus achieved by interweaving and anastomosis of the filaments by numerous tenacular cells or rhizoids (Figs 39F-G, 40F-H, 42F) as well as through investment of the fine tissues of the associated sponge.

Cell dimensions extremely variable, even within a single cell. Filaments of the ultimate branch systems subcylindrical to irregularly shaped, straight to strongly curved, (40-) 55-160 (-210) µm in diameter, 225 µm-12.5 mm long. Cells of the main axes (50-) 130-310 (-455) µm in diameter. Basal cells long and slender, 40-95 µm in diameter, up to 14 mm long.

Cell walls very variable in thickness, in apical cells ranging from 2 to 30 µm, in the main axes up to 40 µm and often closing the entire cell (Fig. 39H). Thick cell walls coarsely striated longitudinally (Fig. 39H, I) and less markedly in the transverse direction.

Chloroplasts elongated or star shaped, 2.5-6.5 µm in diameter with shoots spanning up to 20 µm, forming an open parietal reticulum. Most chloroplasts with a single pyrenoid, 1.9-2.5 µm in diameter.

Short to elongate prismatic calcium oxalate crystals present in a few cells (Figs 39I, 43A-D), 3-18 µm in diameter, up to 15-50 µm long, l/w ratio 1-8; number of crystals per cell 1-5 (-10).

Ecology: *C. vaucheriiformis* generally grows epilithic, only occasionally epiphytic on calcified seaweeds (e.g. *Halimeda opuntia*) in the mid intertidal to shallow subtidal (down to 1 m depth).

Geographical distribution: *C. vaucheriiformis* is widely distributed in the tropical to subtropical Indo-West Pacific (Papenfuss 1950, Gerloff 1960; Sartoni 1992; Silva *et al.* 1987, 1996).

Specimens examined: **Indian Ocean: Maurius**. unknown locality, (leg. Areschoug or Pike, S A2572: lectotype of *Spongocladia vaucheriiformis*; S A2569, A2570 & A2571: syntypes); **Kenya**. Kanamai, Mombasa, (leg. Coppejans, i.1986, HEC 6064); Mc Kenzie Point, Mombasa, (leg. Coppejans, i.1986, HEC 5976); Mwamba Beach, Mombasa: mid to lower intertidal rock pools, seagrass bed, epiphytic on *Halimeda opuntia*, (leg. Coppejans, 12.ix.1991, HEC 8724); Shimoni, Kisite Island, (leg. Coppejans, 9.iii.1988, HEC 7278); Tiwi, between Mombasa and Diani: lower intertidal, epilithic on horizontal substratum, (leg. Coppejans *et al.*, 13.ix.1992, HEC 9423); Vipingo, 35 km N of Mombasa, (leg. Coppejans, 29.vii.1989, HEC 8181); **Mauritius**. unknown locality (leg. Areschoug or Pike, S A2572: lectotype of *Spongocladia vaucheriiformis*; syntypes: S A2569, A2570 & A2571); **Singapore**. unknown locality, (leg. collector unknown, MEL 6835); **Tanzania**. Fungu Achungu, Mnazi Bay, Mtwara area: shallow subtidal, - 8 m, on coral rubble on sand, (leg. Coppejans *et al.*, 11.viii.2000, HEC 14221); Mana Hawanja Island, Mnazi Bay, Mtwara area: subtidal reef slope, - 15 m, epilithic, (leg. Coppejans *et al.*, 5.viii.2000, HEC 14186); Ruvula beach, Mnazi Bay, Mtwara area: shallow subtidal, - 5 m, (leg. Coppejans *et al.*, 26.vii.2000, HEC 12912); S of Ras Ruvula, Mnazi Bay, Mtwara area: low intertidal rock pools, (leg. Coppejans *et al.*, 23.vii.2000, HEC 12843); Chapwani Island, in front of Zanzibar Town, Zanzibar: lower intertidal, epilithic, (leg. Coppejans, 27.vii.1993, HEC 9754); Chwaka Bay, Zanzibar: lower intertidal, shallow rock pools, epilithic, (leg. Coppejans, 24.vii.1993, HEC 9702); Fishermen's resort, Mbweni Cliffs, Zanzibar: drift, epizoic on sponge, (leg. Leliaert, 15.vii.1997, FL 607b); Matemwe, in front of Matemwe Beach Village, Zanzibar: mid intertidal reef flat, (leg. Leliaert & Coppejans, 16.vii.2001, FL 954); Paje, Zanzibar: fringing reef, epizoic on sponge, (leg. Leliaert, 23.vii.1997, FL 683); Uroa, Zanzibar: mid intertidal reef flat, (leg. Leliaert & Coppejans, 19.vii.2001, FL 989); Nungwi, Zanzibar: infralittoral fringe, seaward side of the reef flat, exposed to strong surf, epilithic, (leg. Coppejans & De Clerck, 23.viii.1994, HEC 10570); Mafia Island, Chole Bay in front of Mafia Island Lodge: shallow subtidal seagrass bed, epilithic, (leg. Coppejans & De Clerck, 8.i.1996, HEC 11135); Misali Island, NE coast (W of Pemba Island): shallow intertidal rock pool, epilithic on horizontal substratum, (leg. Coppejans & De Clerck, 21.i.1996, HEC 11394); **Pacific Ocean: Australia**. Goode Island, Queensland, (leg. Powell s.n., MEL 6828); **Indonesia**. Sorong, W

Irian Jaya, (leg. Beccari, v.1872, BM: lectotype of *Spongodendron crassum*); Sorong, W Irian Jaya, (leg. Beccari, v.1872, BM: lectotype of *Spongodendron dichotomum*); Ambon Bay, near Tawiri, (leg. Coppejans *et al.*, 6.ix.1984, Snellius-II 10037 and 10078); NE cape of Komodo Island, (leg. Coppejans *et al.*, 26.x.1984, Snellius-II 10891 and 19.ix.1984, Snellius-II 10908); Taka Garlarang Atoll, NE Taka Bone Rate (Tiger Island), (leg. Coppejans *et al.*, 27.ix.1984, Snellius-II 11347); **Japan**. Iriomote Island - Nadara, (leg. Coppejans, 16.ix.1993, HEC 10097); **New Caledonia**. Poro (leg. Grunow 3558, 9.x.1884, W: holotype of *Spongocladia neocaleonica*, isotype in BM); **Papua New Guinea**. Bagabag, SE point of Christmas Bay, Madang Province, (leg. Coppejans & Prud'homme van Reine, 8.viii.1990, Copp & PvR 13621); Kranket Island, Madang Province, (leg. Coppejans, 23.vi.1988, HEC 7571); Malagere Island, Potsdam Harbour, Madang Province, (leg. Coppejans, 6.vii.1988, HEC 7697); Manam, Madang Province, (leg. Coppejans, 16.vii.1988, HEC 7811); Nagada harbour, on opposite side of CRI buildings, Madang Province, (leg. Coppejans & Prud'homme van Reine, 9.vii.1990, Copp & PvR 13050); Wangat Island, Madang Province, (leg. Coppejans, 22.vi.1988, HEC 7547); **The Philippines**. Mactan Island, (leg. Leliaert *et al.*, 6.viii.1998, PH 654).

Notes:

C. vaucheriiformis is a somewhat unusual member of the genus. In the first place because of its association with sponge tissue and the resulting tough, spongiose thallus morphology. Secondly because of the atypical branching pattern, probably as a consequence of the symbiosis. The branch systems in many parts of the thallus lack cross walls altogether, resulting in an apparently siphonous architecture. Because of its deviant morphology and anatomy, the systematic position of the species has long been undecided. The species was first described in *Spongocladia* by Areschoug (1854). Later, Murray & Boodle (1888a) merged *Spongodendron* Zanardini (including the sponge-associated species *S. crassum* and *S. dichotoma*) with *Spongocladia*, which in its turn, was merged with *Cladophoropsis* by Papenfuss (1958: 104) (without giving any justification) who proposed to conserve the latter. Several authors accepted the merger of both genera (Cribb 1960; Sartoni 1992), while others did not. Millar & Kraft (1994: 430) for example, argued that segregative cell division can been used as a character to discriminate the two genera. We place *C. vaucheriiformis* in *Cladophoropsis* based on the following morphological grounds: 1) the presence of tenacular cells, 2) the presence of prismatic calcium oxalate crystals in the cells, and 3) the typical "*Cladophoropsis*"-type branching which can be observed in at least some parts of the thallus. Based on 18S rRNA gene sequence analysis, Hanyuda *et al.* (2002) demonstrated a close relationship between *C. vaucheriiformis* and *C. peniculum*, with *C. membranacea* forming a sister taxon.

C. neocaledonica was distinguished from *C. vaucheriiformis* by Murray & Boodle (1888a) and Womersley & Bailey (1970) by the unbranched macroscopic thallus and by the larger filament diameter. Cribb (1960), who observed intermediate morphologies in his Queensland material and found similar cell diameters in both species, argued that thallus morphology and differences in cell diameter can hardly be regarded as distinguishing characters and therefore considered both species conspecific.

The conspecificity of *S. crassum* and *C. vaucheriiformis* was proposed by Murray & Boodle (1888a) who compared the types of both species. Zanardini (1878) distinguished *C. dichotomum* from *C. vaucheriiformis* solely by its more slender thallus. Taking into account the great morphological plasticity of *C. vaucheriiformis* (Fig. 38) we propose to also reduce this species to a synonym of *C. vaucheriiformis*.

General references. As *Cladophoropsis vaucheriiformis*: Cribb (1960: 11-12, pl. 4, figs 1-4); Pham-Hoàng (1969: 446, fig. 4.50); Sartoni (1992: 313-314, figs 9C, 10). As *Spongocladia vaucheriiformis*: Murray & Boodle (1888a: 175, figs 8-11); Weber-van Bosse (1890: 79-94, pls. 16-17); Heydrich (1894: 276-281, pl. 14); Okamura (1928: 189-190, 200-201, pl. 250, figs 5-12); Lucas (1935: 196); Børgesen (1946: 17; 1948: 23, figs A, B); Papenfuss (1950: 208, fig. 1a); Gerloff (1960: 612-614, fig. 1); Jaasund (1976: 13, fig. 25); Tseng (1984: 274, fig. 4 on p. 136), Kraft (2000: 576, fig. 26).

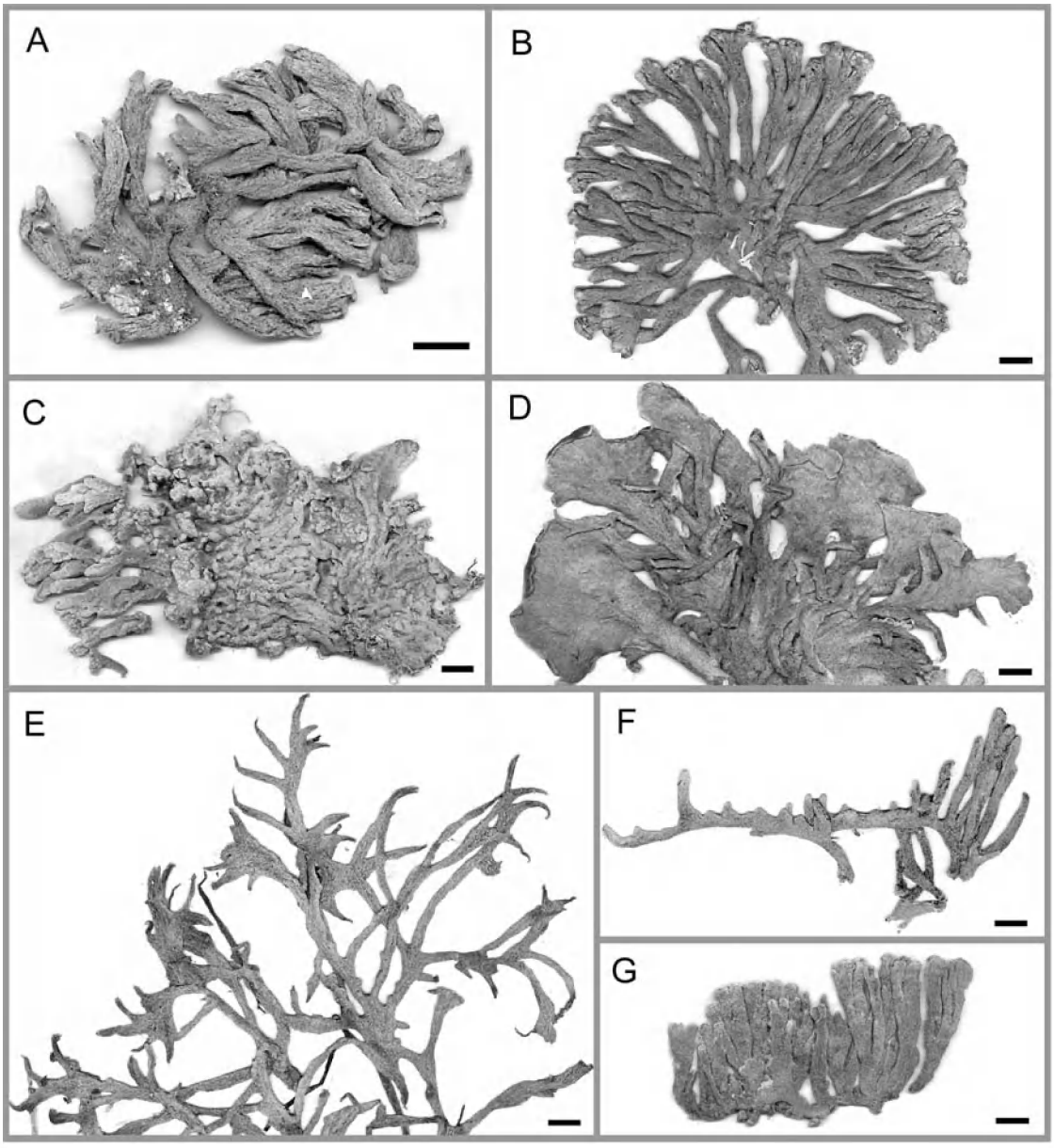


Fig. 38. Thallus morphology of *Cladophoropsis vaucheriiformis*. **A.** Upright thallus with subcylindrical, finger-like, irregularly branched processes (lectotype, S); **B.** Upright thallus with cylindrical, finger-like, dichotomously branched, fastigiate processes (syntype, S A2570); **C.** Prostrate mats with short, papillose protuberances (HEC 9423); **D.** Upright thallus with blade-like outgrowths (HEC 11394); **E.** Upright thallus with cylindrical, irregularly branched processes with pointed tips (HEC 11135); **F.** Young thallus with prostate stolonoids producing upright, cylindrical, finger-like, fastigiate processes (FL 954a); **G.** Older thallus with prostrate stolonoids producing upright cylindrical, finger-like, dichotomously branched, fastigiate processes anastomosing with one another (HEC 7278). Scale bars = 1 cm.

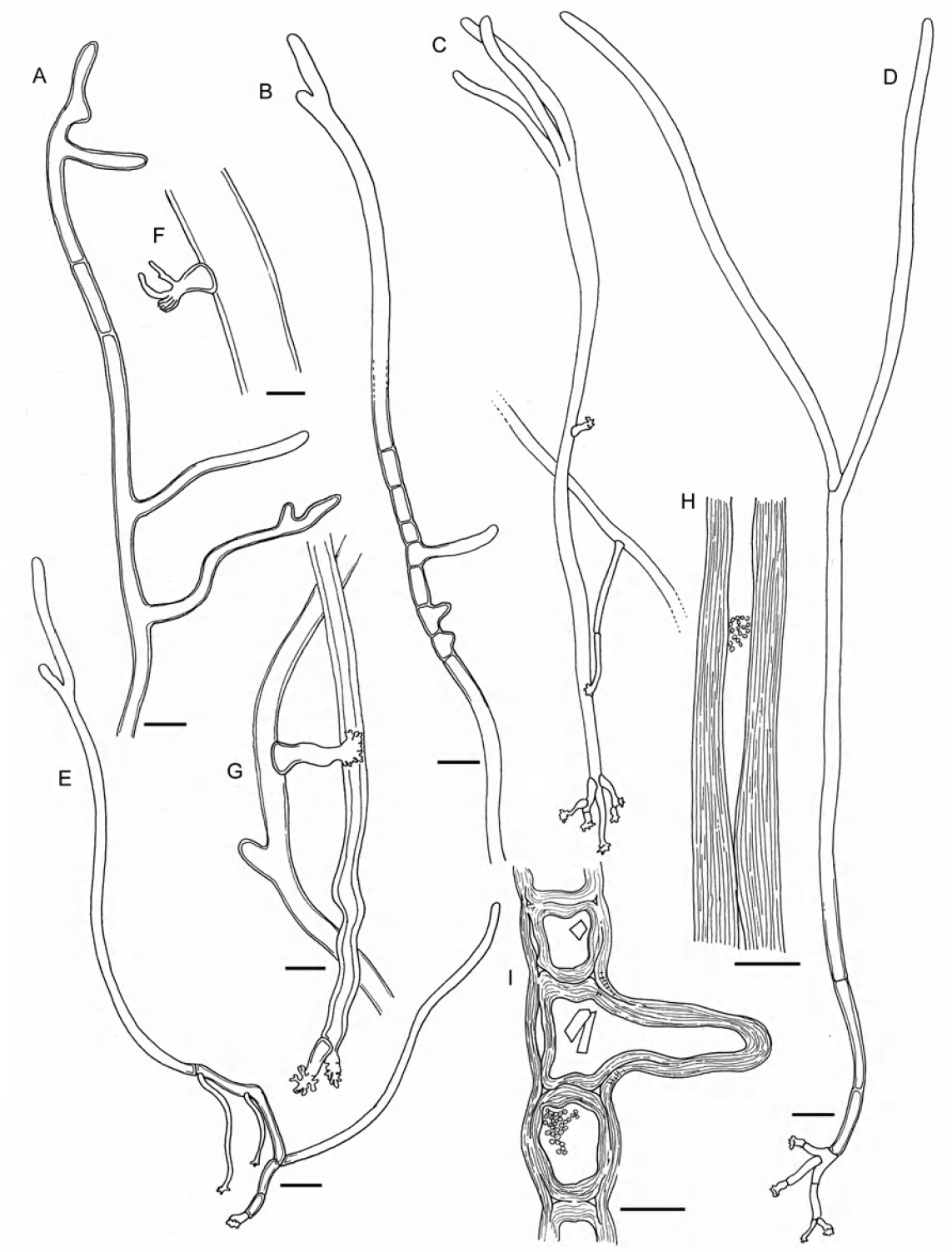


Fig. 39. *Cladophoropsis vaucheriiformis* (lectotype, S). **A-E.** Terminal branch systems and basal type-1 rhizoids; **F-G.** Type-3 tenacular cells; **H.** Detail of the very thick, lamellate cell walls; **I.** Detail of cells divided by segregative cell division with thick, double and lamellate cell walls; cells with chloroplasts and calcium oxalate crystals. Scale bars: A-E = 250 µm; F-G = 100 µm; H-I = 50 µm.

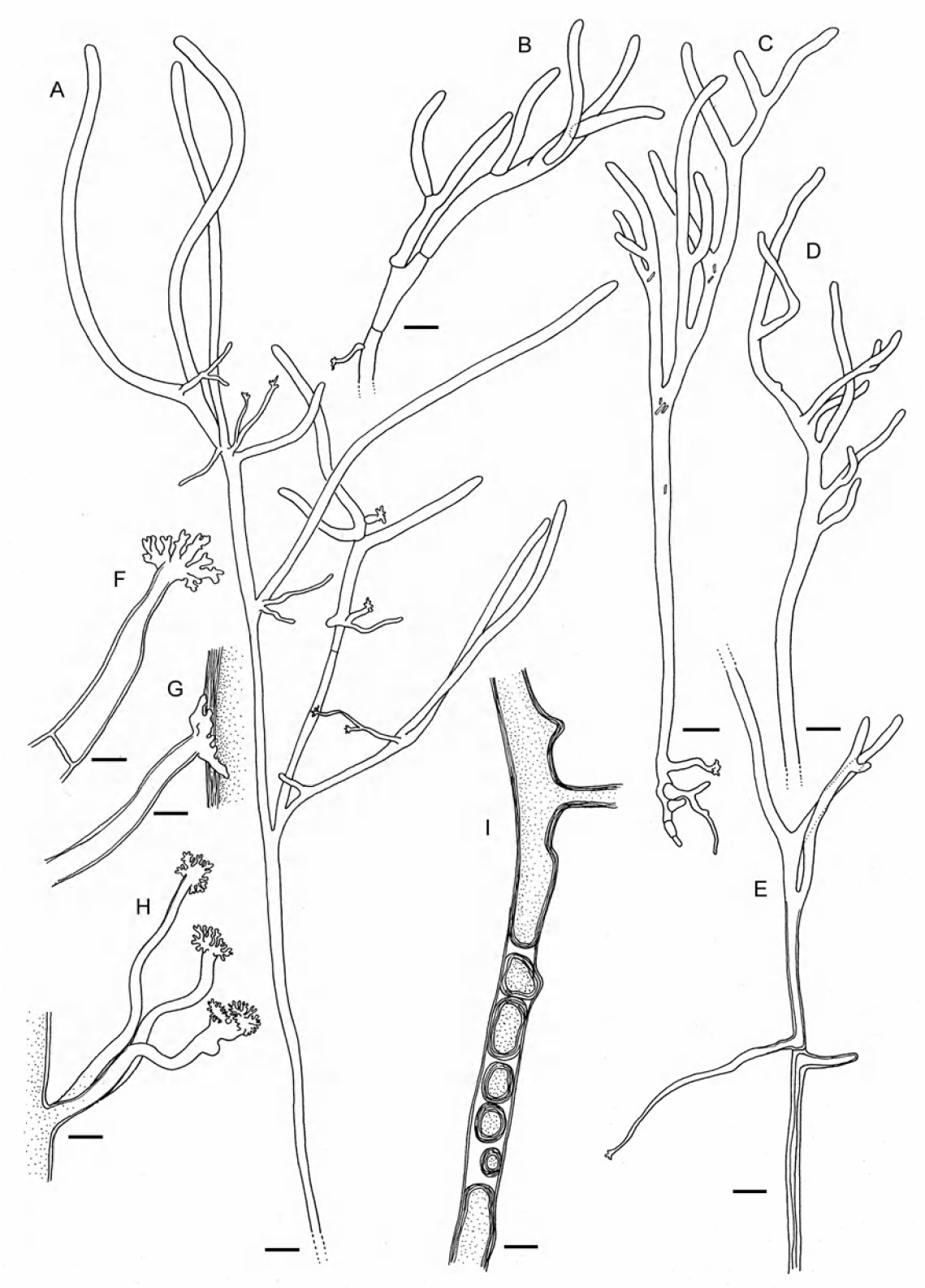


Fig. 40. *Cladophoropsis vaucheriiformis*. **A.** Branch system with numerous rhizoids developing at the base of the laterals (FL 954b); **B.** Septate terminal branch system (HEC 8724); **C.** Young thallus with aseptate branch systems and basal rhizoids (HEC 8724); **D.** Aseptate terminal branch system (FL 989); **E.** Type-2 rhizoid (FL 683); **F-H.** Hapteroidal tips of type-2 rhizoids (HEC 11135); **I.** Detail of filament dividing by segregative cell division (FL 989). Scale bars: A-E = 250 µm; F-I = 100 µm.

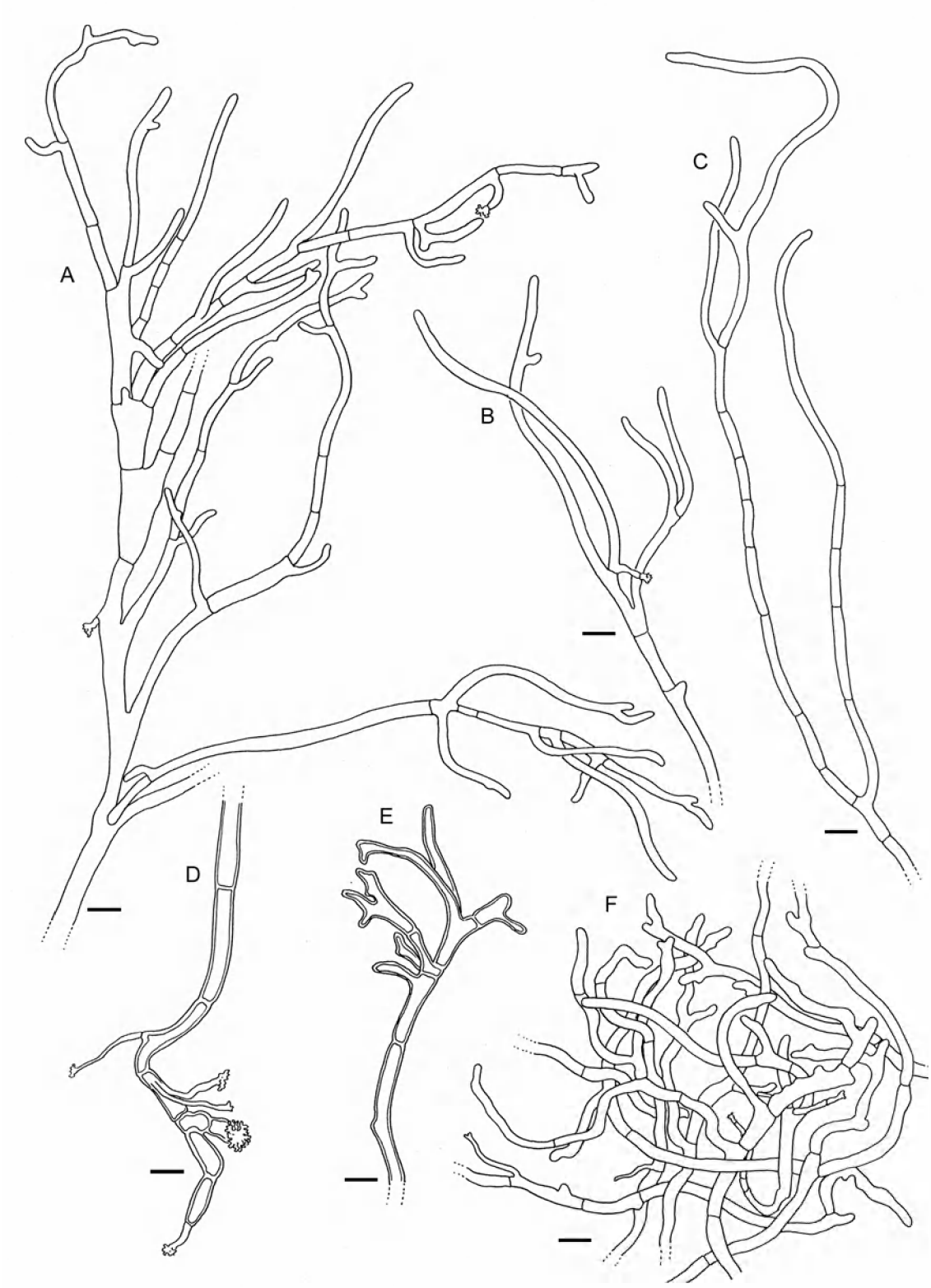


Fig. 41. *Cladophoropsis vaucheriiformis*. **A-C.** Terminal branch systems (HEC 10570); **D.** Basal type-1 rhizoids (HEC 11394); **E.** Terminal cells with thick cell walls (FL 683); **F.** Entangled filaments (FL 607). Scale bars: A-C, E-F = 250 µm; D = 100 µm.

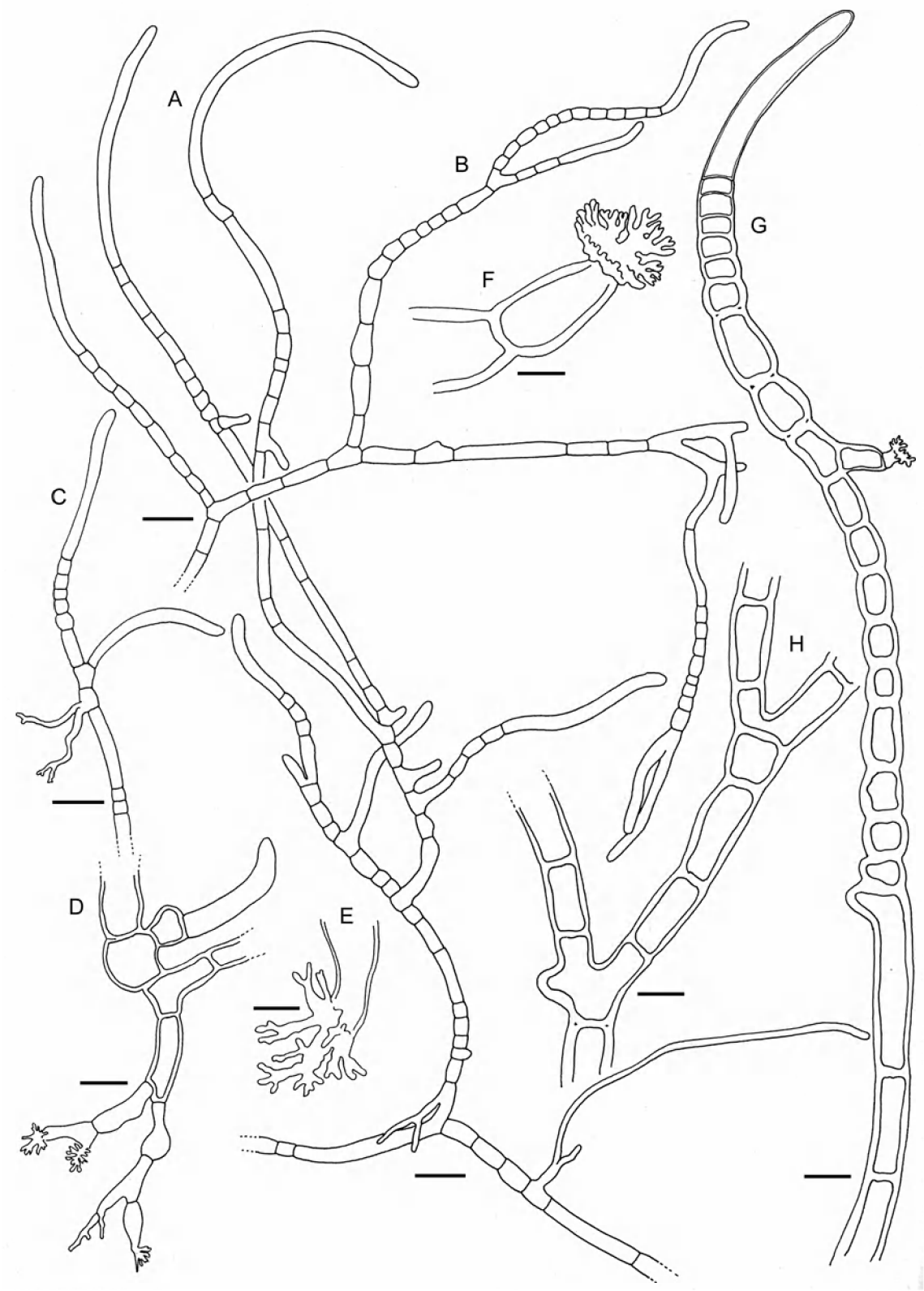


Fig. 42. *Cladophoropsis vaucheriiformis* (FL 954) **A-C.** Terminal branch systems composed of short cells; **D.** Basal type-1 rhizoids; **E.** Detail of hapteroidal tip of a basal rhizoid; **F.** Type-3 tenacular cell; **G.** Apical cell division and subsequent cell elongation in terminal filament; **H.** Pseudodichotomous branch. Scale bars: A-C = 250 µm; D, G-H = 100 µm; E-F = 25 µm.

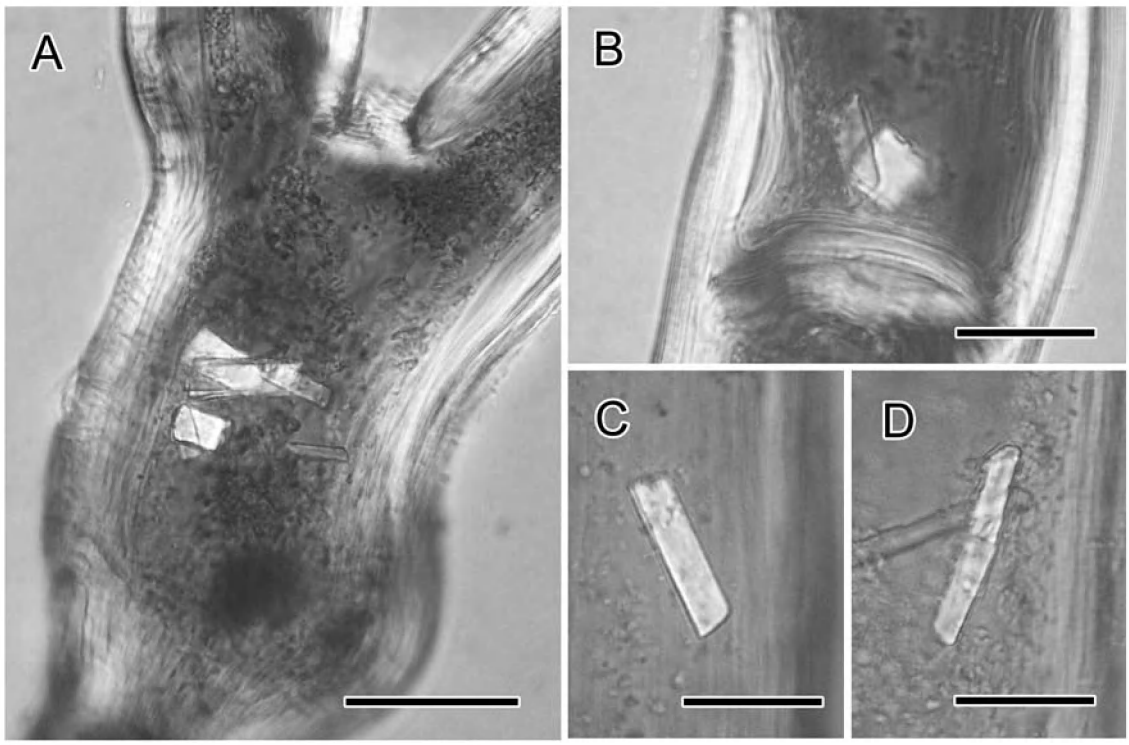


Fig. 43. *Cladophoropsis vaucheriiformis* (FL 954). **A-D.** Prismatic calcium oxalate crystalline cell inclusions in the siphonous filaments; note the extreme thick and lamellate cell walls. Scale bars = 25 µm.

7.3. Section *Rigidae* Leliaert & Coppejans (sect. nov. prov.)

The type and only species ranged in the section is *C. rigida*.

Cladophoropsis rigida (Howe) Leliaert & Coppejans, comb. nov. prov. Figs 44, 45

Siphonocladus rigidus Howe, 1905: 244, pls 13, 14 [Holotype: Key West, Florida, U.S.A., leg. Howe 1597, 30.x.1902, NY!; distributed in the Phycotheca Boreali-Americana as nr 1031 under the name *Siphonocladus tropicus*].

Cladophoropsis palauensis Trono, 1972: 47, pl. 2 [Holotype: reef flat, Iwayama Bay, Palau Island, West Caroline, Caroline Islands, leg. E.G. Meñez, Doty no. D15108, BISH! 586962].

Siphonocladus xishaensis C.F. Chang & B.M. Xia, *in* Chang *et al.*, 1975: 34, 58, pl. I: figs 2-4; text-figs 8, 9: 1-5 [Holotype: Yongxingdao, Xisha Islands, Guangdong Province, China, leg. members of the Institute of Oceanology, iii.1958, AST 58-4074, Herbarium of the Institute of Oceanology, Chinese Academy of Sciences at Qingdao].

Description:

Thallus light green, forming crisp, rigid cushions, up to 8 cm in diameter and 5 cm high, composed of coarse, branching and entangled filaments.

Cell division exclusively by segregative cell division (Fig. 44A, H). Growth by elongation of apical and intercalary cells and subsequent cell division (limited cell enlargement). The diameter of the basal cells about 0.4-2 times that of the apical cells. Distal face of the cross walls often strongly mamillose or tuberculose with elevations, 30-50 µm broad, up to 25 µm high (Figs 44J, 45B, C). Newly formed cells producing a single lateral. Cross wall formation at the base of the laterals markedly delayed, laterals in open connection with the mother cell up to 5200 µm long (l/w ratio 9). Terminal branch systems unilateral to irregular; main filaments generally pseudodichotomously branched. Newly divided cells often fail to form laterals, resulting in uniseriate portions of filaments (Fig. 44A, B, arrows). Filaments frequently becoming two or three cells wide, as a result of longitudinal or oblique cell divisions (Fig. 44A, D, arrowheads). Filaments generally branching up to the 2nd to 4th order. Angle of ramification 30°-90°.

Attachment to the substratum by type-3 tenacular cells developing from the basal cells. Structural reinforcement of the thallus by entangling of the filaments and by anastomosis of adjacent filaments by type-3 tenacular cells which are produced on the apices or laterally on intercalary, lateral and terminal cells, often in clusters of 2 to 9 (Fig. 44E, F, G, I); in average 5-28 % of the cells producing tenacular cells.

Undivided apical and lateral cells slightly sinuous, 350-900 µm in diameter, up to 12.5 mm long, l/w ratio up to 25; recently divided cells 350-1000 µm long, l/w ratio 0.6-1.7. Main filaments one to three cells wide, (350) 550-1200 µm in diameter, individual cells 450-700 µm in diameter, l/w ratio 0.4-3. Tenacular cells 80-120 µm in diameter, 85-150 µm long.

Cell walls conspicuously lamellate, 15-70 (-140) µm thick, sometimes infected with a fungus (possibly *Blodgettiomyces borneti*) forming a network of anastomosing, colourless hyphae.

Chloroplasts polygonal, 5-9 µm in diameter, forming an open parietal reticulum. Most plasts with a single pyrenoid, 2-3 µm in diameter.

Elongate prismatic calcium oxalate crystals present in a small number of cells; number of crystals per cell 1-5; crystals 3-12 µm in diameter, up to 60 µm long, l/w ratio 1-8 (Fig. 45D-F).

Ecology: epilithic in the intertidal to shallow subtidal (down to 1 m depth).

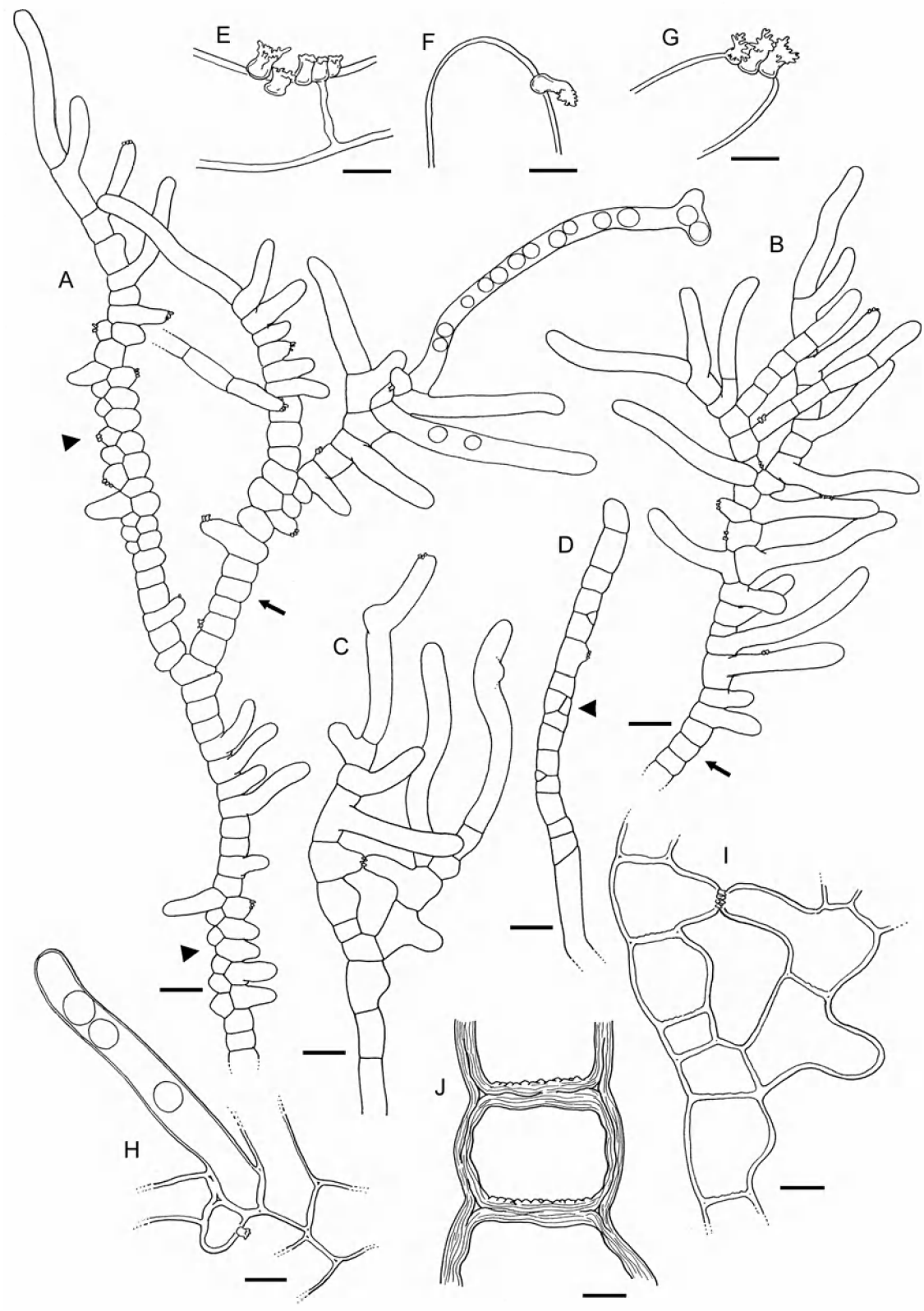


Fig. 44. *Cladophoropsis rigida* (holotype, NY). **A.** Main axes and terminal branch systems with numerous type-3 tenacular cells; apical cell dividing by segregative cell divisions; **B-C.** Terminal branch systems; **D.** Apical cell divided into numerous cells with transverse, oblique and longitudinal cross-walls; **E-G.** Type-3 tenacular cells; **H.** Detail of lateral dividing by segregative cell division; **I.** Detail of pseudodichotomous branching and two laterals anastomosing by type-3 tenacular cells; **J.** Detail of cell walls and mamillose distal sides of cross-walls. Arrows indicating uniseriate portions of filaments; arrowheads indicating filaments of two or three cells wide, owing to longitudinal or oblique cell divisions. Scale bars: A-D = 1 mm; E-G, J = 200 µm; H-I = 500 µm.

Distribution: *C. rigida* is a common species in the Caribbean Sea and the Gulf of Mexico (Taylor 1928; Littler & Littler 2000, as *S. rigidus*). Outside this region the species is also known from China (as *S. xishaensis*) and Micronesia [as *S. rigidus* from the Marshall Islands (Dawson 1956: 31, fig. 9) and as *C. palauensis* from the Caroline Islands]. The Indian Ocean records of *C. rigida* (Seychelles, in Silva *et al*. 1996, as *S. rigidus*) remain uncertain.

Specimens examined: **Carribean Sea: Bahamas.** Cat Island, infralittoral fringe, on sandy bottom, (leg. Howe 1489, 23.xi.1907, NY, PC); **Bermuda.** Agar's Island, at low water mark, (leg. Collins 2169, xii.1915, NY); **Caroline Islands**. Iwayama Bay, Palau Island, West Caroline, reef flat, (leg. Meñez, Doty No. D15108, BISH: holotype of *Cladophoropsis palauensis*); **Gulf of Mexico: U.S.A.** Key West, Florida, infralittoral fringe, on sandy bottom, (leg. Howe 1502, 28.x.1902, NY; leg. Howe 1597, 30.x.1902, NY: holotype of *Siphonocladus rigidus*; PC: isotype).

Notes: *Cladophoropsis palauensis* cannot be distinguished from *C. rigida* and apparently was described in ignorance of the latter. *S. xishaensis* only differs from *C. rigida* in its smaller habit and the absence of lamellate elevations on the cross walls according to Chang *et al*. (1975). Mamillose cross walls however are found not to be a constant character in *C. rigida*. In the young parts of the thallus mamillose elevations are absent or very inconspicuous. It therefore seems likely *S. xishaensis* represents young plants of *C. rigida* where the mamillose cross walls were not yet present or have been overlooked. We have not been able to study the type material.

Mamillose elevations on the cross walls have also been observed in other members of the Cladophorophyceae. In *Valonia cladophora* Kützing (referable to the *Cladophora* section *Aegagropila*) the cross walls form mamillose elevations similar to those in *C. rigida* (unpublished pers. obs.), while in *Valonia trabeculata* Egerod the cross walls form long branched trabeculae (Egerod 1952).

General references. As *S. rigidus*: Howe (1905: 244, pls 13, 14), Taylor (1928: 73, pl. 6, fig. 5; 1960: 114, pl. 6, fig. 7), Dawson (1956: 31, fig. 9), Littler & Littler (2000: 336, fig. on p. 337). As *S. xishaensis*: Tseng (1984: 274, pl. 136, fig. 3).

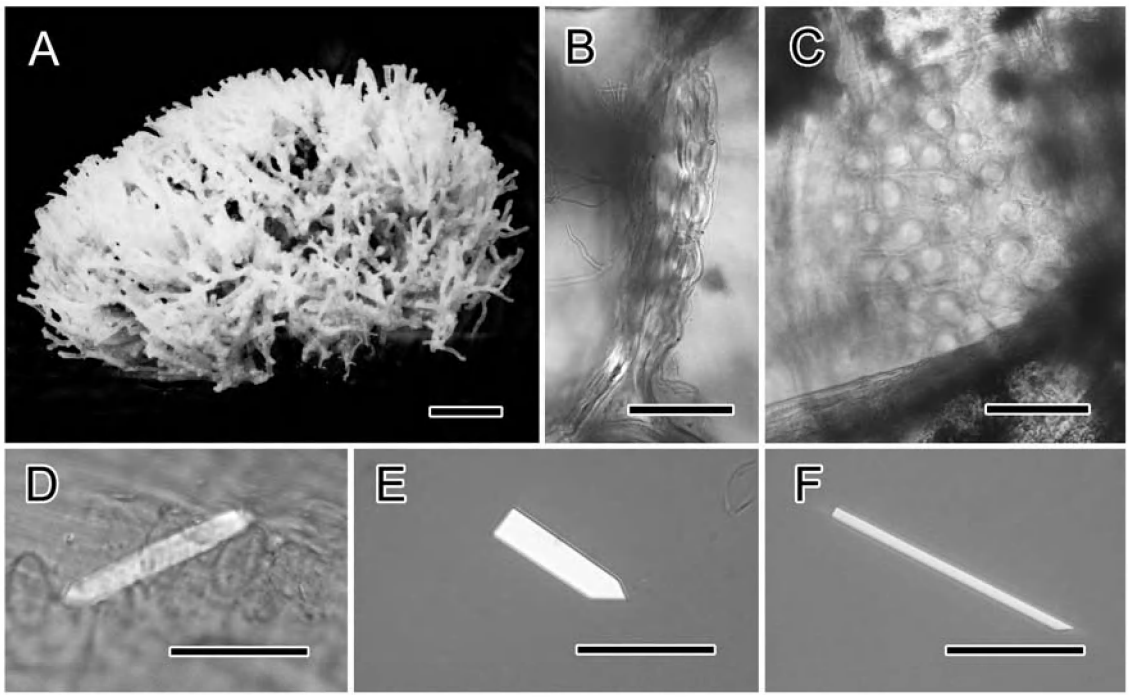


Fig. 45. *Cladophoropsis rigida* (holotype, NY). **A.** Original photograph of the holotype (deposited in NY); **B.** Longitudinal section through a filament showing the elevations of the distal side of a cross-wall; **C.** Surface view of a mamillose side of a cross-wall; **D-E.** Prismatic calcium oxalate crystals. Scale bars: A = 1 cm; B-C = 100 µm; D-E = 25 µm.

7.4. Section *Phyllodictyon* (J.E. Gray) Leliaert & Coppejans stat. nov. & comb. nov. prov.

Thallus forming erect stipitate blades, composed of densely branched filaments, attached to the substratum by branching rhizoids sprouting from the base of the stipe. Stipe unbranched or branched, with or without annular constrictions. Formation of the lamina accomplished by a repetitive process of cell division (by centripetal invagination of the cell walls), opposite formation of laterals, and cell elongation and enlargement (Fig. 46). Young thallus consisting of a unicellular stipe, dividing into two cells; generally a long basal cell and a much shorter distal cell (later becoming the basal cell of the central blade axis). The distal stipe cell elongates, re-divides and the newly formed subapical cell produces a pair of opposite laterals at its distal pole. Older branches normally producing a 2nd (sometimes a 3rd) pair of opposite laterals, under and in the same plane as the first pair. Intercalary cell division generally taking place at regular intervals from the 3rd to 7th cell under the apical cell. Structural reinforcement of the lamina accomplished by attachment of adjacent filaments by type-3 tenacular cells (infrequent in *C. mexicana*); also by type-4 tenacular cells (*C. orientalis* and *C. pulcherrima*).

Three species are ranged under this section: *C. mexicana*, *C. orientalis* and *C. pulcherrima*. The differences between the species are listed in Table 5.

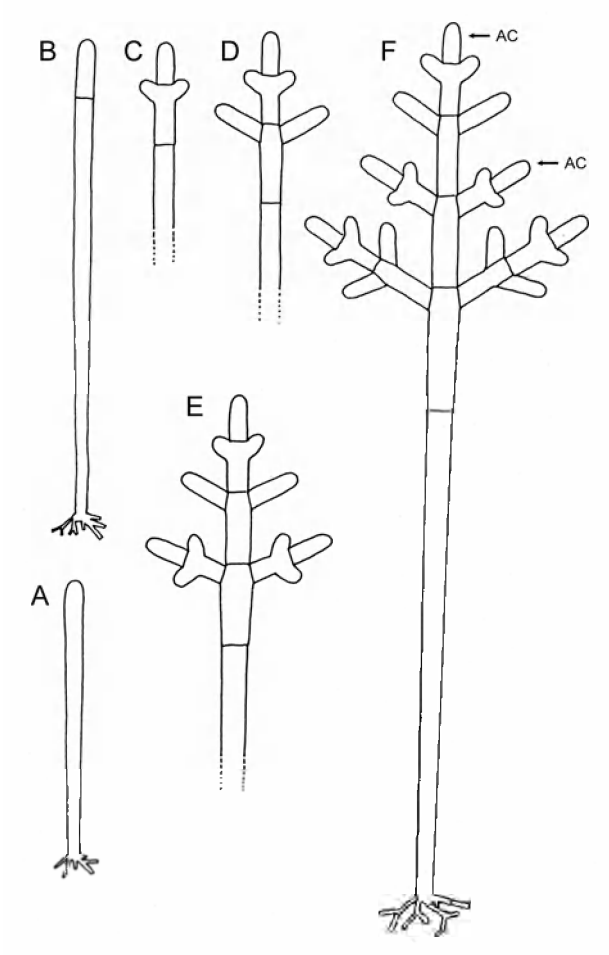


Fig. 46. Schematic representation of the initial developmental stages in the section *Phyllodictyon*. **A.** Young thallus consisting of a single stipe cell; **B.** Subapical, first division of the stipe cell by centripetal wall ingrowths; **C.** Second division, followed by the formation of an opposite pair of laterals; **D-F.** Repetitive process of apical cell division and opposite lateral formation. AC = apical cell.

Table 5. Differences between the species of the section *Phyllodictyon*.

	C. mexicana	*C. orientalis*	*C. pulcherrima*
Thallus height	up to 5 cm	up to 7 cm	up to 36 cm
Maximum number of laterals per cell	4	6	6
Tenacular cells	type-3, rare	type-3 and -4, abundant	type-3 and -4, abundant
Apical cell diameter	950-1120 µm	(70-) 90-170 (-200) µm	200-380 µm
Calcium oxalate crystals	rectangular to irregular	diamond-shaped, sometimes triangular	diamond-shaped or broad hexagonal

Cladophoropsis mexicana (Dawson) Leliaert & Coppejans, comb. nov. prov. Fig. 47

Willeella mexicana Dawson, 1950: 151, fig. 11 [Holotype: Punta Colorado, adjacent to Bahia Bodochibampo, near Guaymas, Sonora, Mexico, leg. E.Y. Dawson 1789, 16.v.1946, AHFH 3766; isotype in L! 952 078 767 as "*Boodleya erecta* Dawson"].

Description:
Thallus dark green (when dried), forming 4-5 cm high clusters of erect stipitate blades. Attachment probably by type-1 rhizoids produced at the proximal pole of the stipe cells (a number of stipe cells were found in the material, all with torn basal parts, Fig. 47A);
Stipe unbranched, blade 1-2 cm high and ca. 1 cm broad, elliptical to irregular in outline; stipe occasionally with laterally produced lenticular cells (Fig. 47B, arrowhead). Initial division of the stipe cell possibly segregative (Fig. 47B, arrow). Blade formation by apical and intercalary cell division (or centripetal invagination of the cell walls), formation of laterals and cell elongation. Each newly formed cell producing a pair of opposite, more or less equally developing laterals at its distal pole. Older cells frequently producing a second pair of laterals under the first pair, all in the same plane. Formation of cross walls at the base of the branches delayed; laterals in open connection with the mother cell up to 2500 µm long (l/w ratio 3.8). Branching up to the 2nd (occasionally 3rd) order. The diameter of the stipe cell 1-1.2 times that of the apical cells. Angle of ramification 15°-50°.
Limited reinforcement of the lamina by infrequent type-3 tenacular cells, produced at the apex of terminal cells (Fig. 47A, arrow).
Apical cells cylindrical with rounded tip, straight, 950-1120 µm in diameter, 1.8-3.2 mm long, l/w ratio 2-3. Cells of the terminal branch systems and basal cells 750-1250 µm in diameter, 2-3.5 (-4) mm long, l/w ratio 1.8-3.5. Stipe cells 1000-1250 µm in diameter; upper stipe cell ca. 2.5 mm long; basal stipe cell up to 18 mm long.
Cell walls 15-25 µm thick in the blade cells, 30-65 µm thick in the stipe cells.
Chloroplasts were not well preserved in the herbarium material and therefore their morphology could not be examined.
Calcium oxalate crystals rectangular to irregular, 8-35 (-60) µm in diameter.

Ecology: The only ecological data are those retrieved from the label of the holotype: epizoic on a sponge as drift.

Geographical distribution: The geographical distribution of *C. mexicana* seems to be restricted to the tropical eastern Pacific Ocean. The species has been recorded from Baja California, and

the Pacific coast of Mexico (Dawson 1950, type; Taylor 1945 as *C. robusta*), El Salvador (Dawson 1961) and the Pacific coast of Panama (Wysor 2002).

Specimen examined: **Pacific Ocean: Mexico.** Punta Colorado, adjacent to Bahia Bodochibampo, near Guaymas, Sonora, (leg. Dawson 1789, 16.v.1946, L 952 078 767: isotype of *Willeella mexicana*).

Notes:

Willeella mexicana was described by Dawson (1950) from nearby the type locality of *Cladophoropsis robusta* and was later placed in synonymy with the latter (as *Pseudostruvea robusta*) by Egerod (1975: 47). The holotype of *C. robusta*, however, does not correspond with its original illustration. This specimen is characterized by laterals, exclusively initiated from lenticular cells (drawings and photographs present in UC and GENT) whereas the original illustration of *C. robusta* shows opposite laterals and delayed cross wall formation (typical *Struveopsis*-type branching) (Setchell & Gardner, 1924: pl. 13: fig. 16). Thallus architecture, branching mode and cell dimensions of this specimen are in agreement with *Valoniopsis pachynema* (G. Martens) Børgesen. Setchell & Gardner could have either misinterpreted the original material, or a wrong specimen might have been indicated as type. In any case *Cladophoropsis robusta* has to be reduced to a synonym of *Valoniopsis pachynema*.

Most records of *Cladophoropsis robusta* (Taylor 1945: 51 and Dawson 1961: 404; Wysor 2002: 96, fig. 8 as *Struveopsis*) are to be regarded as misapplied names for *C. mexicana*. The only record of *C. robusta* outside the eastern Pacific (Islam 1976: Bangladesh) represents an unidentifiable *Cladophora* species.

Wysor (2002) demonstrated, on the basis of SSU sequence analyses, that *C. mexicana* (as *C. robusta*) is closely related to *Phyllodictyon pulcherrimum*. This is endorsed by the presently proposed classification.

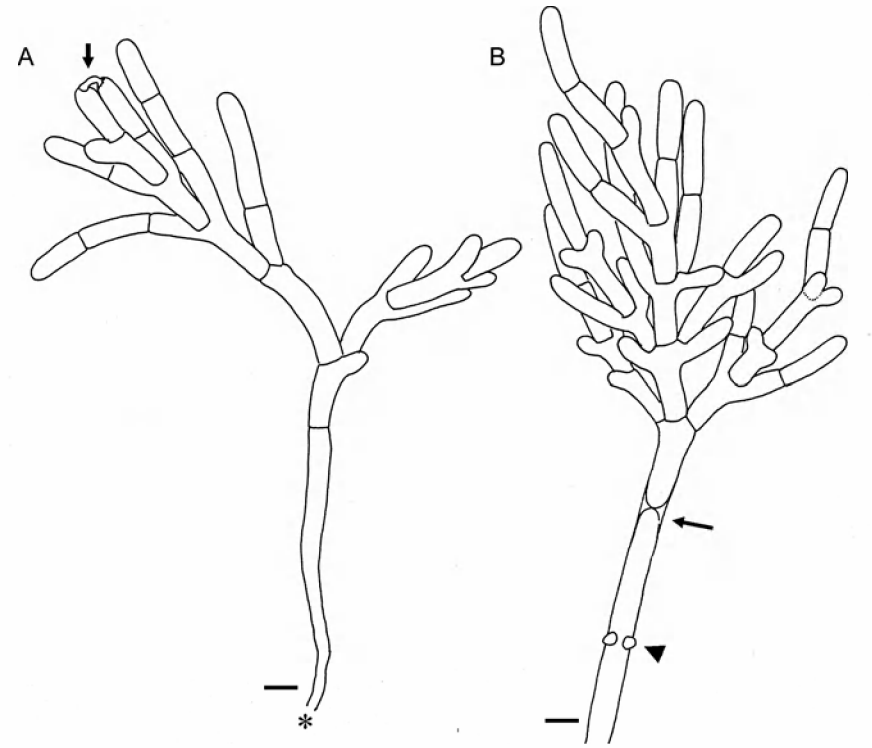


Fig. 47. *Cladophoropsis mexicana* (isotype of *Willeella mexicana*, L 952 078 767). **A.** Young stipitate thallus composed of opposite branches; infrequent anastomosis by a type-3 tenacular cell (arrow); basal attachment structures missing (asterisk); **B.** Stipitate lamina composed of opposite and flabellate branches; note the segregative mode of cell division in the stipe cell (arrow) and the small lenticular cells produced on the stipe (arrowhead). Scale bars = 1 mm.

Cladophoropsis orientalis (A. Gepp & E. Gepp) Leliaert & Coppejans, comb. nov. prov.
Figs 4A-B, 48-51

Struvea orientalis A. Gepp & E. Gepp, 1908: 167-168, pl. 22: figs 6-9 [Holotype: Amirante Islands, Seychelles; leg. J.S. Gardiner, Sealark Expedition, 9.x.1905, BM!].
Phyllodictyon orientale[3] (A. Gepp & E. Gepp) Kraft & Wynne, 1996: 139-140 ("*orientalis*").
Struvea intermedia C.F. Chang & E.Z. Xia, *in* Chang *et al.*, 1975: 43, 59-60, figs 14, 15, Pl. 1, fig. 1 [Holotype: Shidao, Xisha Islands (= Paracel Islands), South China Sea; leg. members of the Institute of Oceanology, AST 58-4264, iv.1858; type deposited in the Herbarium of the Institute of Oceanology, Chinese Academy of Sciences, Qingdao (B.M. Xia, pers. comm.)].
Phyllodictyon intermedium (C.F. Chang & E.Z. Xia) Kraft & Wynne, 1996: 139.
Struvea haterumensis Itono, 1973: 158, figs 15-20 [Holotype: Hateruma Island, at southernmost end of Ryukyu Island, Japan; leg. H. Itono 19732, 10.viii.1972; Herbarium of the Faculty of Fisheries, Kagoshima University].
Phyllodictyon haterumense[1] (Itono) Kraft & Wynne, 1996: 139 ("*haterumensis*").

Description:
Thallus light to medium green, forming erect, stipitate, delicate blades, 3-7 cm high, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe (Figs 50C, 51A). Stipes single or clustered, unbranched (unicellular) or pseudodichotomously branched (multicellular), with or without basal annular constrictions (Figs 50C, 51A). Unbranched stipe cells bearing a single lamina; branched stipes bearing numerous blades at the apical poles which later attach to one another to form a single lamina. Young blades elliptical in outline, reticulate, composed of a prominent central axis and regularly organized, opposite and flabellate branch systems, lying essentially in a single plane (Fig. 51B). Older blades elliptical, reniform or irregular in outline, up to 5 cm long and broad, lacking a percurrent primary axis but consisting of main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders; opposite and flabellate branch systems irregularly organized, lying in a single plane (Fig. 49).
Young stipe cell cylindrical; when reaching a length of 5-8 mm, the distal end of the stipe cell dividing twice, the subapical cell forming a pair of opposite laterals. Blade formation by a repetitive process of apical and intercalary cell division, formation of laterals and cell elongation. Cell division exclusively by centripetal invagination of the cell walls. Each new cell, after being cut from an apical, producing a pair of opposite, more or less equally developing laterals at its apical pole. A second pair of opposite laterals is generally formed under the first pair, from the 3rd to 5th cell under the apical cell; older cells occasionally producing a 3rd pair of laterals. Intercalary cell division generally starting from about the 3rd to 7th cell under the apical cell and taking place at regular intervals, resulting in a regular sequence of opposite and flabellate branches in mature blades (Fig. 49). Formation of cross walls at the base of newly formed laterals somewhat delayed; commonly cross walls are produced after the newly formed apical cell re-divides and forms a pair of laterals; laterals in open connection with the mother cell up to 250-500 µm long (l/w ratio 4.4). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. In mature blades, densely branched filaments resulting in a nearly closed network with small meshes, (20-) 50-500 (-1000) µm in diameter. Blade filaments branching up to the 5th (occasionally to the 7th) order. The diameter of the stipe cell 2.3-8 times that of the apical cells. Angle of ramification 30°-90°.

[3] Epithets in *Phyllodictyon* should receive the neuter ending, thus "orientale" (R. Moe, *pers. comm.*)

Reinforcement of the lamina by type-3 and -4 tenacular cells. Attachment of adjacent filaments by type-3 tenacular cells, borne singly on the tips of apical cells, or laterals in open connection with the mother cell (Figs 50A, D-G, 51C-I). In mature blades, in average 22-37 % of the apical cells producing a type-3 tenacular cell. Type-4 tenacular cells produced at the proximal poles of the basal cells of the main axes (1-5 tenacular cells per cell) and attaching to the cell below (Figs 50A-B, 51A, J-K).

Apical cells cylindrical with rounded tips, straight or slightly curved, (70-) 90-170 (-200) µm in diameter, 120-850 µm long, l/w ratio 1-5.7. Cells of the terminal branch systems cylindrical, (120-) 160-220 (-260) µm in diameter, (150-) 200-800 (-1000) µm long, l/w ratio 1.2-4. Cells of the main axis 220-700 µm in diameter, 300-3000 µm long, l/w ratio 1.5-11. Stipe cells subcylindrical 400-950 µm in diameter (slightly tapering towards the base), 1-2 cm long. Type-3 tenacular cells short to slightly elongated, sometimes rhizoidal, 32-50 µm in diameter at the base, 37-550 µm long. Type-4 tenacular cells 35-60 µm in diameter, 35-190 µm long.

Cell walls 1-2 µm thick in the ultimate branch systems, up to 10 µm thick in the basal branches and stipe cell.

Chloroplasts polygonal to round, forming a more or less open parietal reticulum, 4-6 µm in diameter, each with a single pyrenoid, ca 2 µm in diameter.

Prismatic calcium oxalate crystals present in most blade cells (except the tenacular cells); 1 to 9 per cell in the ultimate branch systems, up to 60 or more in the large basal blade cells, generally diamond-shaped, sometimes triangular, 20-65 µm long, up to 45 µm broad (Fig. 4A-B).

Ecology: *C. orientalis* grows in shallow to deep subtidal biotopes (0.5 to 55 m depth), epilithic on horizontal to overhanging rocky substrates, or epiphytic on stems of seagrasses such as *Thalassodendron ciliatum*.

Geographical distribution: *C. orientalis* possibly has a disjunct tropical Indo-West Pacific distribution. The species has been reported from several Indian Ocean islands: Amirante Islands (type-locality), Aldabra Islands (Rhyne & H. Robinson, 1968: 469), the Seychelles and Maledives (this paper). In the West Pacific Ocean, *C. orientalis* has been recorded from the Xisha Islands in the South China Sea (Chang *et al.* 1975, Tseng 1984, as *Struvea intermedia*), Susaki, Japan (Segawa 1938: 136), the Ryukyu Islands (Itono 1973, as *Struvea haterumensis*) and the Lord Howe Island (Millar & Kraft 1994, Kraft & Wynne 1996: 139 and Kraft 2000: 584, as *Phyllodictyon haterumense*).

Table 6. Comparison of the range of cell dimensions and mesh size of *C. orientalis* with the original descriptions of *Struvea intermedia* and *S. haterumensis*.

	C. orientalis	*S. intermedia*	*S. haterumensis*
Apical cell diameter	70-200 µm	80-160 µm	90-120 µm
Main axes diameter	220-700 µm	330-580 µm	220-400 µm
Stipe cell diameter	400-950 µm	350-580	220-560
Mesh size	90-850 µm	200-650 µm	150-1500 µm

Specimens examined: **Indian Ocean: Maledives.** Bi Ya Doo Island, (leg. Coppejans, 28.iii.1986, HEC 6124; 1.iv.1986, HEC 6154; 8.iv.1986, HEC 6173); **Seychelles.** Amirante Islands, 46 m deep, (leg. Stanley Gardiner, Sealark Expedition s.n., 9.x.1905, BM 563700: holotype of *Struvea orientalis*); Bird Island, dredged, 45-55 m deep, (leg. Coppejans *et al.*, 20.xii.1992, SEY 246 & SEY 301); Desroches Island, between *Thalassodendron*, (leg. Coppejans *et al.*, 30.xii.1992, SEY 556); Ile Desnoeufs, shallow subtidal reef platform, 3-5 m deep, (leg. Coppejans *et al.*, 2.i.1993, SEY 657); Ile Desnoeufs, subtidal, 11-13 m deep, (leg. Coppejans *et al.*, 2.i.1993, SEY 639); Plate

Island, subtidal, 20 m deep, epiphytic on *Thalassodendron ciliatum*, (leg. Coppejans *et al.*, 7.i.1993, SEY 775); Poivre Island, subtidal, 30-40 m deep, (leg. Coppejans *et al.*, 29.xii.1992, SEY 521); **Yemen.** Bindar Fikhah (Bandar Faka), N coast of Socotra, (leg. Leliaert, SOC 195c).

Fig. 48. *Cladophoropsis orientalis* (holotype of *Struvea orientalis*, BM). Scale bar = 1cm.

Notes:
Cladophoropsis orientalis closely resembles *C. pulcherrima*. Both species are characterized by flabellate branching, triangular or diamond shaped crystals, and type-4 tenacular cells. *C. orientalis* only differs from *C. pulcherrima* by the smaller cell diameter, the cells being about twice as narrow. Furthermore both species are geographically separated: *C. pulcherrima* is restricted to the tropical Atlantic ocean, while *C. orientalis* has an Indo-Pacific distribution. Diamond shaped crystals are also typical for *C. gardineri*, but this species can easily be distinguished by the lack of flabellate branches and the lack of type-4 tenacular cells.
According to Chang *et al.* (1975) *Struvea intermedia* closely resembles *C. orientalis* and only differs from it by the larger meshes. Mesh size however is very variable in *C. orientalis*, and related to the age of the lamina (older blades generally having smaller meshes). The mesh size described for *S. intermedia* falls within the range of *C. orientalis* (Table 6) and there are no other grounds for independent recognition of the species. The type specimen of *Struvea haterumensis* consists of a small plants (3-6 mm high) which can be regarded as a young *C. orientalis* thalli.

Type-4 tenacular cells or similar structures are also present in *Apjohnia laetevirens*, *Ernodesmis verticillata* and some *Cladophora* species (e.g. *C. rugulosa*, *C. prolifera* and *C. wrightiana*). The structures in *Ernodesmis* are apparently not homologous with those in *Cladophoropsis* (Leliaert *et al.* 2003). The tenacular cells in *Apjohnia* differ from those in

Cladophoropsis by growing downward into the cross wall of the cell below (in those *C. orientalis* and *C. pulcherrima* the tenacular cells attach to the outer surface of the cell below). In the *Cladophora* species presenting these structures are rhizoidal and not separated by a wall from the parent cell (Papenfuss & Chihara 1975, Leliaert & Coppejans 2003).

General references. As *Struvea orientalis*: A. Gepp & E. Gepp (1909: 377-378, Pl. 47: figs 6-9); Segawa (1938: 136-138, fig. 4). As *S. haterumensis*: Itono (1973: 158, figs 15-20). As *Phyllodictyon haterumense*: Kraft (2000: 584, fig. 29E-I).

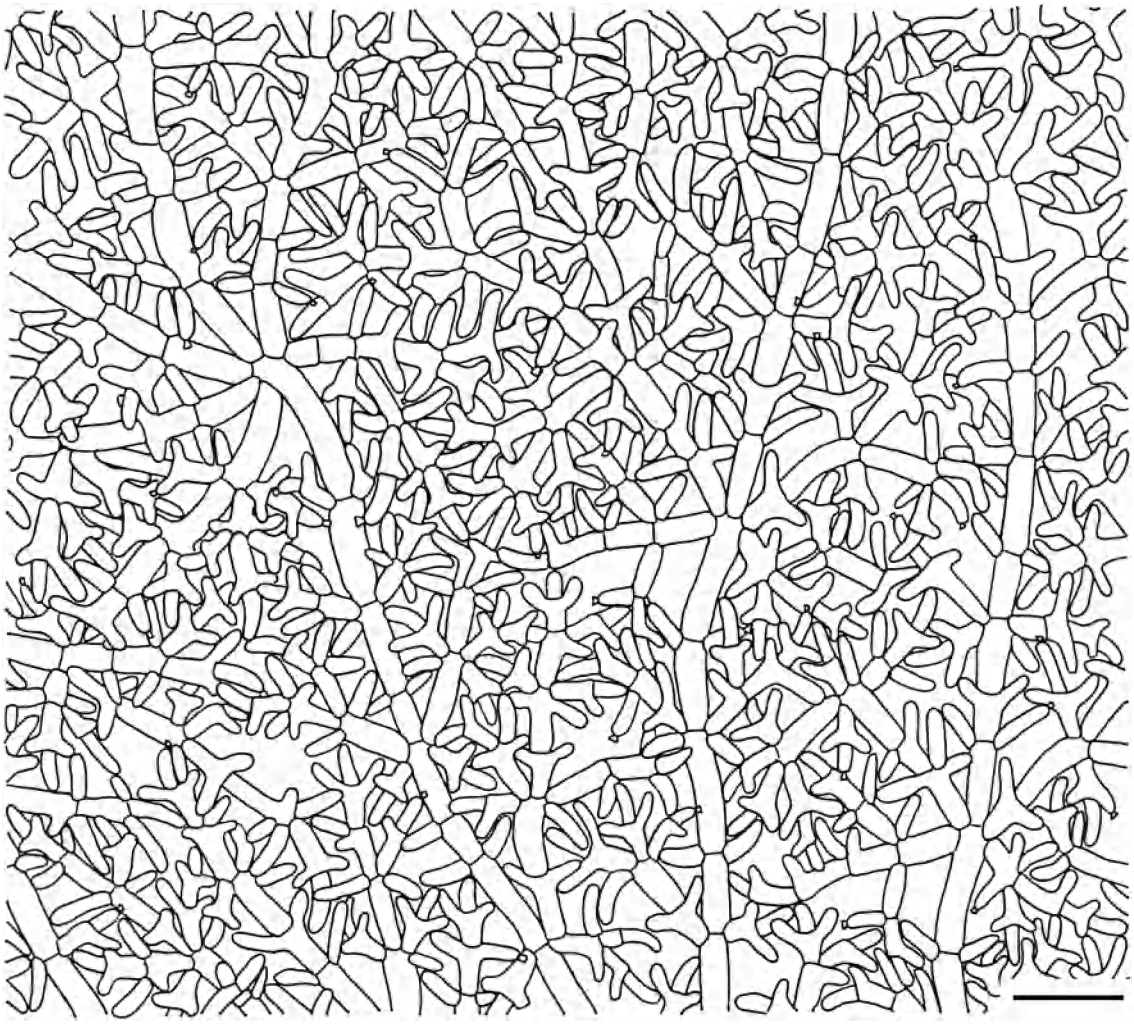


Fig. 49. *Cladophoropsis orientalis* (holotype of *Struvea orientalis*, BM). Portion of mature lamina consisting of main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders. Scale bar = 1 mm.

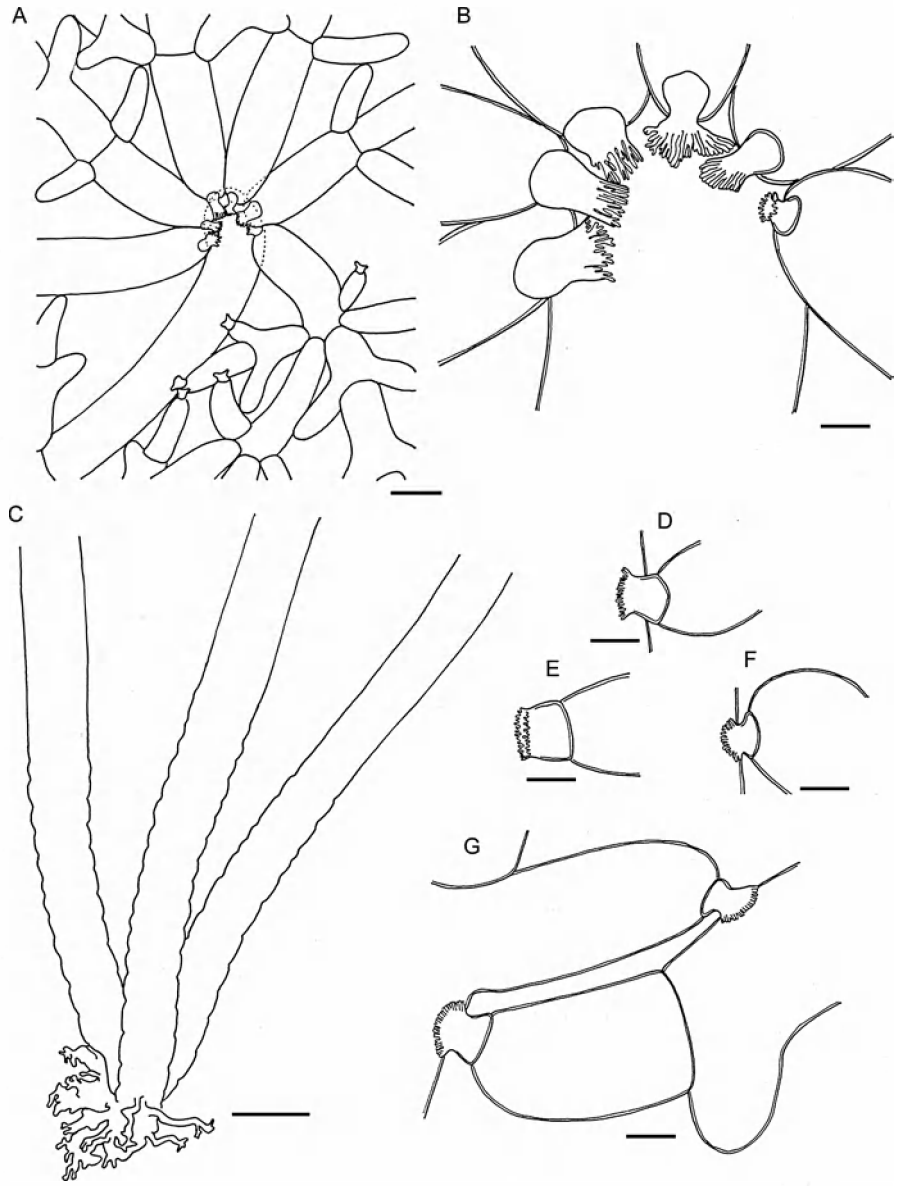
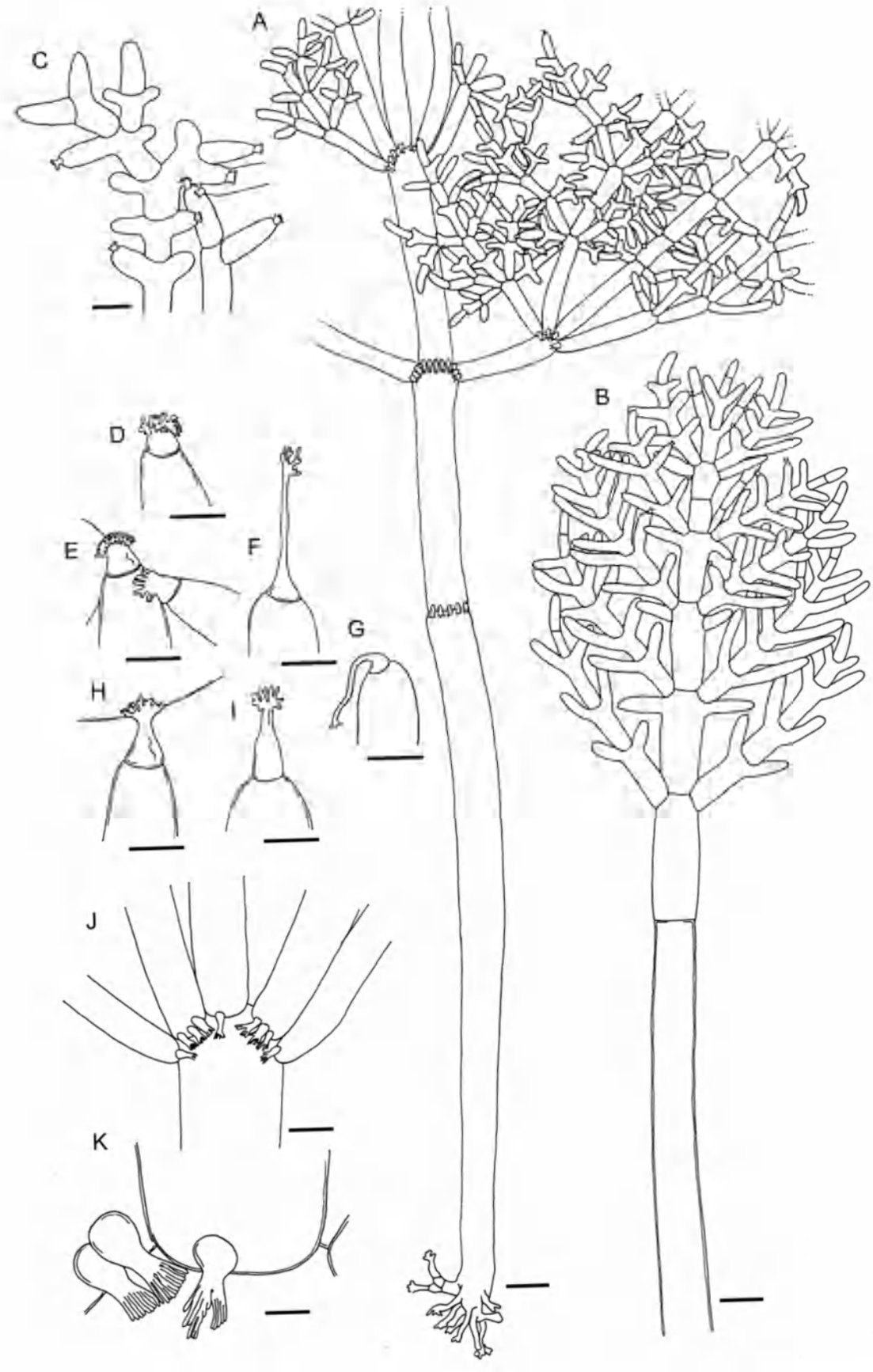


Fig. 50. *Cladophoropsis orientalis* (holotype of *Struvea orientalis*, BM). **A.** Flabellate branching in the main axes; type-4 tenacular cells produced at the proximal poles of the cells and attaching to the cell below; type-3 tenacular produced at the tips of apical cells; **B.** Detail of type-4 tenacular cells; **C.** Proximal pole of the stipe with annular constrictions and producing type-1 rhizoids; **D-G.** Type-3 tenacular cells. Scale bars: A-B = 200 μm; C = 1 mm; D-G = 50 μm.

→ **Fig. 51.** *Cladophoropsis orientalis*. **A.** Cylindrical stipe cell lacking annular constrictions; basal branches of the lamina with type-4 tenacular cells; **B.** Young lamina composed mainly of opposite branches; some cells producing a second pair of laterals; type-4 tenacular cells are not yet developed; **C.** Terminal branches with delayed basal cross-wall formation and type-3 tenacular cells; **D-I.** Variation of type-3 tenacular cells; **J.** Flabellate basal branches producing type-4 tenacular cells; **K.** Detail of type-4 tenacular cells. Scale bars: A-B = 500 μm; C, J = 200 μm; D-I = 100 μm; K = 50 μm.


A
B
C
D
E
F
G
H
I
J
K

Cladophoropsis pulcherrima (J.E. Gray) Leliaert & Coppejans, comb. nov. prov.
Figs 5C-D, 52-55

Phyllodictyon pulcherrimum J.E. Gray, 1866: 70 [Holotype: Gulf of Mexico; leg. A. Menzies 1802, BM!].

Struvea pulcherrima (J.E. Gray) G. Murray & Boodle, 1888b: 281.

Struvea ramosa Dickie 1874: 316 [Lectotype: Bermuda, from 31 fathoms (ca. 57 m depth); leg. Moseley s.n., Challenger Expedition, Herbarium Dickie, BM!. Three specimens, all collected by Mosely from Bermuda are present in BM, the largest one is here indicated as lectotype].

Struvea anastomosans (Harvey) Piccone & Grunow ex Piccone var. *canariensis* Piccone & Grunow, *in* Piccone, 1884b: 20, figs 1, 2 [Lectotype: Arrecife, Lanzarote, Canary Islands, collector unknown, PAD (according to Prud'homme van Reine *et al.* 1994: 112)].

Microdictyon curtissiae Taylor, 1955: 69, figs 1-8, pl. 1.: fig. 2; pl. III [Holotype: south east coast of Florida, USA, herbarium of Mrs. F.A. Curtiss, collected before 1898. The material should be in US but apparently is missing (M. Wynne, pers. comm.). A small portion of the holotype is present in MICH! under the number Taylor 22712, together with Taylor's original notes, photographs and drawing).

Description:

Thallus medium to dark green (when dried), forming erect stipitate blades, up to 36 cm high (Fig. 52), attached to the substratum by branched, multicellular rhizoids arising from the basal pole of the stipe. Stipes single or clustered, unbranched or pseudodichotomously branched, with conspicuous basal annular constrictions (Fig. 55 B). Young blades elliptical in outline, reticulate, composed of a conspicuous central axis and regularly organized, opposite and flabellate branch systems, lying essentially in a single plane. Mature blades elliptic to irregular in outline, up to 30 cm long and 15 (-25) cm broad, lacking a percurrent primary axis and consisting of main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders (Fig. 53).

Young stipe cell cylindrical; when reaching a length of 10-18 mm, the distal end dividing twice by CI, the subapical cell producing a pair of opposite laterals. These first laterals and the central cell generally elongating extremely and initially each producing a separate blade (a large central blade and two smaller lateral blades); these three blades later attaching to one another to form a single one. Blade formation by a repetitive process of apical and intercalary cell division, formation of laterals and cell elongation. Cell division exclusively by centripetal invagination of the cell walls. Each new cell, after being cut off from an apical cell, producing a pair of opposite, more or less equally developing laterals at its apical pole. Later (commonly from the 3rd to 5th under the apical cell onwards) a second pair of opposite laterals is generally formed under the first pair, resulting in flabellate branches; older cells occasionally producing a 3rd pair (Figs 53, 54H). Intercalary cell division generally starting from the 3rd to 5th cell under the apical cell and taking place at regular intervals, resulting in a regular sequence of flabellate and opposite branches in mature blades (Fig. 53). Formation of cross walls at the base of the laterals somewhat delayed; commonly, cross walls are formed after the newly formed apical (or intercalary) cell re-divides and forms a new pair of laterals; laterals in open connection with the mother cell up to 1600 µm long (l/w ratio 6). Older branches laterally inserted with a steeply inclined cross wall cutting them off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. In mature blades, densely branched filaments resulting in a dense network with small meshes, 90-550 µm in diameter. Blade filaments branching up to the 5th order. The diameter of the stipe cell 2.3-6 times that of the apical cells. Angle of ramification 20°-90°.

Reinforcement of the lamina by tenacular cells type-3 and -4. Attachment of adjacent filaments by type-3 tenacular cells, borne singly (rarely in pairs) on the tips of apical cells or laterals in open connection with the mother cell (Figs 54C-E, 55D-G). In mature blades, in average 44-72 % of the apical cells producing a type-3 tenacular cell. Type-4 tenacular cells produced at the proximal poles of the basal cells of the main axes (2-5 tenacular cells per cell) and attaching to the cell below (Figs 54A-B, H, 55H-I).
Zoidangia are transformed cells of terminal branch systems with conical projections on the lateral side of the cell (Fig. 54F-G).
Apical cells cylindrical with rounded tips, straight or slightly curved, 200-380 µm in diameter, 200-2000 µm long, l/w ratio 1-5.7. Cells of terminal branch systems cylindrical, 240-390 µm in diameter, 550-940 µm long, l/w ratio 1.8-3.7. Cells of the main axis cylindrical, 320-900 µm in diameter, 650-4700 µm long, l/w ratio 1.5-10. Stipe cells subcylindrical, 900-1250 µm in diameter in the middle, slightly tapering towards the base to 800-950 µm, 1-6 cm long. Type-3 tenacular cells short to elongated and narrow, 30-114 µm in diameter, 30-95 µm long; type-4 tenacular cells 65-86 µm in diameter, 150-195 µm long.
Cell walls 2-3 µm thick in ultimate branch systems, up to10-16 µm thick in the basal branches and stipe (occasionally up to 60 µm thick in the proximal part of the stipe cell).
Chloroplasts polygonal or round, forming an open to more or less closed parietal reticulum, 3-6 µm in diameter, each chloroplast with a single pyrenoid, ca. 2-3 µm in diameter.
Prismatic calcium oxalate crystals present in most cells of the lamina (except the tenacular cells), 1-20 per cell in the ultimate branch systems, up to 100 or more in the large basal blade cells, generally diamond-shaped or broad hexagonal, 30-65 µm long, up to 45 µm broad (Fig. 5C-D).

Ecology: *C. pulcherrima* is an exclusively deep-water species, growing between 21-100 m depth, epilithic.

Geographical distribution: *C. pulcherrima* is a relatively rarely collected but widely distributed species in the (sub)tropical western Atlantic [ranging from North Carolina (Humm & Cerame-Vivas 1964, Schneider & Searles 1991); Gulf of Mexico (Taylor 1928, Dawes 1974); Caribbean Sea (Taylor 1960, Littler & Littler 2000); Bermuda (Taylor 1960, as *S. ramosa*)], the Canary Islands (type locality of *Struvea anastomosans* var. *canariensis*), the Cape Verde Islands and Macaronesia (this paper). The records from the Gulf of California, Mexico (Dawson 1966), the Philippines (von Westerhagen 1974) and Kenya (Isaac 1967) remain doubtful. The Seychelles record from Coppejans *et al.* (1994: 182) is referable to *C. gardineri*, while the Maldives and Seychelles records from Titlyanova & Butorin (1978) are most probably misapplied names for *C. orientalis*.

Specimens examined: **Atlantic Ocean: Bermuda.** unknown locality, (leg. Moseley, Challenger Expedition s.n., herbarium Dickie, BM 563707; syntype of *Struvea ramosa*); unknown locality, subtidal, 57 m deep, (leg. Moseley, Challenger Expedition s.n., herbarium Dickie, BM 563708; syntype of *S. ramosa*); unknown locality, (leg. Moseley, Challenger Expedition s.n., herbarium Dickie, BM 563706; lectotype of *S. ramosa*); **Canary Islands.** Gran Tarajal, Fuerteventura, dredged, 45-80 m deep, (leg. ? 234, 26.viii.1977, L 477098); Pt. Lantaill, E of Gran Tarajal, Fuerteventura, dredged, (leg. ? 145, 27.viii.1977, L 485047); **Cape Verde Islands.** NW of São Vicente, subtidal, 45-50 m deep, (CANCAP expedition 3021, 21.vi.1982, L 997 063 421); NW of São Vicente, subtidal, 54-62 m deep, (CANCAP expedition 7749, 22.vi.1982, L 988 111 065); S of São Vicente, subtidal, 50-60 m deep, (CANCAP expedition 7403, 19.vi.1982, L 997 062 499); SE of Cima, subtidal, 30-90 m deep, (CANCAP expedition 8986, 24.viii.1986, L 997 063 044); **Macaronesia.** S of Lanzarote, subtidal, 35-70 m deep, (CANCAP expedition 2567, 14.v.1980, L 997 063 261); S of Lanzarote, subtidal, 82 m deep, (CANCAP expedition 3021, 16.v.1980, L 986 324 808); SE of Lanzarote, subtidal, 41-50 m deep, (CANCAP expedition 2941, 20.v.1980, L 997 063 309); SE of Lanzarote, subtidal, 42-60 m deep, (CANCAP expedition 3021, 20.v.1980, L 997 063 325); **Carribean Sea: Puerto Rico.** Guanica Harbor, in shallow water, in *Rhizophora* association, (leg. Howe 7031, 23.vi.1915, NY); Playa de Guanica, in shallow water, (leg. Howe 7228, 29.vi.1915, NY); **Gulf of Mexico: U.S.A.** SE coast of Florida, (leg. Curtiss s.n., before 1898, Herb. Taylor no. 22712, MICH; part of the holotype of *Microdictyon curtissiae* Taylor);

Jupiter Inlet, Florida, (leg. Hall s.n., NY); unknown locality, (leg. Menzies s.n., 1802, BM 563705; holotype of *Phyllodictyon pulcherrimum*).

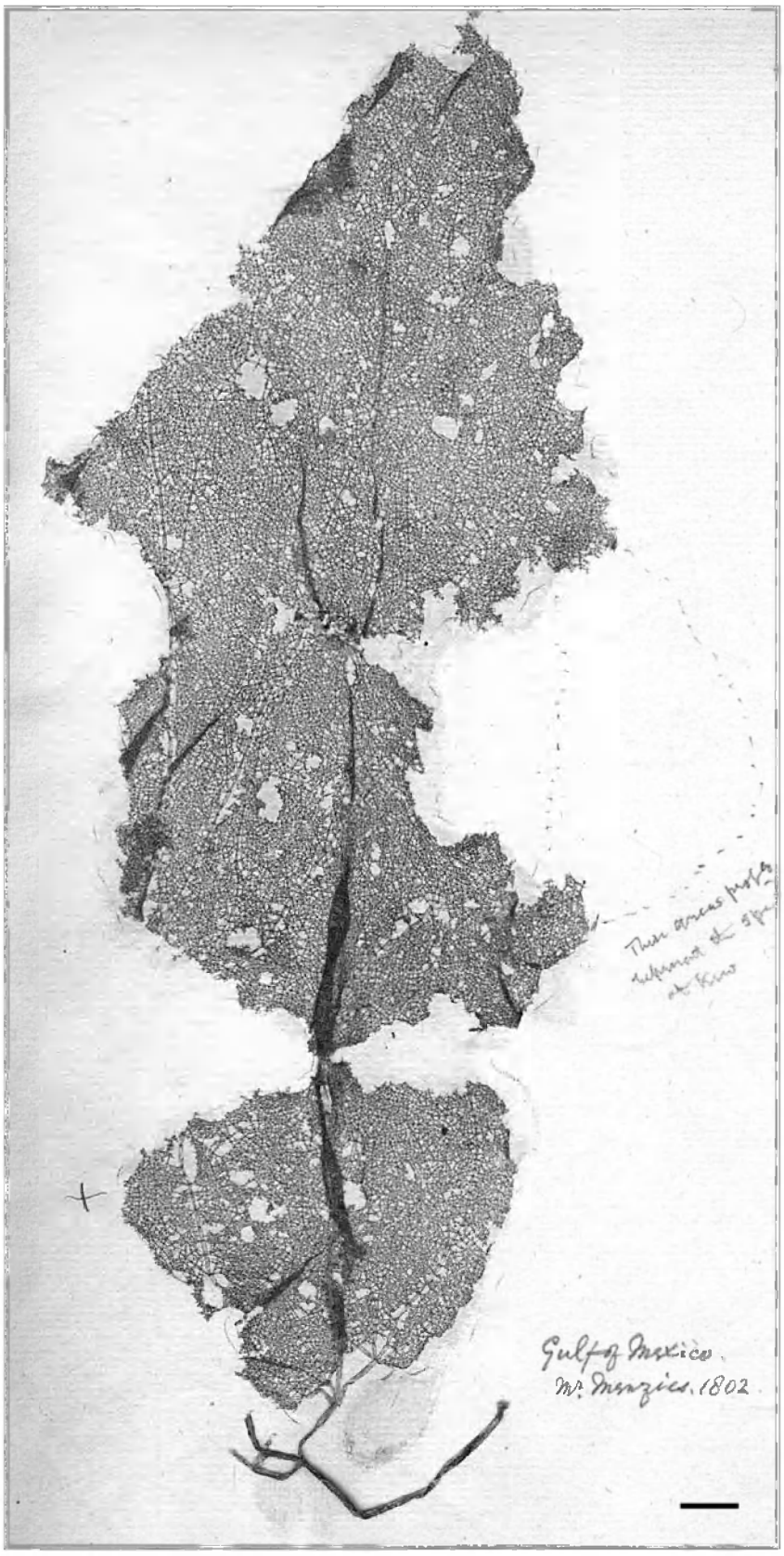


Fig. 52. *Cladophoropsis pulcherrima* (holotype of *Phyllodictyon pulcherrimum*, BM). Scale bar = 1 cm.

Notes:
Phyllodictyon pulcherrimum is the type and only species described by Gray (1866: 70) in his new genus *Phyllodictyon*. The species was very soon transferred to *Struvea* by Murray & Boodle (1888b: 281), and recently returned to *Phyllodictyon* by Kraft & Wynne (1996: 139) on the basis of mode of cell division which takes place exclusively by CI.

Struvea ramosa has been distinguished from *C. pulcherrima* by the formation of three separate blades borne on the end of a distally branched (trifurcate) stipe, while in *C. pulcherrima* the blades are joined to form a single lamina. Schneider & Searles (1991: 81) demonstrated that thalli in the Carolinas showed both conditions with intermediates between both types, and reduced *S. ramosa* to a synonym of *Struvea pulcherrima*. The type material of *S. ramosa* consists of eight plants showing this morphological range: young plants with three separate blades and older thalli with fused blades. The holotype of *C. pulcherrima* consists of a very large plant with a single blade of 25 cm high.

Struvea anastomosans var. *canariensis* (from the Canary Islands) was reduced to a synonym of *Struvea ramosa* (until then only known from the Caribbean) by Murray & Boodle (1888b: 266-267) who made a thorough comparison of specimens from both localities. The synonymy has been accepted by Børgesen (1925: 72-73) and later authors.

Microdictyon curtissiae was described as a netlike blade (7 cm long and 3.5 cm broad) composed of branched and anastomosing filaments in a single plane. Branching pattern is regularly opposite and flabellate, and anastomosis is accomplished by means of type-3 tenacular cells (Taylor 1955). Examination of the type material shows that the cells contain diamond-shaped crystals, similar to those present in *C. pulcherrima*. This type of crystals does not occur in the genus *Microdictyon*, nor do type-3 tenacular cells. Since all characters and cell dimensions of *M. curtissiae* (except for the apparently absence of a stipe) fall within the limits of *P. pulcherrimum*, this species most likely represents a portion of the lamina of the latter. A specimen identified as *M. curtissiae* by Littler & Littler (US! 24011) is referable to the *montagnei* phenodeme of the *C. composita* complex (see there).

General references. As *Phyllodictyon pulcherrimum*: Kraft & Wynne (1996: 131, 134-135, Figs 26-28). As *Struvea pulcherrima*: Murray & Boodle (1888b: 265-282, Pl. 16: fig. 4); Taylor (1960: 123); Dawes (1974: 92; 1981: 125, fig. 5-17); Schneider & Searles (1991: 80-81, fig. 70). As *S. ramosa*: Murray & Boodle (1888b: 265-282, Pl. 16: fig. 3); Taylor (1942: 21).

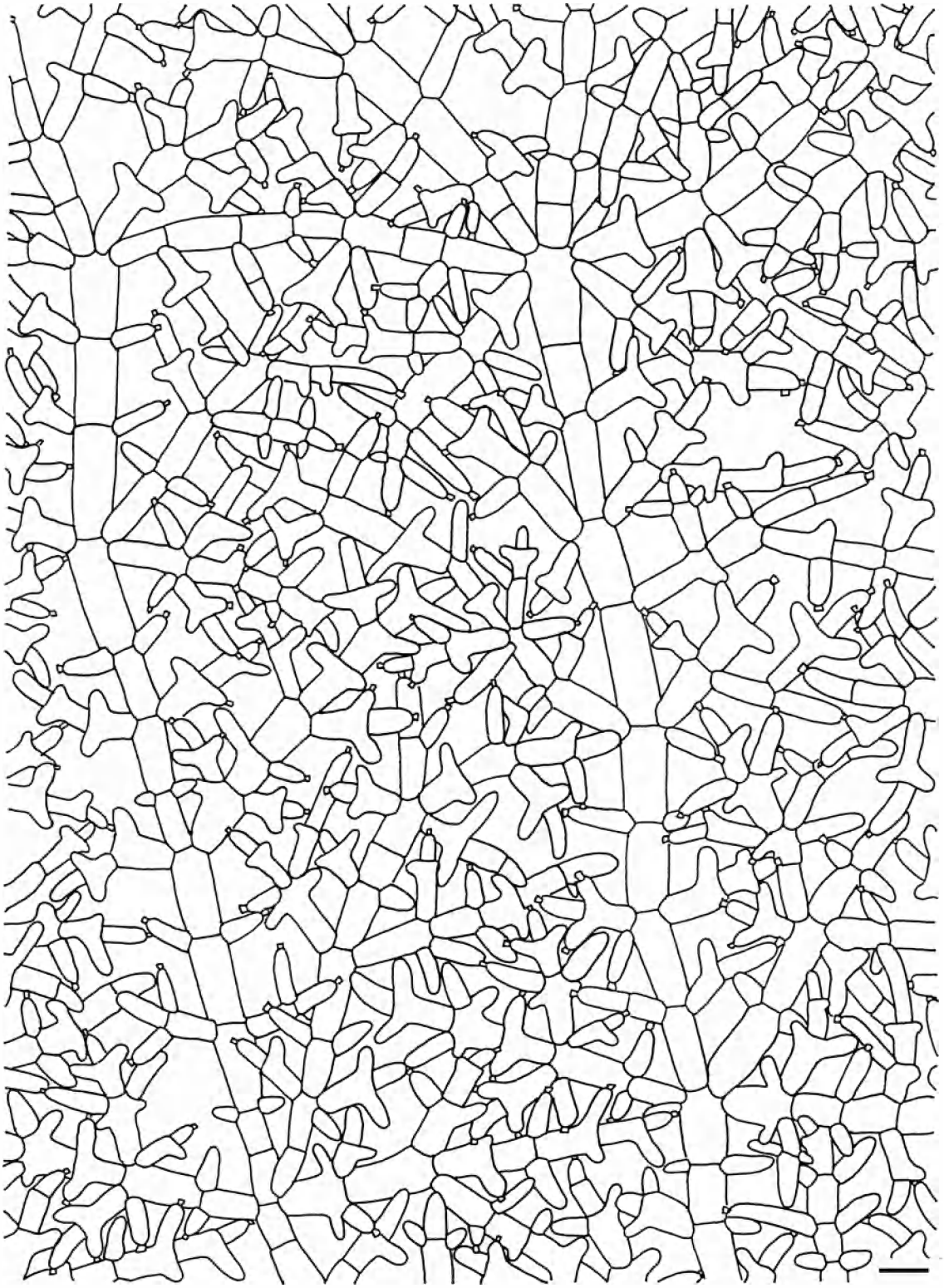


Fig. 53. *Cladophoropsis pulcherrima* (holotype of *Phyllodictyon pulcherrimum*, BM). Portion of mature lamina consisting of main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders. Scale bar = 500 μm.

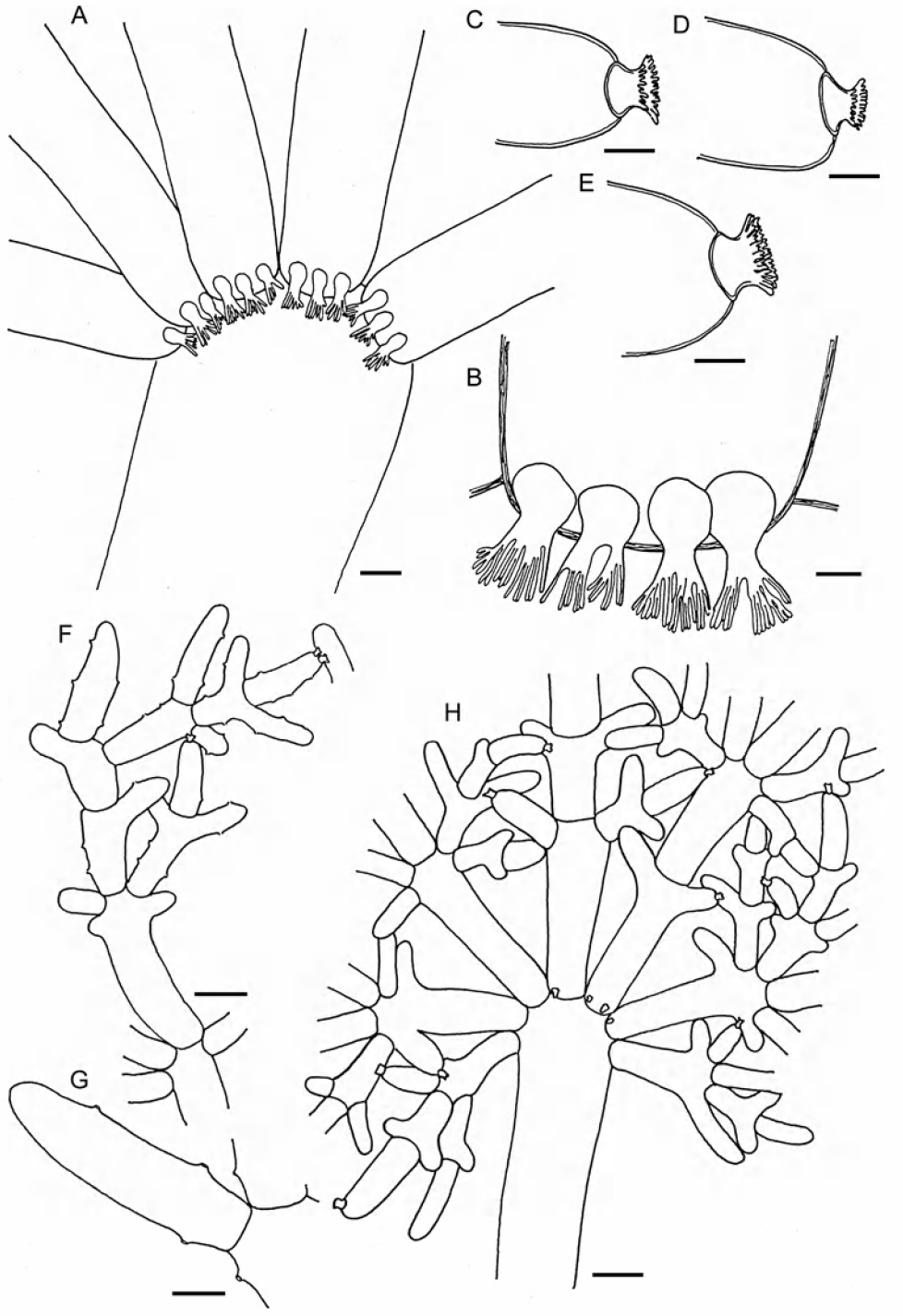


Fig. 54. *Cladophoropsis pulcherrima* (holotype of *Phyllodictyon pulcherrimum*, BM). **A.** Flabellate branching in the main axes; type-4 tenacular cells produced at the proximal poles of the cells and attaching to the cell below; **B.** Detail of type-4 tenacular cells; **C-E.** Type-3 tenacular cells; **F.** Sporangia in terminal branch-systems with conical projections on the lateral sides of the cells; **G.** Detail of sporangium; **H.** Flabellate branches with developing type-4 tenacular cells. Scale bars: A, H, F = 500 µm; B = 50 µm; C-E = 25 µm; G = 200 µm.

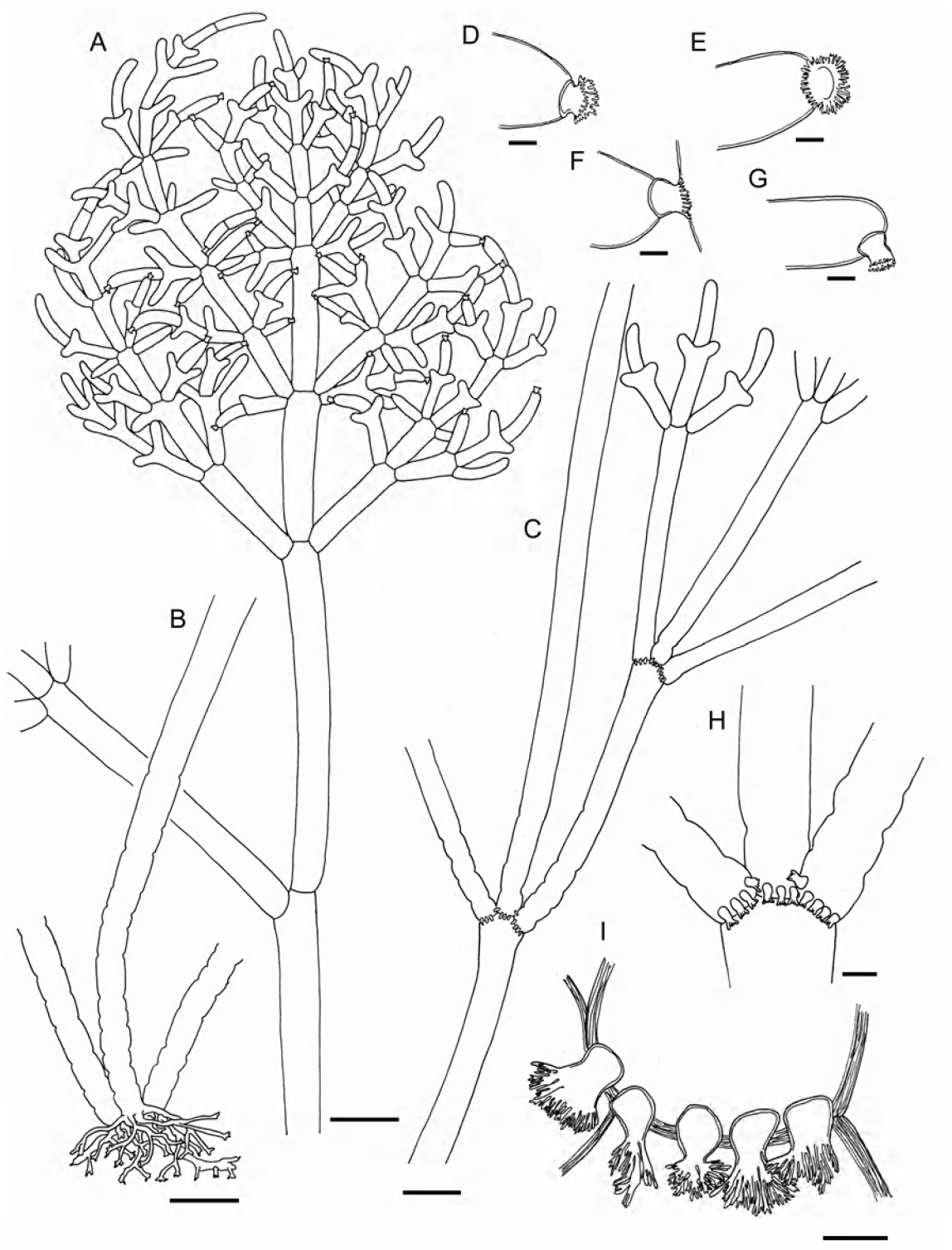


Fig. 55. *Cladophoropsis pulcherrima* (lectotype of *Struvea ramosa*, BM). **A.** Young lamina; **B.** Stipes with basal annular constrictions producing type-1 rhizoids; **C.** Basal branches of a mature lamina with basal annular constrictions and type-4 tenacular cells; **D-G.** Type-3 tenacular cells; **H-I.** Type-4 tenacular cells and lamellated cell walls. Scale bars: A-C = 1 mm; D-G = 50 μm; H = 200 μm; I = 100 μm.

7.5. Section *Struvea* (Sonder) Leliaert & Coppejans stat. nov. & comb. nov. prov.

Thallus forming erect stipitate blades composed of densely branched filaments, attached to the substratum by branching rhizoids sprouting from the base of the stipe. Stipes generally unbranched, with or without annular constrictions. Formation of the lamina is essentially similar as in the section *Phyllodictyon* but cell division is, at least in the initial stages of blade development, exclusively segregative (Fig. 56). Young thalli consisting of an unbranched stipe composed of a single cell. When reaching its full size, the distal end of the stipe is divided simultaneously into a series of cells (later becoming the cells of the central axis of the lamina). Each cell producing a pair of equally developing opposite laterals which elongate and form the primary laterals. Segregative cell division is repeated in the primary laterals. The apical cell of the central axis behaving like a primary lateral in regard to the timing of its own internal segregative division. The process of cell division, formation and elongation of laterals is repeated in the secondary, and higher order laterals. Branching pattern very regular in young blades but possibly becoming irregular in older blades of *C. papuensis* and *C. gardineri*, where cell division takes place by centripetal wall ingrowths. Structural reinforcement of the lamina accomplished by attachment of adjacent filaments by type-3 tenacular cells. The primary laterals curving upwards, and attaching to the acropetally adjacent primary laterals, resulting in a more or less closed, crenate blade margin. Tips of the second-order laterals generally attaching to cells of the most closely adjacent primary laterals or the base of a secondary lateral, often resulting in a zigzag appearance (especially obvious in *C. plumosa*) (Fig. 66C). Apical cell of higher order laterals attaching to adjacent cells in a more irregular way.

Four species are recognized in the section: *C. elegans*, *C. gardineri*, *C. papuensis* and *C. plumosa*. The differences between the species are summarized in Table 7.

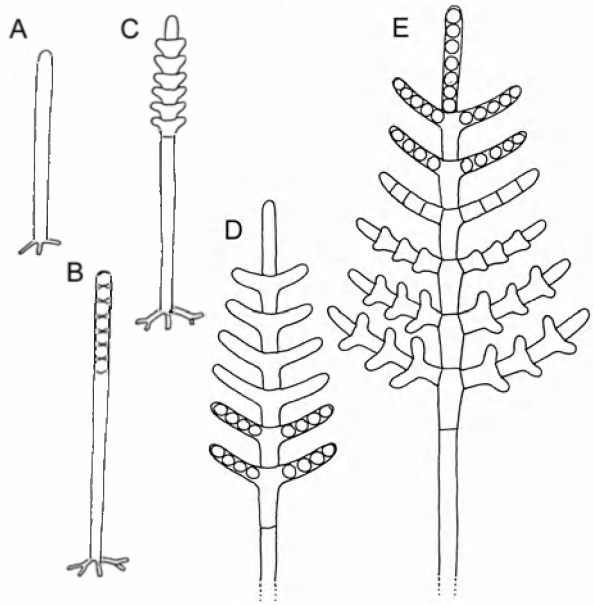


Fig. 56. Schematic representation of the initial developmental stages in the section *Struvea*. **A.** Young thallus consisting of a single stipe cell; **B.** Segregative cell division in the distal end of the stipe cell resulting in a series of cells (later becoming the central axis); **C.** Each cell producing a pair of equally developing opposite laterals which elongate and form the primary laterals; **D-E.** Segregative cell division and formation of laterals repeated in the primary laterals and apical cell of the central axis.

Table 7. Differences between the species in the section *Struvea*.

	C. elegans	*C. gardineri*	*C. papuensis*	*C. plumosa*
Thallus height	1-4 (-8) cm	up to 20 cm	5-16 cm	3-15(-20) cm
Stipe cell: shape and maximum diameter	subcylindrical, slightly attenuating towards both extremities, with basal annular constrictions, 600-1300 (-2000) µm in diam.	subcylindrical, slightly attenuating towards both extremities, with basal annular constrictions, 1500-2000 µm in diam.	subcylindrical, without annular constrictions, 380-700 (-820) µm in diam.	broad in the middle, markedly attenuating towards both extremities, 800-3500 (-5000) µm in diam.
Mode of cell division	SCD[1]	SCD in the initial lamina development; CI[2] in older blades	SCD in the initial lamina development; CI in older blades	SCD
Apical cell diameter and l/w ratio	190-315 µm l/w ratio: 1-8	200-400 µm l/w ratio: 1.2-11	(150-) 180-270 (-370) µm l/w ratio: 3-18 (-42)	240-600 µm l/w ratio: 1-3
Diameter of cells of the central axis (µm)	400-800 (-1125) µm l/w ratio: 1-2 (-6)	550-800 µm l/w ratio 1-10	370-670 µm l/w ratio 1.8-11	600-1500 µm l/w ratio 0.5-1.3
Calcium oxalate crystals	absent	diamond-shaped or triangular	diamond-shaped	diamond-shaped (occasionally triangular or pentagonal)

[1] SCD: segregative cell division.
[2] CI: centripetal invagination of cell walls.

Cladophoropsis elegans (Børgesen) Leliaert & Coppejans, comb. nov. prov. Figs 57-59

Struvea elegans Børgesen, 1912: 264, figs 13, 14 [Lectotype: off America Hill, north-coast of St. Jan, leg. Børgesen 2055, C!. In the original description several localities are mentioned in the Virgin Islands between St. Jan and St. Thomas. From these localities 11 specimens, comprising 7 herbarium numbers, are present in C: Børgesen 1762, 1809, 1867, 1901, 1950, 2055, 2222. Børgesen 2055 has been indicated as lectotype by A. Millar (annotation of 22.vii.1987)].

Struvea tuticorinensis Børgesen, 1933: 3-4, fig. 2, pl. 1 [Lectotype: Tuticorin, Tamil Nadu, South India; leg. Børgesen 5673, C!. Two sheets and two microscopic slides, all from the same locality and numbered Børgesen 5673, are present in C; one of the herbarium sheets (including a cluster of stipitate plants and two origingal photographs) is here indicated as lectotype; the other sheet and both slides then become isolectotypes].

Phyllodictyon tuticorinense[1] (Børgesen) Kraft & Wynne 1996: 140 ("*tuticorinensis*").

Struvea japonica Okamura & Segawa, *in* Segawa, 1936: 178, figs 4, 5 [Holotype: Tôzi, Island of Miyake, Izu Province, Japan, dredged from 18-37 m, herbarium of the Mitsui Institute of Marine Biology, Susaki, Izu, Japan].

Phyllodictyon japonicum (Okamura & Segawa) Kraft & Wynne, 1996: 139.

Struvea japonica var. *okiensis* Kajimura, 1978: 60, pl. I: fig. 1, text-fig. 1, 2 [Holotype: off Tsuma, Oki Islands, Japan, on *Lithophyllum okamurai* at depth of 40 m; leg. Kajimura, 2.vii.1976. The location of the holotype is uncertain].

Description:

Thallus medium to dark green, forming 1-4 (-8) cm high stipitate blades, attached to the substratum by branching, multicellular rhizoids sprouting from the base of the stipes (Figs 57, 59B). Stipes single or clustered, unbranched or occasionally branched, with a few basal annular constrictions, bearing reticulate, unistratose blades with a prominent central axis, triangular, ovate or lanceolate in outline, up to 4 (-6) cm long and 1-2.5 (-3) cm broad (Figs 57, 58A).

Young, unicellular stipes cylindrical, with a few (up to 8) basal annular constrictions. Distal end of fully grown stipes (about 2-4 cm high), dividing into numerous (9-17) cells by segregative cell division, followed by the formation of equally developing opposite pairs of laterals (Fig. 59A, F). The lowest cell of the central axis about 3 times longer than the other cells (Fig. 58A). Further development of the blade by a repetitive process of segregative cell division of the laterals and apical cells, formation and elongation of opposite laterals, and limited enlargement of the filaments. Division of the primary laterals starting proximally and progressing acropetally. Division of higher order laterals not strictly acropetal, resulting in a more irregular branch-pattern in older blades. Laterals in open connection with the mother cell, up to 900 µm long (l/w ratio 10). Often only the distal end of a lateral divided into a number of cells, leaving the basal part in open connection with the mother cell (Fig. 58A, arrowhead). All branches lying essentially in one plane. Branching up to the 3rd (sometimes 4th order). The diameter of the stipe cell 2.5-8 times that of the apical cells. Angle of ramification: 65°-90°.

Structural reinforcement of the lamina by type-3 tenacular cells borne singly on the tips of the apical cells or laterals in open connection with the mother cell (Figs 58B-D, 59C-E). In mature blades, in average 27-42 % of the apical cells terminating by a tenacular cell. Generally, the primary (and higher order) laterals arching upwards and the apical cells attaching to the acropetally adjacent primary laterals by tenacular cells. Branching in the marginal cells often unilateral and adaxial (Fig. 58A, arrow), resulting in more or less entire and crenate blade margins.

[1] Epithets in *Phyllodictyon* should receive the neuter ending (R. Moe, pers. comm.)

Zoidangia as transformed cells of terminal branch systems with conical projections on the lateral side of the cell (Fig. 58E, F).
Apical cells straight or curved, 190-315 µm in diameter, 300-2250 µm long, l/w ratio 1-8. Cells of the terminal branch systems subcylindrical to cupiform, 200-575 µm in diameter, 225-1350 µm long, l/w ratio 1-3. Cells of the central axis cupiform, 400-800 (-1125) µm in diameter, 600-1800 (-6000) µm long, l/w ratio 1-2 (-6). Stipe cell 0.6-1.3 (-2) mm in diameter, 1.5-6 cm long. Tenacular cells short to elongate, rhizoidal, ending in a broader lobed disc, 45-63 µm in diameter at the base, 50-90 (-300) µm long.
Cell walls with longitudinal and transverse striations in surface view, 2.5-5 µm thick in cells of the ultimate branches; 10-18 µm in the stipe.
Chloroplasts polygonal, 4-6 µm in diameter, forming a more or less closed parietal reticulum. Each chloroplast containing a single pyrenoid, 1.5-2.8 µm in diameter.
Crystalline cell inclusions absent.

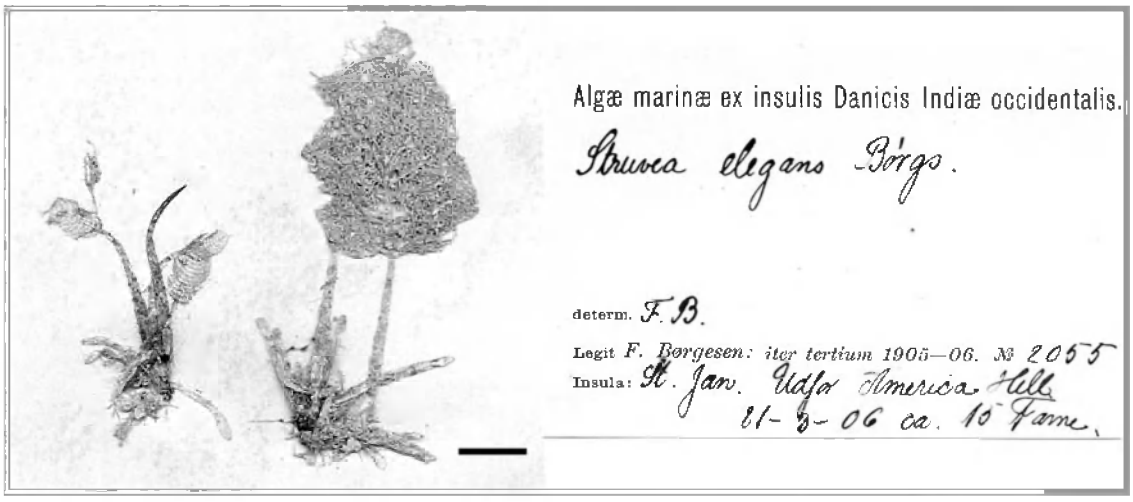


Fig. 57. *Cladophoropsis elegans* (lectotype of *Struvea elegans*, C). Scale bar = 1 cm.

Ecology: *S. elegans* is restricted to the subtidal, between 12-40 m depth, epilithic (see also Børgesen 1912, 1913; Taylor 1928, 1960, Littler & Littler 2000).

Distribution: *C. elegans* is widely distributed in the Caribbean region, where it has been reported from several localities, including the Virgin Islands (type locality), Florida (Taylor 1928) and Puerto Rico (Almodovar & Ballantine 1983). In the Indian Ocean the species is known from India as *S. tuticorinensis*. Other Indian Ocean records of *C. elegans* [Seychelles (Kalugina-Gutnik *et al.* 1992: 25) and Réunion (Payri 1985: 640)] remain uncertain since no description or illustration were provided. In the Pacific Ocean, *C. elegans* is known from Japan (as *S. japonicum*) and Papua New Guinea (Leliaert *et al.* 1998: 187).

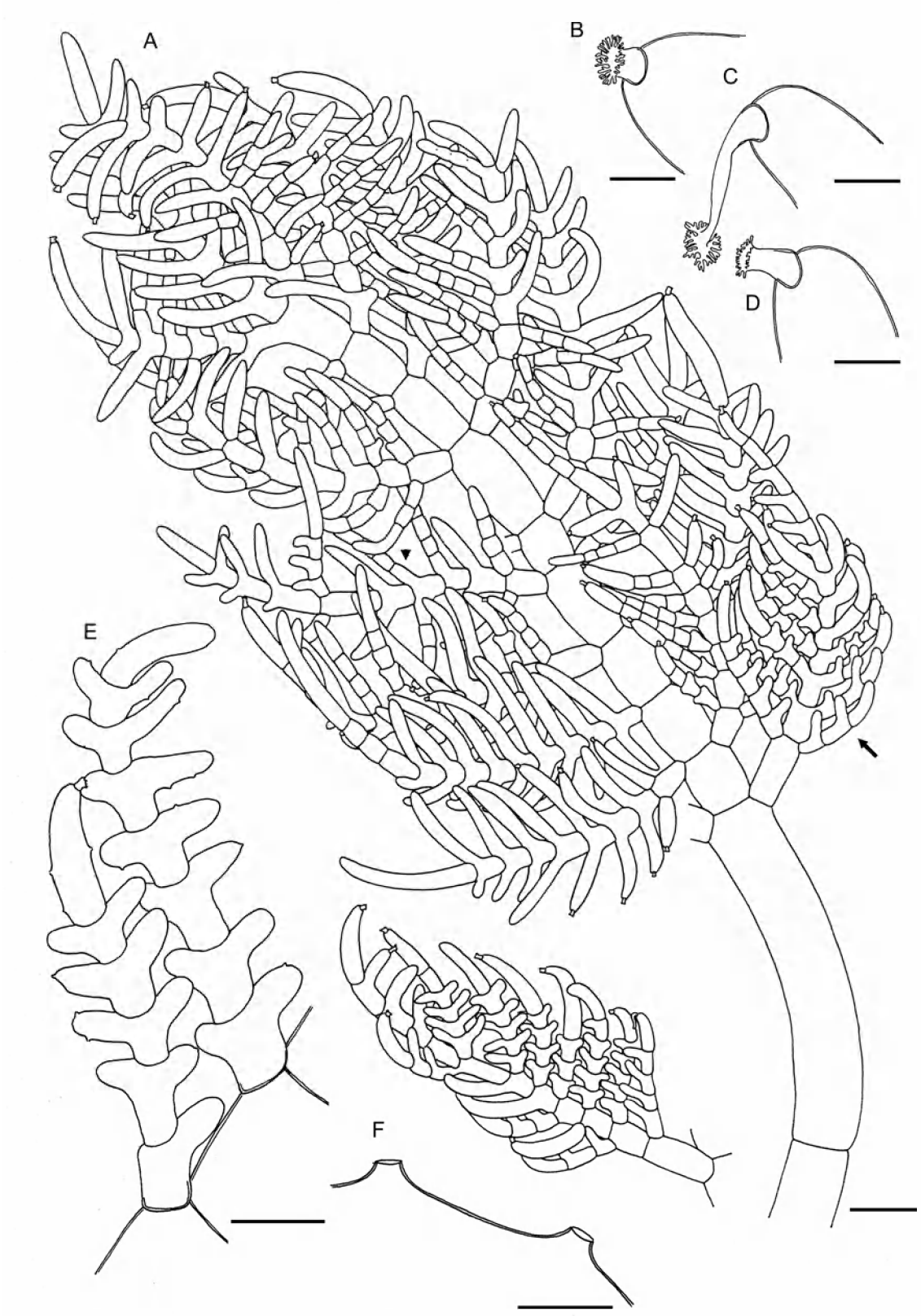


Fig. 58. *Cladophoropsis elegans* (lectotype of *Struvea elegans*, C). **A.** Mature lamina composed of regular, opposite branches (marginal branches occasionally unilateral, arrow); often only the distal end of a lateral is divided into a number of cells, leaving the basal part in open connection with the mother cell (arrowhead); **B-D.** Type-3 tenacular cells; **E.** Sporangia with conical projections on the lateral sides of the cells; **F.** Detail of conical projections with pores. Scale bars: A = 1 mm; B-D = 100 µm; E = 500 µm; F = 50 µm.

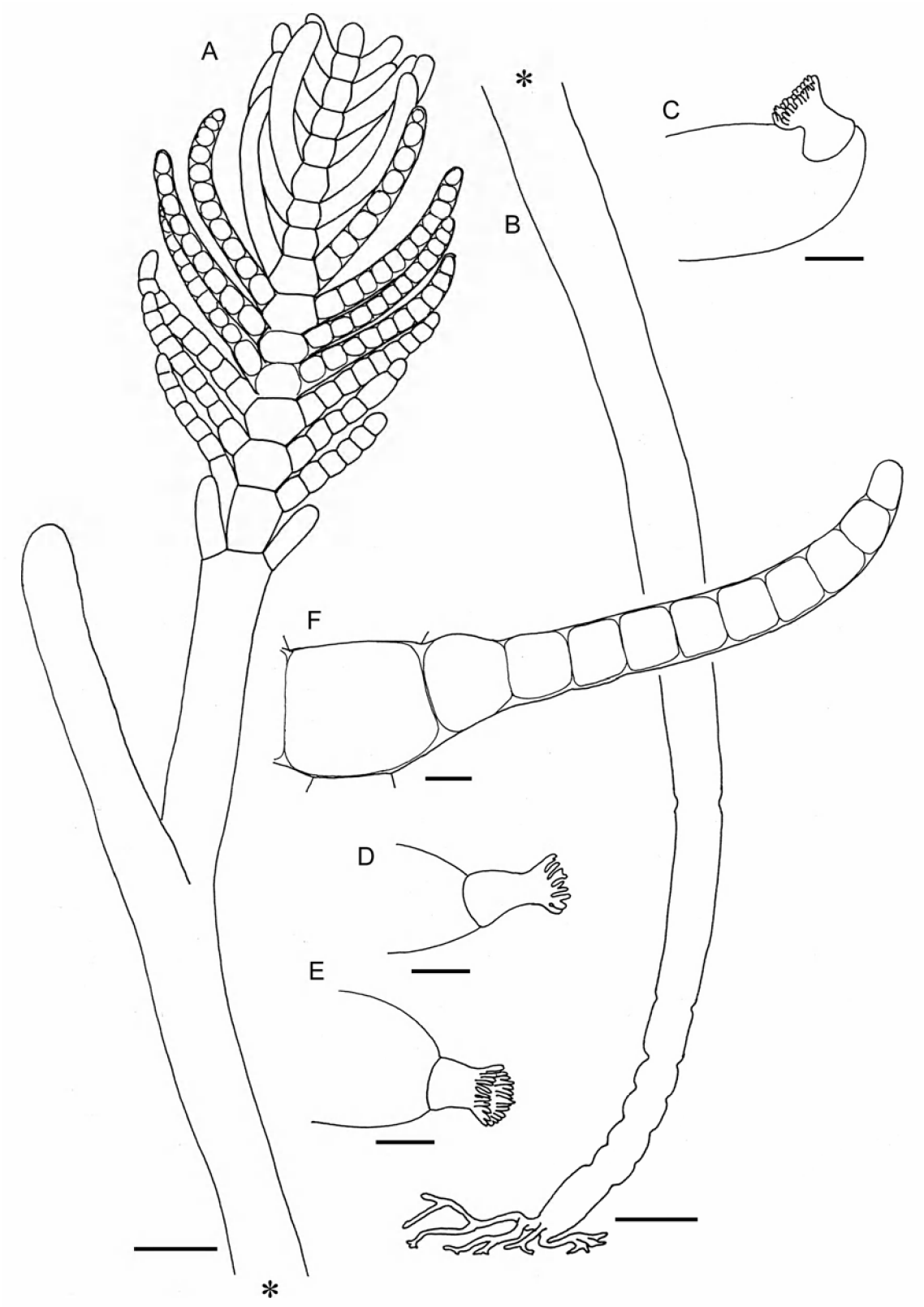


Fig. 59. *Cladophoropsis elegans* (lectotype of *Struvea tuticorinensis*, C). **A-B.** Young stipitate lamina composed of a central axis and primary laterals undergoing segregative cell division; stipe with basal annular constrictions and type-1 rhizoids; **C-E.** Type-3 tenacular cells; **F.** Detail of primary lateral dividing by segregative cell division. Scale bars: A-B = 1 mm; C-E = 50 µm; F = 200 µm.

Specimens examined: **Carribean Sea: Virgin Islands.** Cruz Bay, St. Jan, (leg. Børgesen 2055, 21.iii.1906, C: lectotype of *S. elegans*); Cruz Bay, St. Jan, (leg. Børgesen 1762, 5.iii.1906; Børgesen 1809, 6.iii.1906; Børgesen 1867, 8.iii.1906; Børgesen 1901, 9.iii.1906; Børgesen 2222, 29.iii.1906, C: syntype of *Struvea elegans*); near Thatch Cay, St. Thomas, (leg. Mortensen 1950, 12.iii.1906, C: syntype of *S. elegans*); **Indian Ocean: India.** Tuticorin, Tamil Nadu, South India, subtidal, 20 m deep, (leg. Børgesen 5673, 1927-1928, C; holotype of *Struvea tuticorinensis*); **Pacific Ocean: Papua New Guinea.** Laing Island, Port Moresby area, epilithic on vertical walls of rock boulders, shallow subtidal, (leg. Coppejans, viii.1986, HEC 6450, HEC 6460); N Motupore Island, (leg. Coppejans, vi.1986, HEC 6348); Loloata Island, SE reef, Port Moresby area, subtidal outer reef slope, 12 m deep, epilithic on horizontal dead coral, (leg. Coppejans & De Clerck, 5.viii.1994, HEC 10437); Loloata Island, W end of the reef platform, Port Moresby area, subtidal outer reef slope, 12 m deep, epilithic on horizontal fossil coral, (leg. Coppejans & De Clerck, 31.vii.1994, HEC 10366); Motupore Island, Port Moresby area, subtidal, 15-30 m deep, epilithic on fossil coral wall, (leg. Coppejans & De Clerck, 23.vii.1994, HEC 10236); N Laing Island, Port Moresby area, outer reef, (leg. Coppejans, vi.1980, HEC 4395 & HEC 4413); N of Pig (Tab) Island, Madang Province, inner slope of the reef, (leg. Coppejans & Prud'homme van Reine, 5.viii.1990, Copp & PvR 13587).

Notes:

Børgesen (1913) elaborately described and illustrated his new species, giving full details on mode of cell division, branching systems, cell walls and chloroplasts. *C. elegans* resembles young thalli of *C. papuensis* but differs by the annular constrictions in the stipe, and the lack of calcium oxalate crystals (Table 7).

Børgesen (1933) distinguished *Struvea tuticorinensis* from *C. elegans* only by its smaller thallus. The type of *S. tuticorinensis* however can be regarded as a young thallus of *C. elegans*. Kraft & Wynne (1996: 140) transferred *S. tuticorinensis* to *Phyllodictyon*, based on the erroneous presumption that the cells in this species divide by centripetal wall ingrowth. The original illustration and the type material of *S. tuticorinensis* clearly show a segregative mode of cell division.

We have not seen the type of *S. japonicum* but based on the original description and illustration, this species probably represents a large *C. elegans* thallus with blade filaments being somewhat irregularly organized. *S. japonica* var. *okiensis* also lies within the circumscription of *S. japonica*.

General references. As *Struvea elegans*: Børgesen (1912: 264, figs 13, 14; 1913: 51-54, figs 37, 38), Taylor (1928: 74, Pl. 6, figs 6, 7; 1960: 123, Pl. 9, figs 1, 8, 9); Leliaert *et al.* (1998: 187-188, figs 28, 29); Littler & Littler 2000: 328, fig. on p. 329).

Cladophoropsis gardineri (A. Gepp & E. Gepp) Leliaert & Coppejans, comb. nov. prov. Figs 4E-F, 60-62

Struvea gardineri A. Gepp & E. Gepp, 1908: 166-167, pl. 22: fig. 5 [Holotype: Cargados Carajos; leg. J.S. Gardiner 10, Sealark Expedition, 1905, BM!. Two specimens, matching the original prologue, are present in BM: one consisting of a stipitate blade, the second one of a portion of a large lamina, lacking a stipe. The first plant is illustrated in the original publication and is here regarded as holotype].

Phyllodictyon gardineri (A. Gepp & E. Gepp) Kraft & Wynne, 1996: 139.

Description:

Thallus light to medium yellow-green (when dried), forming erect stipitate blades, up to 20 cm high, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe (Figs 60A, 62A, F).

Stipe single, unbranched, with annular constrictions over the entire length, bearing a reticulate lamina, composed of branched filaments, essentially lying in a single plane. Young blade with a prominent central axis, elliptical to obovate in outline, with an entire, crenate margin, 13-50 mm long, 9-30 mm broad, composed of strictly opposite branching systems (Fig. 62A). Mature blade irregular in outline, about 17 cm long and 15 cm broad, lacking a percurrent primary axis and composed of more irregular branch systems (Fig. 60B).

Formation of the lamina by a repetitive process of cell division, formation and elongation of laterals. Growth in the initial stages of blade formation mainly by apical cell division, accomplished SCD (dividing the cells simultaneously into 3-5 cells) (Fig. 62G). Growth in older

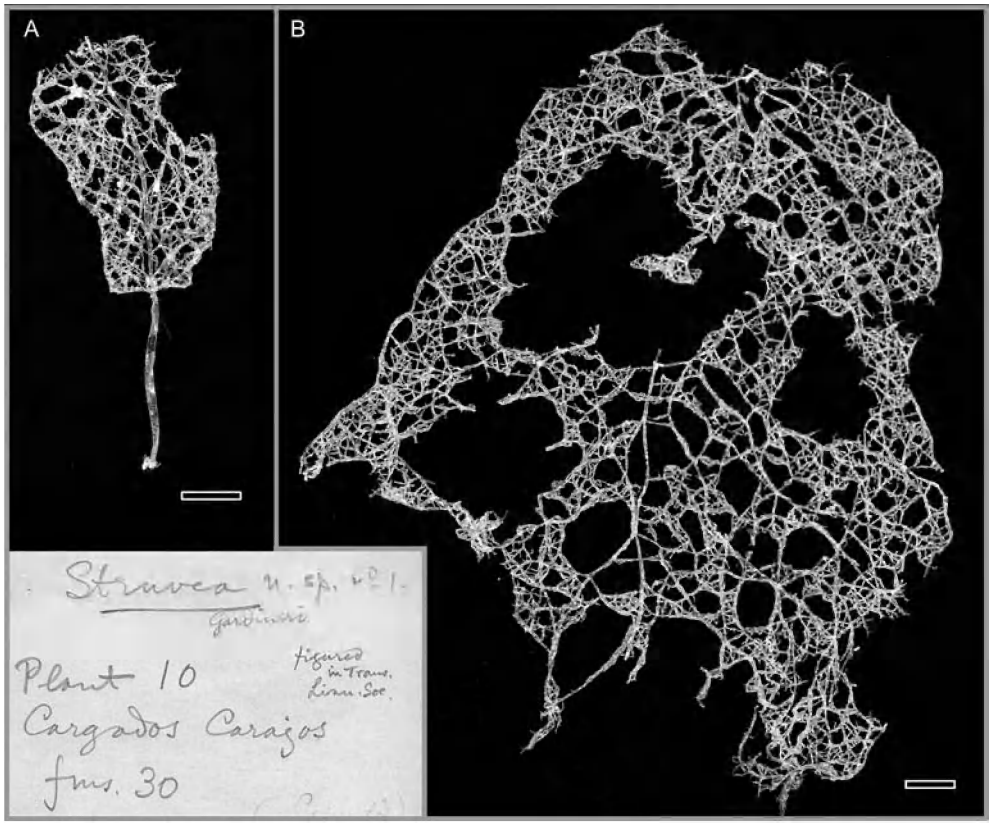


Fig. 60. *Cladophoropsis gardineri*. **A.** Young, stipitate lamina with entire margin; stipe cell with annular constrictions over the entire length (holotype of *Struvea gardineri*, BM); **B.** Portion of older blade (paratype of *Struvea gardineri*, Gardiner s.n., BM). Scale bars = 1 cm.

blades mainly by cell elongation; apical and intercalary cell divisions only by CI (Fig. 61A). Generally, each new cell producing a pair of opposite, more or less equally developing laterals at its apical pole; occasionally only a single lateral produced. Formation of cross walls at the base of the laterals (by CI or SCD) somewhat delayed; laterals in open connection with the mother cell up to 1400 µm long (l/w ratio 5). Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Branching up to the 5th order. The diameter of the stipe cell 3.8-10 times that of the apical cells. Angle of ramification 30°-90°.

Structural reinforcement of the lamina by attachment of the adjacent cells by type-3 tenacular cells, terminally, laterally or basally inserted on the apical cells; laterals in open connection with the mother cell, or intercalary cells. Adjacent cells frequently attached laterally by two or three (sometimes four) type-3 tenacular cells born on a single cell (Figs 61B-D, 62B-E). In mature blades, in average 30-55 % of the apical cells producing one or more tenacular cells.

Apical cells subcylindrical to tapering with rounded tip, slightly constricted at the base, straight or slightly curved, 200-400 µm in diameter, 400-3450 µm long, l/w ratio 1.2-11. Cells of terminal branch systems cylindrical, 300-600 µm in diameter, 750-3000 µm long, l/w ratio 1-5. Cells of the main axis 550-800 µm in diameter, 550-7000 µm long, l/w ratio 1-10. Stipe cell 1500-2000 µm in diameter in the middle part, slightly tapering towards both extremities to 800-1400 µm, 2.5-3 cm long. Tenacular cells 100-125 µm in diameter, 120-150 µm long.

Cell walls relatively thin, ca. 2 µm in the apical cells and terminal branches, up to 20 µm in the older filaments and stipe cell.

Chloroplasts were not well preserved in the herbarium material and therefore their morphology could not be examined.

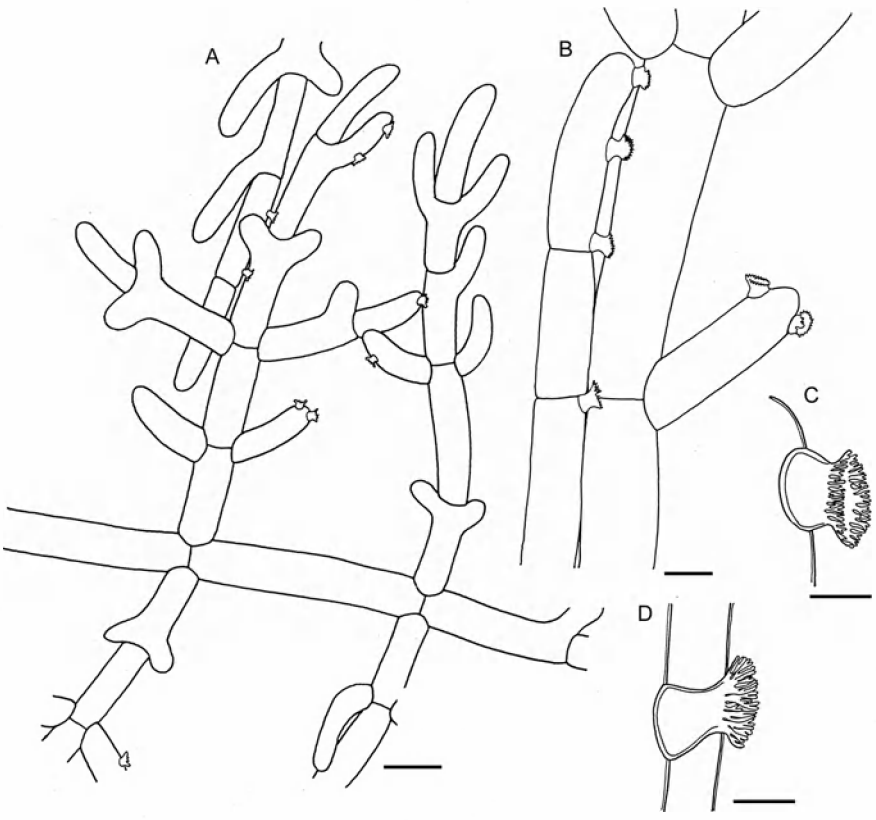


Fig. 61. *Cladophoropsis gardineri* (paratype, Gardiner s.n., BM). **A.** Branch-systems of a mature lamina, laterals mainly opposite; **B.** Adjacent cells attached laterally by a number of type-3 tenacular cells, **C-D.** Type-3 tenacular cells. Scale bars: A = 1000 µm; B = 250 µm; C-D = 100 µm.

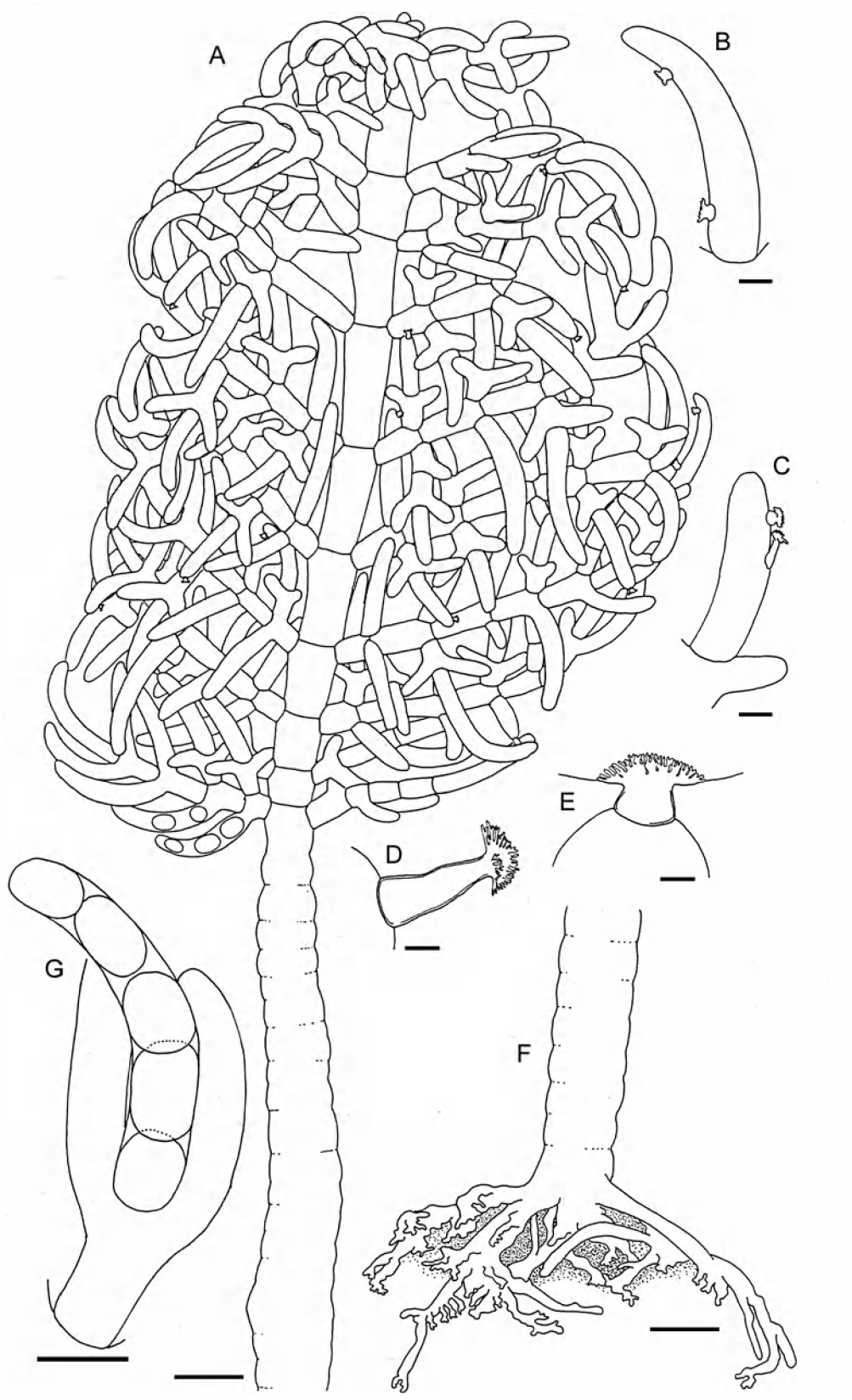


Fig. 62. *Cladophoropsis gardineri* (SEY 771B, Seychelles). **A.** Young blade with an entire, crenate margin and prominent central axis, composed of regular opposite branch systems; stipe with annular constriction over the entire length; **B-E.** Type-3 tenacular cells formed laterally or terminally; **F.** Base of the stipe with annular constrictions (over the entire length), attached by type-1 rhizoids. **G.** Apical cell undergoing segregative cell division. Scale bars: A, F, G = 500 µm; B-E = 50 µm.

Prismatic calcium oxalate crystals present in most blade cells (except the tenacular cells), up to 5 crystals per cell; crystals diamond-shaped or triangular, 20-50 µm in diameter, 30-75 µm long, l/w ratio 1.5-2 (Fig. 4E-F).

Ecology: The type specimens were collected by dredging, down to 55-80 m depth. The plant from the Seychelles (SEY 771) grew epiphytic on the seagrass *Thalassodendron ciliatum* at 20 m depth.

Geographical distribution: *C. gardineri* was, until now, only known from the single type collection on the Cargados Carajos shoals, 480 km N of Mauritius. The collection from the Seychelles indicates that this poorly known, deepwater species might have a wider Indian Ocean distribution.

Specimens examined: **Indian Ocean: Cargados Carajos**. 30 fms (ca. 55 m) deep, (leg. Gardiner 10, Sealark Expedition, 1905, BM, holotype of *Struvea gardineri*); 44 fms (ca. 80 m) deep, (leg. Gardiner s.n., Sealark Expedition, 1905, BM, paratype of *S. gardineri*); **Seychelles**. NW side of Plate Island, 20 m deep, epiphytic on *Thalassodendron ciliatum*, (leg. Coppejans *et al.*, 7.i.1993, SEY 771).

Notes:
Due to the limited number of specimens available, we are unable to describe the entire development of the lamina. Kraft & Wynne (1996: 139) transferred *Struvea gardineri* to *Phyllodictyon* on account of the cell division which, they presumed, does not take place by a process of segregative cell division. The mode of cell division cannot be retrieved from the original description and illustrations, but examination of young thalli (the type and the Seychelles material) clearly shows that the blade cells initially divide by CI or SCD.

C. gardineri can be easily distinguished from other stipitate blade-forming species by the large apical cell diameter (200-400 µm), the regular opposite branching pattern (at least in young blades), the laterally placed tenacular cells and the large diamond-shaped crystalline cell inclusions. *C. gardineri* resembles *C. plumosa* in general habit and crystal morphology but can be distinguished by the subcylindrical stipe, and the placement and number of tenacular cells per cell (laterally and up to three in *C. gardineri* versus distally and maximum one in *C. plumosa*).

Diamond-shaped or triangular crystals also occur in *C. orientalis* and *C. pulcherrima*. These two species can be easily distinguished from *C. gardineri* by their mode of cell division (exclusively by centripetal wall ingrowths), flabellate branching pattern and the much thinner filaments.

The record of *C. gardineri* from Papua New Guinea (Leliaert *et al.* 1998: 187, figs 25-27, as *Struvea gardineri*) is a misapplied name for *C. papuensis*. Both species grow in deep water, and have comparable cell dimensions and a similar branching pattern. *C. gardineri* differs from the Papuan species mainly by the entire blade margin and the annulated stipe-cell.

General references. As *Struvea gardineri*: A. Gepp & E. Gepp (1908: 166-167, pl. 22: fig. 5; 1909: 376-377, Pl. 47: fig. 5).

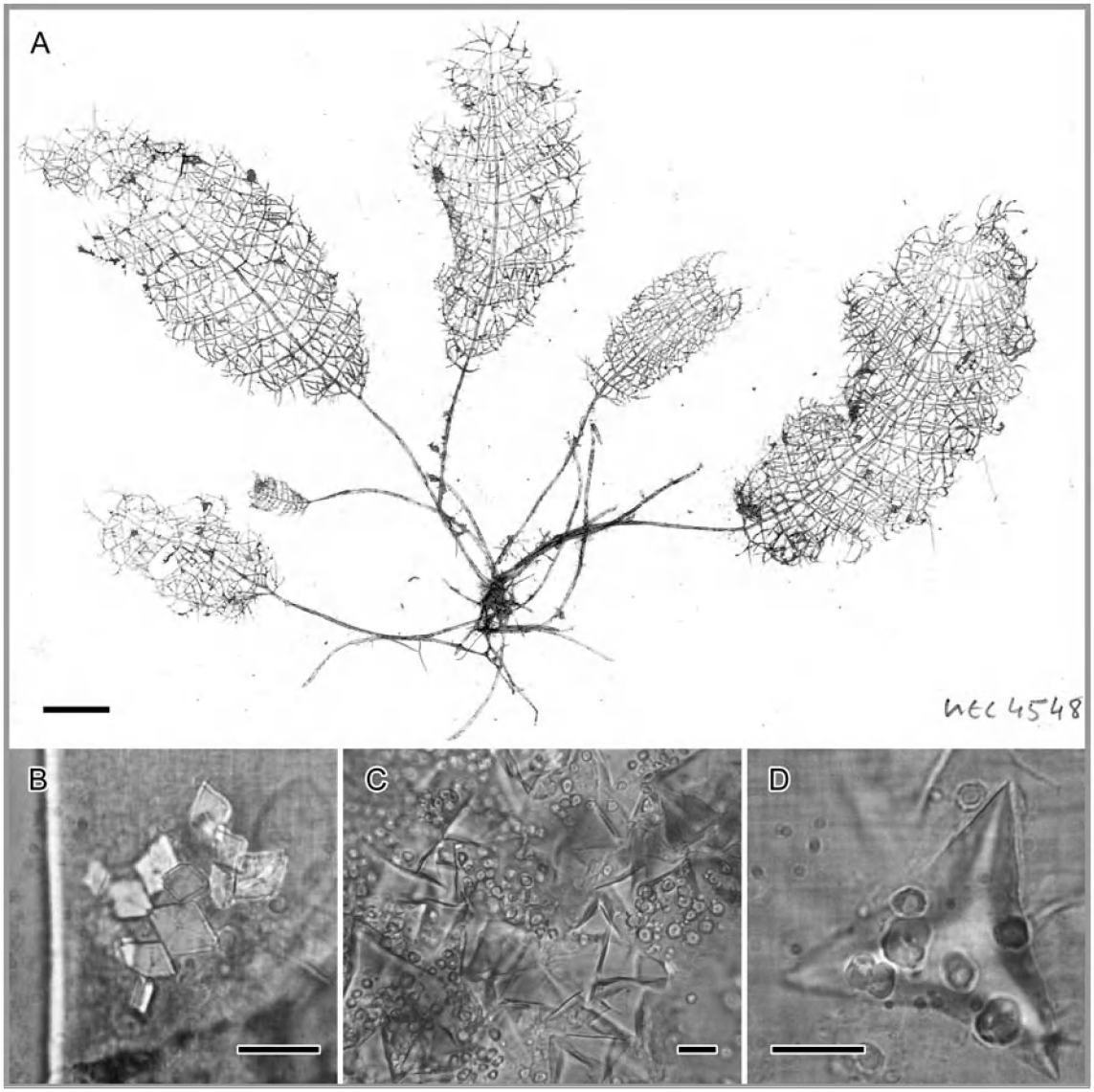


Fig. 63. *Cladophoropsis papuensis* (holotype, HEC 4548). **A.** Habit; **B.** Diamond-shaped calcium oxalate crystals in the blade cells; **C-D.** Tetrahedral protein crystals in the stipe cell. Scale bars: A = 1 cm; B-D = 10 µm.

Cladophoropsis papuensis Leliaert & Coppejans, sp. nov. prov. Figs 63-65

Holotype: Laing Island, Hansa Bay, Madang Province, Papua New Guinea, leg. Coppejans, vi.1980, HEC 4548 (GENT).

Description:
Thallus light to medium green (when dried), forming erect, stipitate, reticulate blades, 5-16 cm tall, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe (Fig. 63A). Stipes clustered, unbranched, lacking annular constrictions. Blades with a percurrent central axis, composed of branched filaments, lying essentially in a single plane and forming a reticulum (Fig 64B); blades sometimes slightly spirally twisted. Young blades composed of regularly opposite branch systems, obovate to triangular in outline, with an open margin. Mature blades elliptical in outline, commonly 3.5-7.3 cm high and 1.4-3.6 cm broad, l/w ratio1.7-2.5. Older blades with more irregular branch systems, up to 11 cm high and 6.5 cm broad.

Young stipes cylindrical and unicellular; when fully grown (about 3-5 cm long), the distal end dividing into numerous (up to 20) cells by segregative cell division, followed by the formation of equally developing, opposite pairs of laterals (Fig. 64A). Initial development of the lamina by apical cell divisions, accomplished by SCD (dividing the cells simultaneously into 3-5 cells), formation of opposite laterals, and subsequent cell elongation and enlargement (Fig. 64B-D). Growth in older blades mainly by cell elongation; cells dividing exclusively by CI; newly formed subapical cells producing one or two (opposite) laterals. All branches lying essentially in a single plane (Fig. 65A). Formation of cross walls at the base of the laterals (by CI or SCD) markedly delayed; laterals in open connection with the mother cell up to 2200 µm long in young blades (l/w ratio 10), up to 7000 µm long in the older blades (l/w ratio 32). Older branches laterally inserted with a steep cross wall cutting it off from the parent cell; this cross wall soon becoming partly fused with the cell above the parent cell. Blade filaments branching up to the 3rd order (in older blades up to the 4th order). The diameter of the stipe cell 1.4-4.6 times that of the apical cells. Angle of ramification 40°-70°.
Structural reinforcement of the lamina by attachment of adjacent filaments by type-3 tenacular cells, borne (sub-)terminally on apical cells or laterals in open connection with the mother cell; generally one, sometimes 2 per cell (Fig. 65B-E). In mature blades, in average 8-30 % of the apical cells producing a tenacular cell.
Apical cells tapering, with rounded tips, straight or strongly curved, (150-) 180-270 (-370) µm in diameter, 700-4750 (-8125) µm long, l/w ratio: 3-18 (-42). Cells of terminal branch systems cylindrical, 200-400 µm in diameter, 500-1750 µm long, l/w ratio 1.7-6. Cells of the central axis 370-670 µm in diameter, 870-4500 µm long, l/w ratio 1.8-11; basal cell of the central axis (350-) 420-650 (-820) µm in diameter, 1800-4250 µm long, l/w ratio 4.8-6.8. Stipe cells 380-700 (-820) µm in diameter, 40-50 mm long. Tenacular cells short to narrowly elongated (15-) 45-55 µm in diameter, 65-250 (-350) µm long.
Cell walls 2-4 µm thick in the terminal branch systems, 5-14 (-32) µm thick in the cells of the central axis and stipe.
Chloroplasts polygonal, 4-7 µm in diameter, forming an open to more or less closed parietal reticulum. Each chloroplast containing a single pyrenoid, 1.5-3 µm in diameter.
Prismatic calcium oxalate crystals present in most blade cells (except the tenacular cells); number of crystals per cell ranging from a few to 30; crystals diamond-shaped, relatively small (compared to the size of the cells), 5-13 µm long, up to 9 µm broad, l/w ratio 1-1.5 (Fig. 63B).
Tetrahedral protein crystals abundant in the stipe cells, less frequent in the basal cells of the lamina, up to 28 (-40) µm in diameter (Fig. 63C-D).

Ecology: The only three specimens of *C. papuensis* were collected subtidally at 15-30 m depth, on sandy substratum.

Geographical distribution: *C. papuensis* is only known from the type locality.

Specimens examined: **Pacific Ocean: Papua New Guinea.** Laing Island, Hansa Bay, Madang Province, (leg. Coppejans, vi.1980, HEC 4548: holotype; viii.1980, HEC 4696; 14.vii.1988, HEC 7760).

Notes:
As in *C. gardineri*, the segregative mode of cell division is obvious in young blades whereas in older thalli, cell division takes place by centripetal wall ingrowths. Young thalli of *C. papuensis* most closely resembles *C. elegans*, which grows at similar depths, but differs from it by the much larger thalli, the longer blade cells, the lack of annular constrictions in the stipe, and the presence of calcium oxalate crystals in the blade cells and protein crystals in the stipe cells.

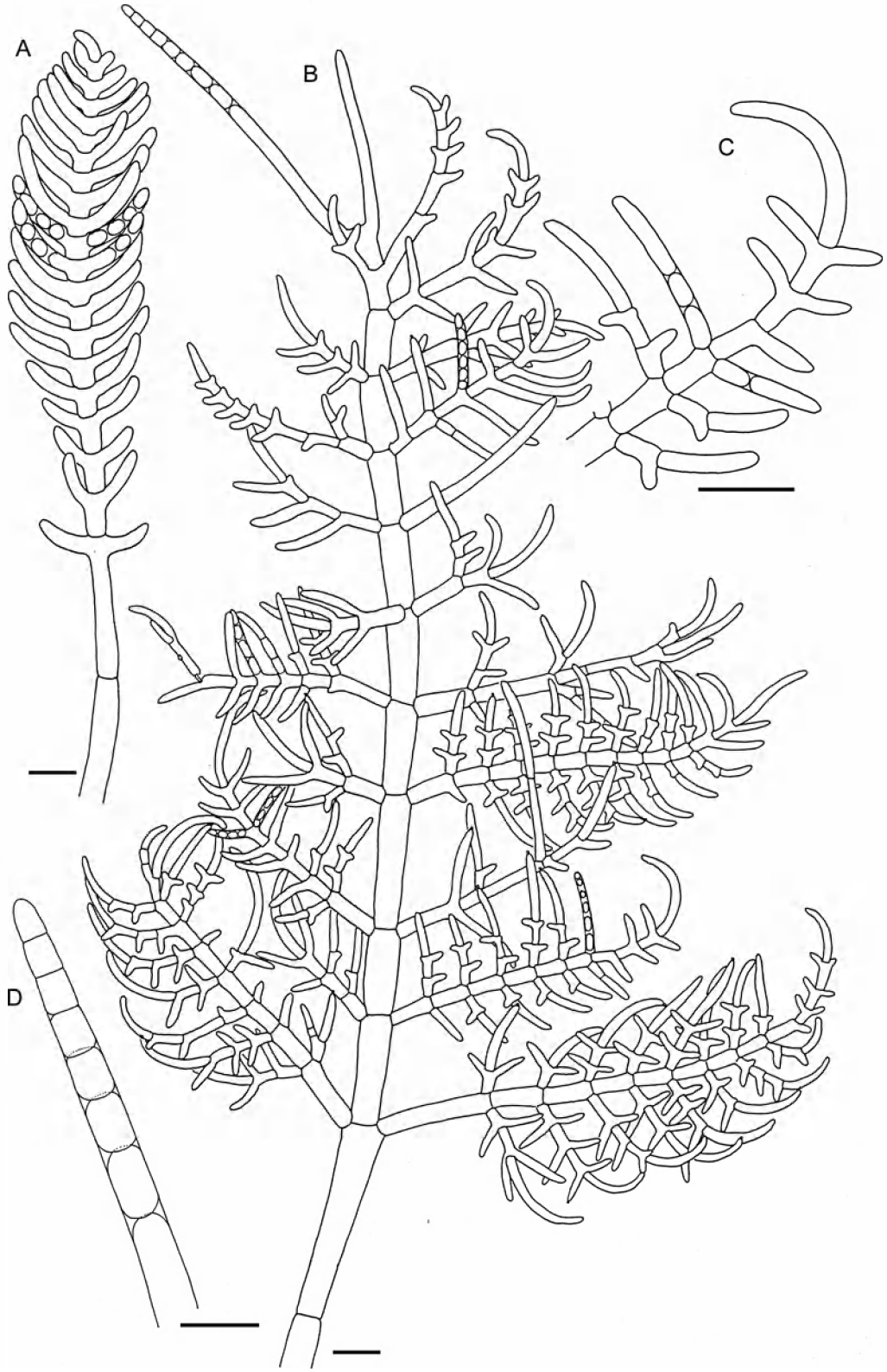


Fig. 64. *Cladophoropsis papuensis* (holotype, HEC 4548). **A.** Young lamina composed of a central axis and primary laterals undergoing segregative cell division; **B.** Older lamina composed of regular opposite branch-systems; **C.** Terminal branch with branchlets; **D.** Distal end of a lateral undergoing segregative cell division. Scale bars = 1 mm.

Leliaert *et al.* (2003) found both species to be very closely related, and forming a sister group to a clade consisting of taxa belonging to the *C. composita* complex.

C. papuensis has been briefly described under the misapplied name *Phyllodictyon gardineri* in Leliaert *et al.* (1998) and as *Phyllodictyon* sp. in Coppejans *et al.* (2001). The plant illustrated as *Phyllodictyon* sp. in (Littler & Littler 2003: 202, fig. on p. 203) is possibly referable to *C. papuensis*.

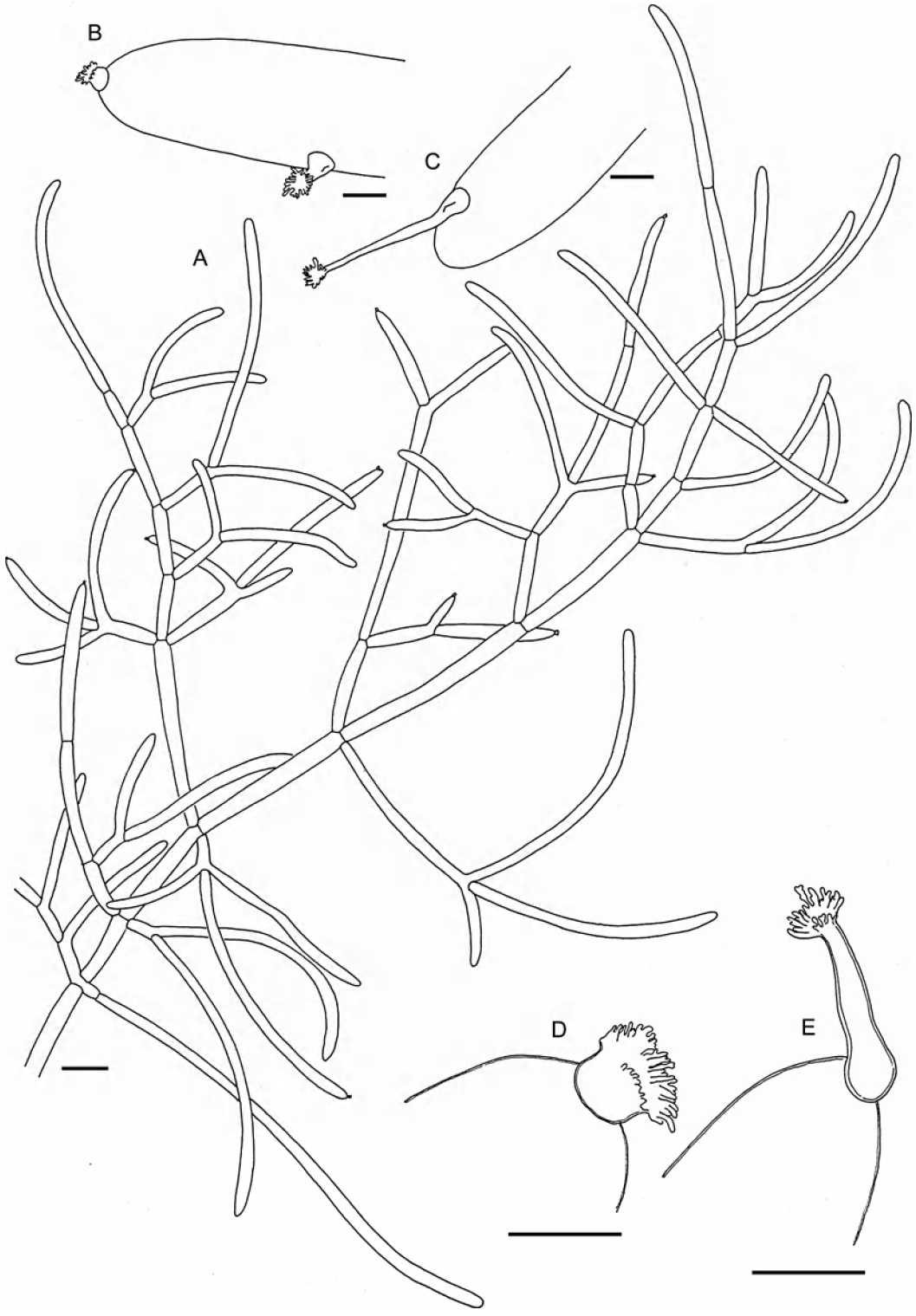


Fig. 65. *Cladophoropsis papuensis* (HEC 4696). **A.** Opposite to irregular branching in a mature lamina; **B-E.** Type-3 tenacular cells, sometimes extremely elongate. Scale bars: A = 1 mm; B-E = 100 µm.

Cladophoropsis plumosa (Sonder) Leliaert & Coppejans, comb. nov. prov.

Figs 4G, 66, 67

Struvea plumosa Sonder, 1845: 50 [Lectotype: Western Australia; leg. L. Preiss s.n., herbarium Sonder, MEL! 502116. Three specimens with Sonder's handwriting from 'Novae Hollandiae' were found in BM (Sonder 1846), S (Sonder s.n.), and MEL 502116 (Sonder s.n.). The latter is here indicated as the lectotype; the same herbarium sheet also contains two drawings by Sonder (in pencil), a copy of Kützing's (1856) plate 90, and annotations in Kützing's handwriting].

Struvea macrophylla Harvey, 1855b: 564 [Holotype: Champion Bay, Western Australia; leg. Drummond s.n., herbarium Harvey, TCD. The specimen has been removed from the mounting sheet in Harvey's bound book of algae and is most probably lost (J. Parnell pers. comm.)].

Valonia radicans Grunow, *in* Piccone, 1884a: 293 [Type: Adelaide, S Australia, in W according to Womersley 1956].

Description [we also refer to the excellent illustrations of Womersley (1984: 218-220, fig. 73B, C) and Kraft & Wynne (1996: 131, figs 1-15)]:

Thallus light to medium green, forming 3-15(-20) cm high, single to densely clustered stipitate blades, attached to the substratum by branching, multicellular rhizoids arising from the base of the stipes. Stipes unbranched, widest in the middle part, with annular constrictions over the entire length or confined to their upper and lower, narrower parts. Mature blades with a prominent central axis, composed of regular, opposite branch systems lying essentially in one plane, elliptical, ovate to elongate in outline, 1-10 (-17) cm long and 0.5-4 (-12) cm broad (Fig. 66). Blade margins with a closed, crenate contour. Thallus sometimes limited to stipes.

Young stipes unicellular, club-shaped, later becoming elongated-clavate with basal annular constrictions, with the apex remaining smooth and obtuse. Stipe reaching 5 cm high becoming distally attenuated with annular constrictions; distally a series of 6-22 cells being formed by segregative cell division; each of these cells (later becoming the cells of the central axis of the lamina) producing more or less equally developing, opposite laterals which then elongate and form the primary laterals. Segregative cell division repeated in the primary (and higher order) laterals, starting with the proximal laterals and progressing acropetally. The apical cell of each primary lateral behaving as a secondary lateral in regard to the timing of its own internal segregative divisions. In these cells inner (adaxial) unilateral branches are produced, giving the blade margin a smooth but crenate contour (Figs 66C, D, 67). Cross wall formation at the base of the laterals markedly delayed; laterals in open connection with the mother cell, up to 2200 µm long (l/w ratio 6). Growth by division of the apical cells and subsequent cell elongation and enlargement. Branching up to the 4th (sometimes 5th) order in large blades. The diameter of the stipe cell 3-13 times that of the apical cells. Angle of ramification: 50°-60°.

Structural reinforcement of the lamina by type-3 tenacular cells, borne singly on apical cells or laterals in open connection with the mother cell. Most primary laterals terminating in tenacular cells, placed on the tip of the apical cell. The primary laterals arching upwards, and attaching to the acropetally adjacent primary laterals. Tips of the second-order laterals attaching to cells of the most closely adjacent primary laterals or the base of a secondary lateral resulting in a zigzag appearance. Apical cell, of higher order laterals, attaching to adjacent cells in a more irregular way (Fig. 67). In mature blades, in average 56-78 % of the apical cells terminated by a tenacular cell.

Apical cells straight or curved, 240-600 µm in diameter, 350-1400 µm long, l/w ratio 1-3. Cells of the terminal branch systems: 350-600 µm in diameter, 300-750 µm long, l/w ratio 0.7-1.5. Cells of the central axis: 600-1500 µm in diameter, 600-1200 µm in length, l/w ratio 0.5-1.3.

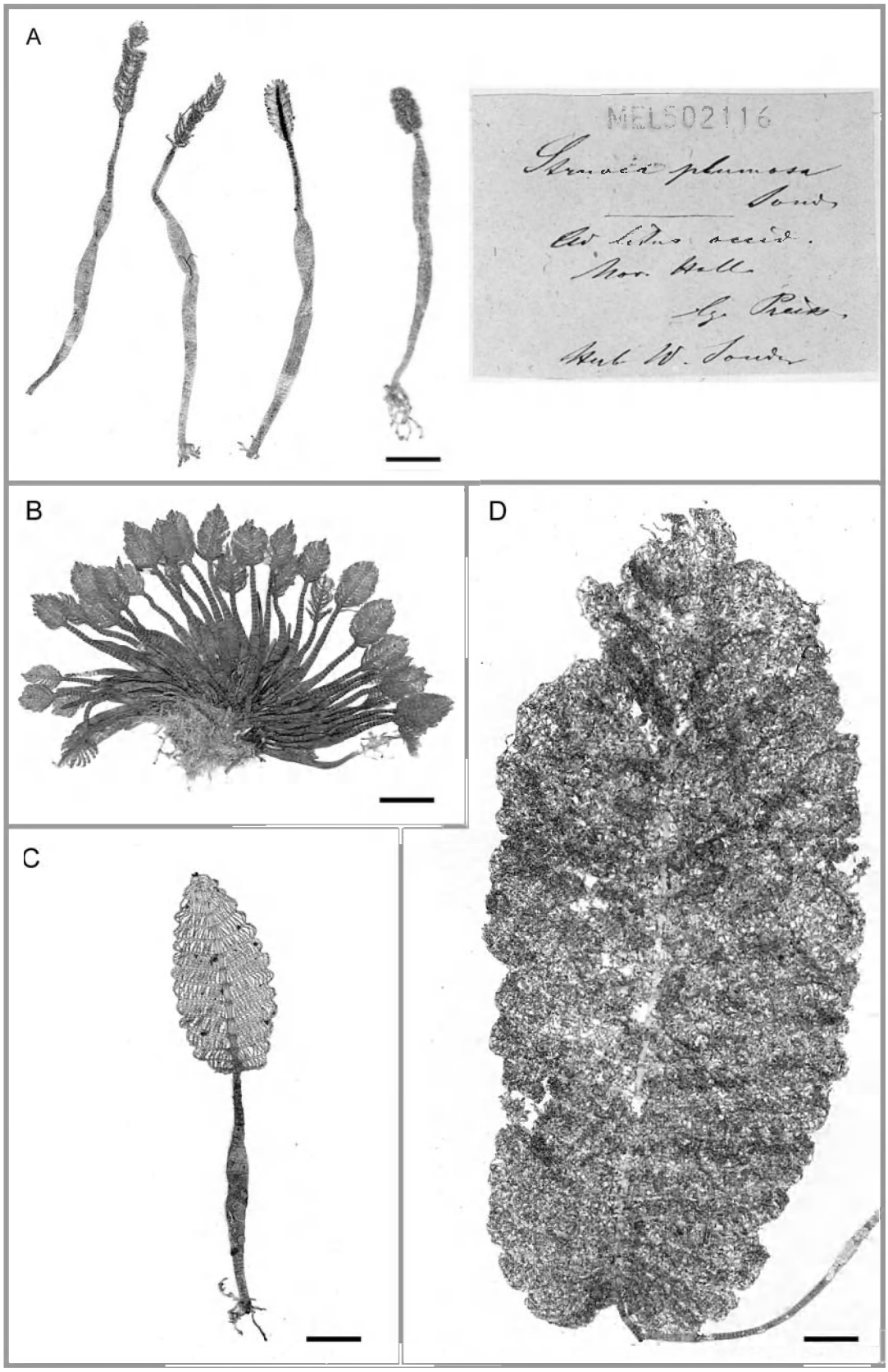


Fig. 66. *Cladophoropsis plumosa*. **A.** Lectotype of *Struvea plumosa* (MEL); **B.** Clustered, markedly annulated stipes bearing young blades (MEL 666897); **C.** Mature lamina with a prominent central axis and regular, opposite branch-systems lying essentially in one plane (MEL 666898); **D.** Large blade from Champion Bay, Western Australia (MEL 666902). Scale bars = 1 cm.

Stipe cell 0.8-3.5 (-5) mm in diameter, tapering towards both extremities to 640-1125 µm, 1-8 cm long. Tenacular cells 110-150 µm in diameter, 60-75 µm long.
Cell walls relatively thick, 6-8 µm in the terminal branch systems, up to 40 µm thick in the cells of the central axis and stipe.
Chloroplasts polygonal or round, 2.5-5.5 µm in diameter, each with a single pyrenoid, ca. 2 µm in diameter, forming an open to more or less closed parietal reticulum.
Prismatic calcium oxalate crystals present in most cells of the thallus (except for the young laterals and tenacular cells), 1-5 per cell, generally diamond-shaped (occasionally triangular or pentagonal), 5-27 (-32) µm in diameter (Fig. 4G).

Ecology: Low intertidal rockpools to deep subtidal (down to 33 m depth), epilithic (Womersley 1984: 220).

Distribution: *C. plumosa* is a common Australian species, occurring from Champion Bay (Geraldton, W Australia) around Australia to Encounter Bay (Victor Harbour, S Australia).

Specimens examined: **Indian Ocean: Western Australia.** Champion Bay, Western Australia, (unknown collector, no. 26, MEL 666902); Fremantle, (leg. Harvey 56a, MEL 666900 & S); Fremantle, (leg. Harvey, Harvey's Australian Algae no. 21, 1853, AK 26763); Fremantle, low intertidal rock pools, (leg. Harvey 567a, BM 563704); Swan River, (leg. Drummond s.n., BM 563701); (leg. Preiss s.n., BM 563702: syntype of *S. plumosa*); **South Australia.** Elliston, inner reef pools, (leg. Womersley A15 194e, 15.i.1951, S); Elliston, low intertidal, (leg. Womersley, Marine algae of southern Australia 169, 9.i.1976, AK 144137, L 353318 & MEL 666897); Head of Great Australian Bight, (leg. Womersley 234/b2 (A19,144), 4.ii.1954, MEL 666899); Nuarlunga Reef, (leg. Ashby A65c, 28.i.1944, AKU VWL7640); Pt. Sinclair, low intertidal, (leg. Womersley s.n., 25.i.1951, L 952 74 205); unknown locality (M); Venus Bay, reef pools, (leg. Womersley A 15, 168 c, S); Ward Island, W of Flinders Island, (leg. Sheperd A50877, 3.iii.1980, MEL 666898); Ward Island, W of Flinders Island, (leg. Shepherd 169b, 3.iii.1980, L 366042); Ward Island, W of Flinders Island, subtidal, 13-17 m deep, (leg. Shepherd 169b, 9.i.1976, AK 154665); **unknown Australian locality.** (leg. Berger s.n., 1854, M); (leg. Preiss s.n., L 937 183 106); (leg. Preiss s.n., L 937 183 108); (leg. Preiss s.n., MEL 502116: lectotype of *S. plumosa*); (leg. Preiss s.n., S: syntype of *S. plumosa*); (leg. von Mueller 249, MEL 666901); (unknown collector, M); (unknown collector, MEL 666896).

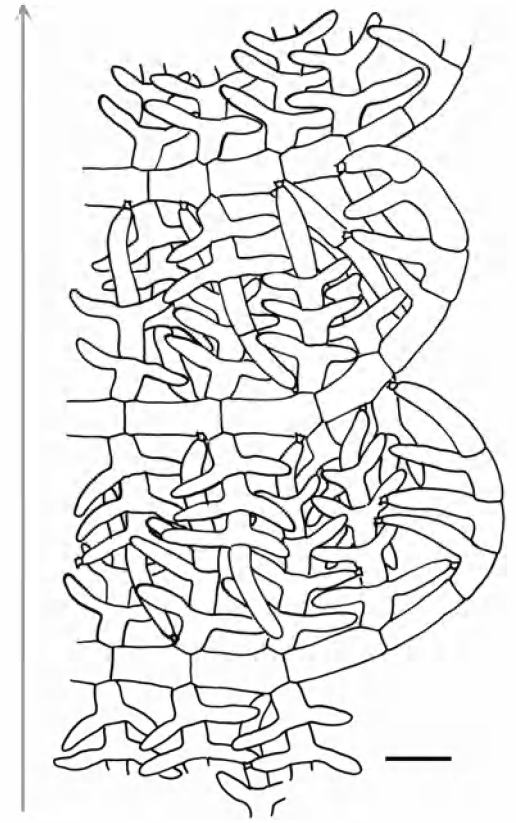


Fig. 67. *Cladophoropsis plumosa* (MEL 666898). Opposite branchlets in the middle part of the lamina and adaxial, unilateral branchlets forming the blade margin. The grey arrow represents the direction of the central axis. Scale bar = 1 mm.

Notes:
Struvea plumosa is the only species described by Sonder (1845: 4) in his new genus *Struvea*. The original description of the species is very cryptic and it was not until Kützing (1856: Tab. 90) and Harvey (1858: Pl. 32) illustrated the species, that the genus became better known. In their structural and systematic account of the genus *Struvea*, Murray & Boodle (1888b: 265-282, Pl. 16: fig. 1) described and illustrated the species in great detail. According to Womersley (1984: 220) *C. plumosa* is one of the most distinctive of the southern Australian marine algae and shows remarkable seasonal development of the stipitate, reticulate blades from the densely massed stipes. Near the distribution margins, in shallow water and in winter, the thallus of *C. plumosa* often remains limited to the stipes (Womersley 1984: 218). This growth form is scarcely recognizable as "*Struvea*" and is remarkably similar to the stipes of *Apjohnia laetevirens* Harvey. Mature thalli of *C. plumosa* can easily be distinguished from the other species in the sections *Struvea* and *Phyllodictyon* by the very coarse stipe with distinct annular constrictions, tapering towards both extremities.

Harvey (1855b) distinguished *S. macrophylla* from *S. plumosa* on the basis of the larger thallus size, the more complicated branch pattern, and the longer blade cells. Murray & Boodle (1888b: 269) noted that the developmental stages in both species were similar, and they believed that both species were closely related. Comparing a range of specimens, Womersley (1956: 377-378) regarded *S. macrophylla* as an older state of *S. plumosa*.

Valonia radicans is referable to the young developmental stages of *C. plumosa* (i.e. young stipes consisting of an elongate, clavate vesicle) according to Womersley (1956: 377).

General references. As *Struvea plumosa*: Kützing (1856: 31, Tab. 90); Harvey (1858: Pl. 32); Murray & Boodle (1888b: 265-282, Pl. 16: fig. 1); Womersley (1956: 377-378; 1984: 218-220, fig. 73B, C); Kraft & Wynne (1996: 131, figs 1-15); Huisman (2000: 242, + 2 figs). As *S. macrophylla*: Harvey (1858: Pl. 7); Murray & Boodle (1888b: 265-282, Pl. 16: fig. 2).

7.6. Section *Chamaedoris* (Montagne) Leliaert & Coppejans stat. nov. & comb. nov. prov.

Thallus forming erect, stipitate capitula, composed of branched filaments, attached to the substratum by branching rhizoids sprouting from the base of the stipe. Stipe unicellular, with numerous annular constrictions over the entire length. Distal end of the stipe with or without small superimposed cells, formed by segregative cell division of the stipe cell. Capitulum filaments developing from the distal end of the stipe cell and from superimposed cells. Growth of the capitulum by apical and intercalary cell divisions (by centripetal invaginations of the cell walls), cell elongation and formation of a single lateral; older cells may produce a second, opposite lateral. Reinforcement of the capitulum by entangling of the filaments and by anastomosis of adjacent filaments by type-3 tenacular cells, produced laterally.

The section contains four species, namely *C. auriculata*, *C. delphinii*, *C. arbuscula* and *C. peniculum*. The differences between the four species are listed in Table 8.

Table 8. Comparison of the 4 species in the section *Chamaedoris*.

	C. auriculata	*C. delphinii*	*C. arbuscula* (= *Chamaedoris orientalis* Okamura & Higashi)	*C. peniculum*
Thallus height	4-12 cm	4-8 cm	5-20 cm	2-10 cm
Number of superimposed cells on the stipe cell	1-2	none	13-28	0-3
Capitulum shape and dimensions	flat, auriculate, 2-12 cm in diam.	globose, up to 1.5 cm in diam.	oblong to globose, up to 2.5-10 cm long, 2-4 cm in diam.	cup-shaped to sub-globose, 3-10 cm in diam.
Diameter capitulum filaments	60-155 µm	60-200 µm	320-490 µm	80-175 µm
Prismatic calcium oxalate crystals	absent	absent	elongate prismatic	diamond shaped
Tetrahedral protein crystals	present	present	absent	absent
Ecology	low intertidal to subtidal (-18 m)	mid intertidal rock pools to subtidal (-15 m)	shallow subtidal (-6 m)	shallow to deep subtidal (-50 m)
Type locality* and geographical distribution	India*, tropical East Africa	Madagascar*, (sub)tropical southern East Africa and Mauritius	Taiwan*, tropical West Pacific Ocean	Florida*, Caribbean and South Pacific

Cladophoropsis auriculata (Børgesen) Leliaert & Coppejans, comb. nov. prov.

Figs 68-70

Chamaedoris auriculata Børgesen, 1933: 5-9, text-figs 3-5 [Lectotype: Dwarka, Gujarat, India, leg. Børgesen 5447, C!. Four herbarium specimens, all from the same locality with number Børgesen 5447, are present in C; the largest specimen is here indicated as lectotype; the others becoming isolectotypes].

Description:

Thallus medium to dark green, forming erect, stipitate capitula, 4-12 cm high, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe cells; rhizoids giving rise to new stipe cells. Stipe cells single to densely clustered (a few to over 100), single-celled, with annular constrictions over the entire length, unbranched or occasionally branched. Capitulum flat, growing eccentrically to one side, penicillate to spatulate when young, later becoming auriculate to peltate, diameter up to 12 cm, about 2-4 mm thick (Fig. 68).

Young stipes cylindrical, gradually becoming annularly constricted from the base upwards. When reaching their full size, one or two small cells being formed at the swollen apex of the stipe cell by segregative cell division, followed by the formation of the capitulum. Capitulum filaments arising in whorls from the swollen apex of the stipe cell and from the one or two small cells formed at the top of the stipe (Fig. 69I). Cell division of the capitulum filaments by centripetal invagination of the cell walls or by segregative cell division (Fig. 69D-F). Growth of the capitulum by apical and intercalary cell division, followed by cell-elongation. Each new cell, after being divided from the apical cell, giving off one lateral at its apical pole; the basal cells of the capitulum possibly forming a second lateral (Fig. 69A-C, J-K). Filaments of young or small capitula often fastigiate (Fig. 69A-B); filaments of larger capitula generally curved or sinuous (Fig. 69C, J-K). Cross wall formation at the base of the laterals markedly delayed; l/w ratio of laterals in open connection with the mother cell up to 80. Branching of the capitulum filaments up to the 4th order. The diameter of the basal capitulum cells 2-5 times that of the apical cells. Angle of ramification 4°-60°.

Structural reinforcement of the capitulum achieved by entanglement of the filaments (filaments often sinuous, facilitating entanglement) and by anastomosis of adjacent cells by means of laterally inserted, type-3 tenacular cells (Fig. 69L-P, 70A-B), often extremely elongated and rhizoidal (Fig. 69G). Filaments of adjacent capitula possibly becoming intricated and attaching by type-3 tenacular cells (Fig. 68E-F).

Apical cells of the capitulum filaments 60-130 µm in diameter, 110 µm -11 mm long; cells of the main capitulum filaments 72-155 µm in diameter, 135 µm - 11 mm long; basal capitulum cells 220-360 µm in diameter, 300-2250 µm long. Diameter of stipe cell 900-1500 µm in the middle part, slightly tapering towards both extremities, 2-7.5 cm long. Tenacular cells 32-75 µm in diameter, 50-400 µm long.

Cell wall thickness of the capitulum filaments increasing from 2-8 µm in the terminal branch systems to 25-40 µm in the basal filaments. Cell walls of the stipe cell markedly stratified, up to 75 µm thick.

Chloroplasts rounded, 2.6-4 µm in diameter, forming an open to relatively closed parietal network. Most chloroplasts containing a single pyrenoid, ca. 1.3 µm in diameter.

Tetrahedral protein crystals abundant and scattered among the chloroplasts of the stipe cell; less frequent in the capitulum filaments; up to 45 µm in diameter. Star-shaped clusters of fine needle-shaped crystals (possibly silica) present in the capitulum filaments, ca. 40 µm in diameter. Calcium oxalate crystals absent.

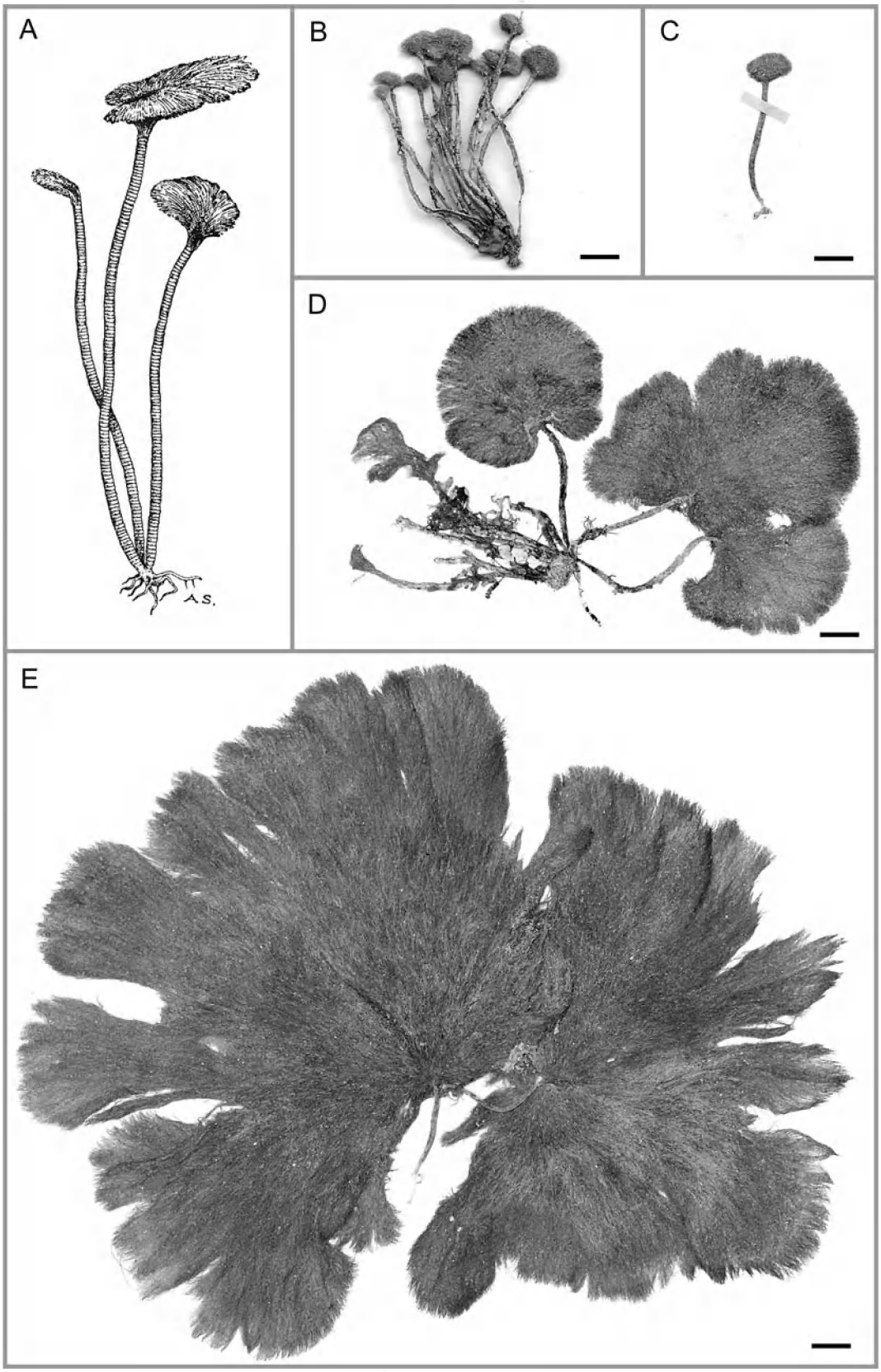


Fig. 68. *Cladophoropsis auriculata*. **A.** Original drawing of the type material (Børgesen 1933); **B.** Clustered stipes forming small, auriculate capitula (lectotype, C); **C.** isolectotype (C). **D-E.** Plant from deep water forming large, often intricated capitula (SOC 370). Scale bars = 1 cm.

Ecology: Low intertidal to subtidal (down to 18 m deep), epilithic on vertical or horizontal substratum, or epiphytic on e.g. stems of the seagrass *Thalassodendron* stems. Plants from deeper water form large flat capitula. The stipes are often completely epiphytized by crustose coralline rhodophytes.

Geographic distribution: Besides numerous records from India, *C. auriculata* is a common species along the tropical African coast where it has been reported for Somalia (Sartoni 1992), Kenya (Isaac 1967, Coppejans *et al.* 2000: 63), Tanzania including Zanzibar and Mafia Island (Coppejans *et al.* 2000: 63), Mozambique, South Africa and Socotra (this paper).

Specimens examined: **Indian Ocean: India**. Dwarka, (leg. Børgesen 5447, 1927-1928, C: holotype *Chamaedoris auriculata*); **Kenya**. Kanamai, shallow subtidal, 1 m deep, outer side of the reef, (leg. Coppejans, 13.ix.1991, HEC 8760); Nyali Reef, Mombasa, subtidal, wave exposed seaward side of the reef, epilithic, (leg. Coppejans, 26.ix.1991, HEC 8877); Kanamai, (leg. Coppejans, 29.vii.1987, HEC 7032); Mambrui, 10 km N of Malindi, (leg. Coppejans, 27.xii.1988, HEC 8169); **Mauritius**. unknown locality, (leg. Collins s.n., NY); Gabriel Island, (leg. Pike s.n., 8.iii.1871, NY); Fort George, (leg. Pike s.n., 1872, NY); **Mozambique**. Praia Chokas, N of Lumbo, (leg. Papenfuss & Scagel PR-28-6, 15.xi.1962, L 385004); **South Africa**. Linkia Reef, subtidal, 15 m deep, epilithic, (leg. Coppejans *et al.*, 15.viii.1999, KZN 0694); Kosi Bay, KwaZulu-Natal, intertidal rock pools, (leg. Coppejans *et al.*, 16.viii.1999, KZN 0765); Bhanga Nek, KwaZulu-Natal, intertidal, (leg. Coppejans *et al.*, 15.viii.1999, KZN 0710); Treasure Beach, Bluff, Durban, KwaZulu-Natal, infralittoral fringe rock pools, epilithic on vertical & overhanging walls, (leg. Coppejans *et al.*, 3.viii.1999, KZN 0083); **Sri Lanka**. unknown locality, (leg. Pike, 1861, NY); **Tanzania**. Chole Bay, Mafia Island, infralittoral fringe, horizontal coral substratum, (leg. Coppejans & De Clerck, 9.i.1996, HEC 11155); Ras Fumba, Zanzibar, shallow subtidal, 1 m deep, epilithic on vertical coral walls, (leg. Coppejans & De Clerck, 25.viii.1994, HEC 10635); Nungwi, Zanzibar, shallow subtidal, 5 m deep, seaward side of the reef, (leg. Coppejans & De Clerck, 23.viii.1994, HEC 10556); in front of Bahari Beach Hotel, Kunduchi, N of Dar es Salaam, shallow subtidal, 2 m deep, epilithic on rock covered with *Jania*, in *Thalassodendron* bed, (leg. Coppejans & De Clerck, 3.i.1996, HEC 11046); in front of Sea Safari Lodge, Ruvula beach, Mnazi Bay, Mtwara area, subtidal, 18 m deep, on coral fragments, (leg. Coppejans *et al.*, 24.vii.2000, HEC 12880; 9.viii.2000, HEC 14201); Ruvula beach, Mnazi Bay, shallow subtidal, 3 m deep, epiphytic on a *Thalassodendron* stem, (leg. Coppejans *et al.*, 13.viii.2000, HEC 14241); S coast of Mbutya Island, shallow subtidal, 4 m deep, epiphytic on *Thalassodendron* stem, (leg. Leliaert, 11.vii.2001, FL 906); Kunduchi, N of Dar es Salaam, shallow subtidal, wave exposed, epilithic, (leg. Dargent, 5.viii.1997, HEC 12178); **Yemen**. W of Rhiy di-Diblih, Nogid, S coast of Socotra, subtidal, 6 m deep, epilithic on sand covered rock, between dense seaweed vegetation (leg. Leliaert, 15.iii.1999, SOC 344, SOC 398); Mahfirhin, Socotra, subtidal, 10 m deep, epilithic on sand covered rock, (leg. Leliaert, 16.iii.1999, SOC 438); Steroh, Nogid, S coast of Socotra, subtidal, 15 m deep, epilithic, (leg. Leliaert, 14.iii.1999, SOC 370); 3 km W of Bidholih, Nogid, S coast of Socotra, subtidal, 15 m deep, epilithic on horizontal rock, (leg. Leliaert, 14.iii.1999, SOC 395, SOC 396); Ghubbah di-Net, SW coast of Socotra, subtidal, 6 m deep, epilithic on vertical rock wall, (leg. Leliaert, 3.iii.1999, SOC 273); Quray, East of Qatanhin, Socotra, (leg. Schils, 9.iv.2000, sMM 226, sMM 239); East of Bedolah, Socotra, (leg. Schils, 1.v.2000, sMM 476); Bay of Mahfirin, Socotra, subtidal, (leg. Schils, 22.iv.2000, sMM 349, sMM 394); West of Bedolah, Socotra, (leg. Schils, 30.iv.2000, sMM 466).

Note: As pointed out by Børgesen (1933: 8) the main difference between *C. auriculata* and *C. peniculum* is the shape of the capitulum which is relatively constant in both species. In *C. auriculata* the capitulum filaments are formed in whorls on the apical part of the stipe and on the small, apical, superimposed cell(s), and grow out to one side, resulting in an eccentric capitulum. Older capitula are auriculate and sometimes become secondarily peltate by closure and anastomosis of the auriculate ends (Fig. 68E). In *C. peniculum* the capitulum filaments are also formed in whorls on the apical part of the stipe and on the superimposed cells, but in this species the filaments do not grow unilateral, resulting in a flat, peltate or cup-shaped capitulum. *C. delphinii* differs from *C. auriculata* by the ball-shaped capitula, the absence of superimposed cells on the stipe, and the slightly thicker capitulum filaments. The distinction between both species is somewhat blurred up by Sartoni (1992) who erroneously illustrates *C. delphinii* with superimposed cells on the stipe.

General reference: Sartoni (1992: 308, figs 8A, 9A).

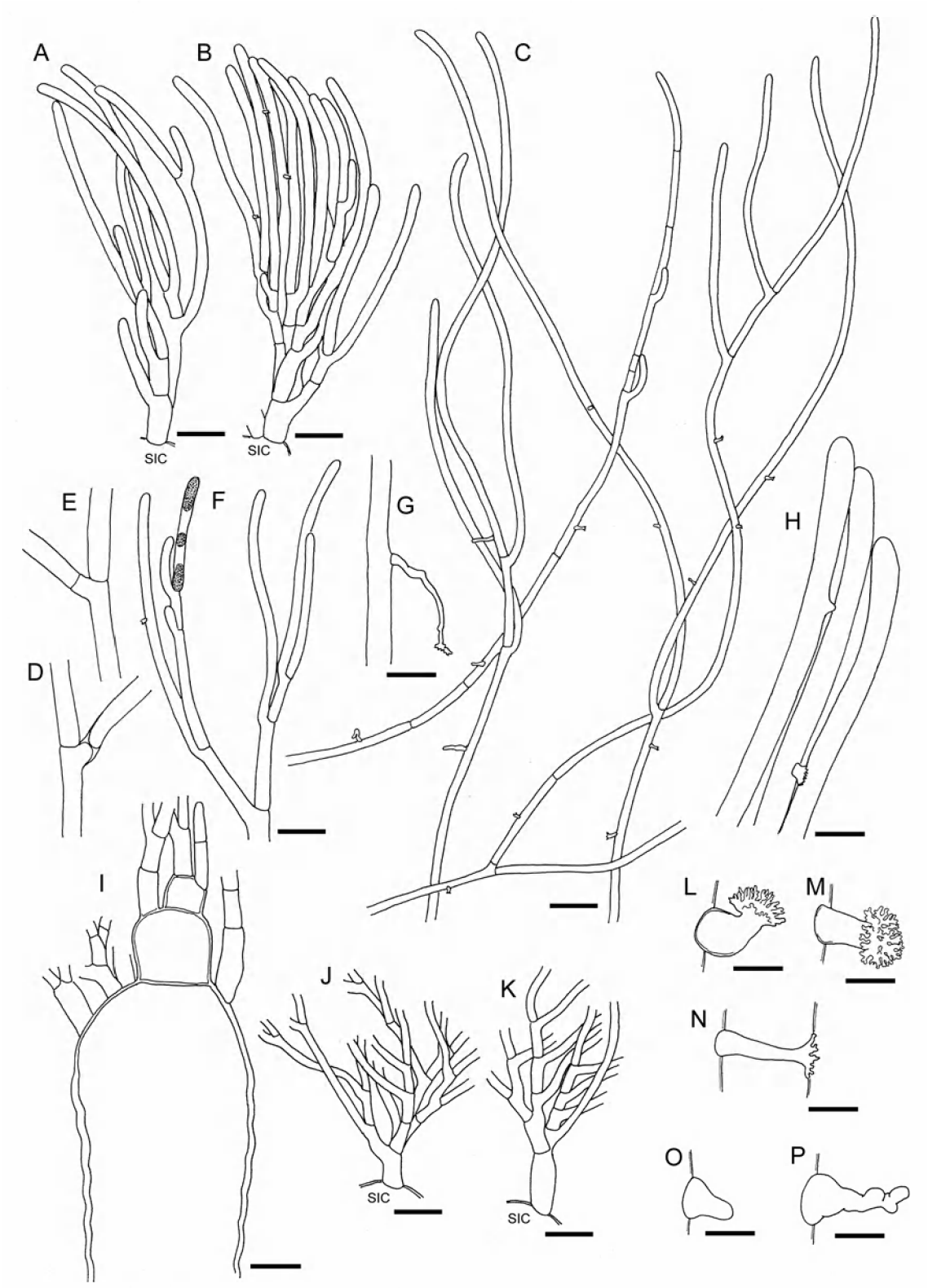


Fig. 69. *Cladophoropsis auriculata.* **A-B.** Unilaterally branched filaments of a small capitulum; **C.** Filaments of a large capitulum with numerous, laterally formed tenacular cells; **D-E.** Cross wall at the base of a lateral, formed by segregative cell division; **F.** Apical cell undergoing segregative cell division; **G.** Extremely elongated (rhizoidal) type-3 tenacular cell; **H.** Fastigiate filaments attaching by a type-3 tenacular cell; the upper tenacular cell undeveloped; **I.** Distal end of annulated stipe and two superimposed cells, producing whorls of capitulum filaments; **J-K.** Basal branches of the capitulum; **L-N.** Type-3 tenacular cells; **O-P.** Developing tenacular cells. (A-B: KZN 83; C-P: SOC 396). Scale bars: A-C, F, I-K = 500 µm; D-E, G-H = 200 µm; L-P = 50 µm. SIC = superimposed cell.

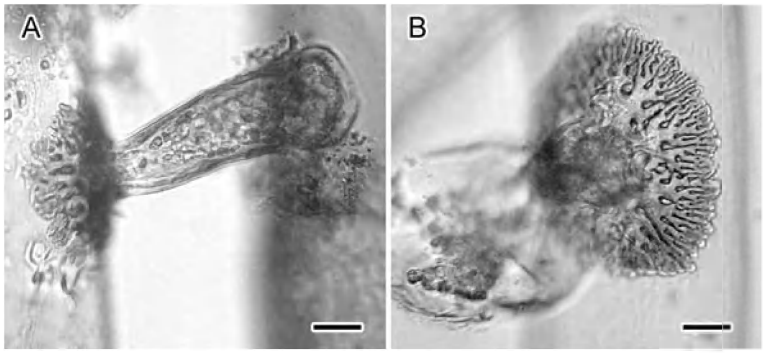


Fig. 70. *Cladophoropsis auriculata*. **A-B.** Type-3 tenacular cells (KZN 694). Scale bars = 20 µm.

Cladophoropsis delphinii (Hariot) Leliaert & Coppejans, comb. nov. prov. Figs 71, 72

Siphonocladus delphinii Hariot, 1902: 470 [Holotype: Fort-Dauphin, Madagascar, leg. M. Ferlus, herbier général, case 69, PC!. The holotype consisting of a single capitulum lacking a stipe. One microscopic slide, made from the holotype material by Børgesen and consisting of capitulum filaments only, is present in C!].

Chamaedoris delphinii (Hariot) J. Feldmann & Børgesen, *in* Børgesen, 1940: 16-20, 21, footnote, fig. 5, pl. 1.

Description:

Thallus dark green, erect, forming erect stipitate capitula, 4-7 (-8) cm high (Fig. 71), attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe cell (Fig. 72D); rhizoids giving rise to new stipe cells. Stipes single to densely clustered (a few to over 100), single-celled, with annular constrictions over the entire length. Young capitula penicillate, becoming ball-shape when older (incurving filaments), 5-15 (-18) mm in diameter, 2-15 (-23) mm high.

Young stipes cylindrical to slightly clavate, gradually becoming annularly constricted from the base upwards. When fully grown, filaments are formed unordered at the apex of the stipe to form the capitulum (Fig. 72C). Cell division of the capitulum filaments by centripetal invagination of the cell walls or by segregative cell division. Growth of the capitulum mainly by apical cell division, followed by cell-elongation. After being cut off from the apical cell, each new cell producing one lateral at its apical pole; the basal cells of the capitulum possibly forming a second lateral (Fig. 72A-B). Cross wall formation of the branches delayed; l/w ratio of laterals in open connection with the mother cell up to 38. Branching of the capitulum filaments up to the 3rd order. Diameter of the basal capitulum cells 2-6 times that of the apical cells. Angle of ramification 15°-60°.

Structural reinforcement of the capitulum mainly by entanglement of the filaments (facilitated by the curved or sinuous filaments), in some plants also by anastomosis of capitulum filaments by means of laterally inserted type-3 tenacular cells (Fig. 72E-F).

Apical capitulum cells 60-130 µm in diameter, 220-5250 µm long; cells of the main capitulum filaments 90-200 µm in diameter, 150-6000 µm long; basal capitulum cells 160-400 µm in diameter, 250-1250 µm long. Diameter of the stipe cell 1300-1650 µm at the apex, tapering to 400-950 µm at the base, 2-7 cm long. Tenacular cells 40-70 µm in diameter, 70-400 µm long.

Cell wall thickness of the capitulum filaments increasing from 2-6 µm in the terminal branch systems to 8-35 µm in the basal filaments. Cell walls of the stipe markedly stratified, up to 55 µm thick.

Chloroplasts polygonal to rounded, 4-7 μm in diameter, forming an open parietal reticulum. Most chloroplasts containing a single pyrenoid, 1.5-2.8 μm in diameter.
Protein crystals abundant and scattered among the chloroplasts of the stipe cell, less frequent in the capitulum filaments. Protein crystals tetrahedral when small, growing into 4-armed structures, up to 85 μm in diameter. Star-shaped clusters of fine needle-shaped crystals (possibly silica) present in the capitulum filaments, ca. 40 μm in diameter. Calcium oxalate crystals absent.

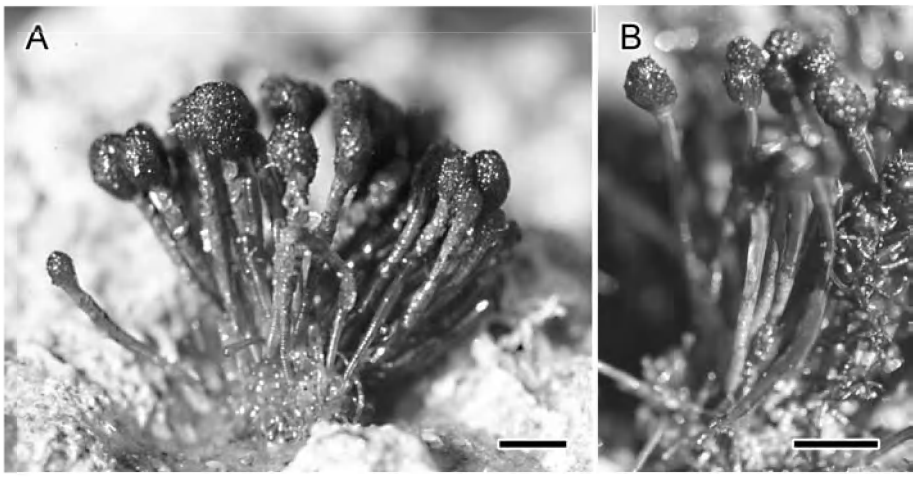


Fig. 71. *Cladophoropsis delphinii*. **A-B.** Habit (A: KZN 769; B: KZN 215). Scale bars = 1 cm.

Ecology: Epilithic in mid to low intertidal rock pools or subtidal (down to 15 m deep), on vertical or horizontal substrates. The stipes are often completely covered by the crustose coralline red algal epiphyte *Pneophyllum amplexifrons* (Harvey) Chamberlain & Norris (Chamberlain & Norris 1994: 10, fig. 4).

Geographic distribution: *C. delphinii* is a common species along the (sub)tropical southern East African coast [Mozambique (Isaac 1956: 172, pl. XXXVIII), South Africa (Papenfuss 1952: 167)], Madagascar (type locality) and Mauritius (Børgesen 1940: 16). The records from the tropical East African coast remain doubtful [Somalia (Sartoni, 1992: 311), Kenya (Gerloff 1960: 611), Tanzania (Jaasund, 1976: 11)].

Specimens examined: **Indian Ocean: Madagascar**. Balise, N of Tuléar, subtidal, 15 m deep, on horizontal rock substratum, (leg. Coppejans *et al.*, 20.viii.2002, HEC 15087); Fort-Dauphin, (leg. Ferlus s.n., PC: holotype *Chamaedoris delphinii*); Plage de Monseigneur, Fort Dauphin, low intertidal rock pools, epilithic on horizontal rock substratum, (leg. Coppejans *et al.*, 31.viii.2002, HEC 15236); unknown locality, (leg. Børgesen s.n., C); **Mauritius**. unknown locality, (unknown collector, NY); **Mozambique**. Ponta Abril, (leg. Isaac 699, 22.vii.1956, L 095901); Santa Maria, near Inhaca Island, (leg. Isaac 146, 19.vi.1954, L 095898); **Rodrigues**. Cotton Bay, mid intertidal rock pools, epilithic on vertical walls, (leg. Coppejans, 18.ix.2001, HEC 14617); **South Africa**. Bluff, Durban, KwaZulu-Natal, (leg. Weber-van Bosse s.n., 1894, L 936 73 446); Durban, (unknown collector, S); Durban, KwaZulu-Natal, (leg. Krauss 326.1, BR); Durban, KwaZulu-Natal, (leg. Weber-van Bosse s.n., 1894, BR); Isipingo, KwaZulu-Natal, (leg. Weber-van Bosse s.n., 1894, L 936 73 463; 1894, NY; xi.1894, BR); Isipingo, KwaZulu-Natal, mid- to low intertidal pools, epilithic on vertical walls, (leg. Coppejans, 21.i.1995, HEC 10945); Island Rock, KwaZulu-Natal, intertidal rock pools, (leg. De Clerck & Cocquyt, 14.viii.2000, KZN 1704); Kosi Bay, KwaZulu-Natal, intertidal rock pools, (leg. Coppejans *et al.*, 16.viii.1999, KZN 0763); Mabibi, KwaZulu-Natal, infralittoral fringe rock pools, (leg. Coppejans *et al.*, 9.viii.1999, KZN 0372; leg. De Clerck & Cocquyt, 13.viii.2000, KZN 1652); Mission rocks, KwaZulu-Natal, intertidal rock pools, (leg. De Clerck & Cocquyt, 17.viii.2000, KZN 1765); Mission Rocks, KwaZulu-Natal, mid- to low intertidal pools, epilithic on vertical walls, (leg. Coppejans, 23.xi.1995, HEC 11028.1); Mission Rocks, KwaZulu-Natal, shallow subtidal, (leg. Bolton, 8.vii.1998, KZN 1047); Palm Beach, KwaZulu-Natal, intertidal rock pools, (leg. Coppejans *et al.*, 19.viii.1999, KZN 0853); Palm Beach, KwaZulu-Natal, intertidal rock pools, (leg. Coppejans *et al.*, 19.viii.1999, KZN 0839); Rabbit Rock, intertidal, (leg. Coppejans *et al.*, 13.viii.1999, KZN 0541); Rabbit Rock, intertidal, (leg. Coppejans *et al.*, 13.viii.1999, KZN 0539); Sodwana Bay, 2 Mile Reef, KwaZulu-Natal, subtidal, 12 m deep, (leg. De Clerck & Leliaert, 10.ii.2001, KZN 2110); Sodwana Bay, KwaZulu-Natal, intertidal pools, (leg. Coppejans *et al.*, 8.viii.1999, KZN 0215); St. Lucia, KwaZulu-Natal, (unknown collector, BR); Wahlberg, (unknown collector, S).

Note: Although Hariot (1902: 470) provided a fairly detailed original description of *Siphonocladus delphinii*, it was only after Børgesen's (1940) publication that this species became widely known as *Chamaedoris delphinii* (see the large number of records of this species in Silva *et al*. 1996). *C. delphinii* differs from the other species in the section primarily by the lack of small super-imposed cells on the stipe.

General reference: Børgesen (1940: 16-20, fig. 5).

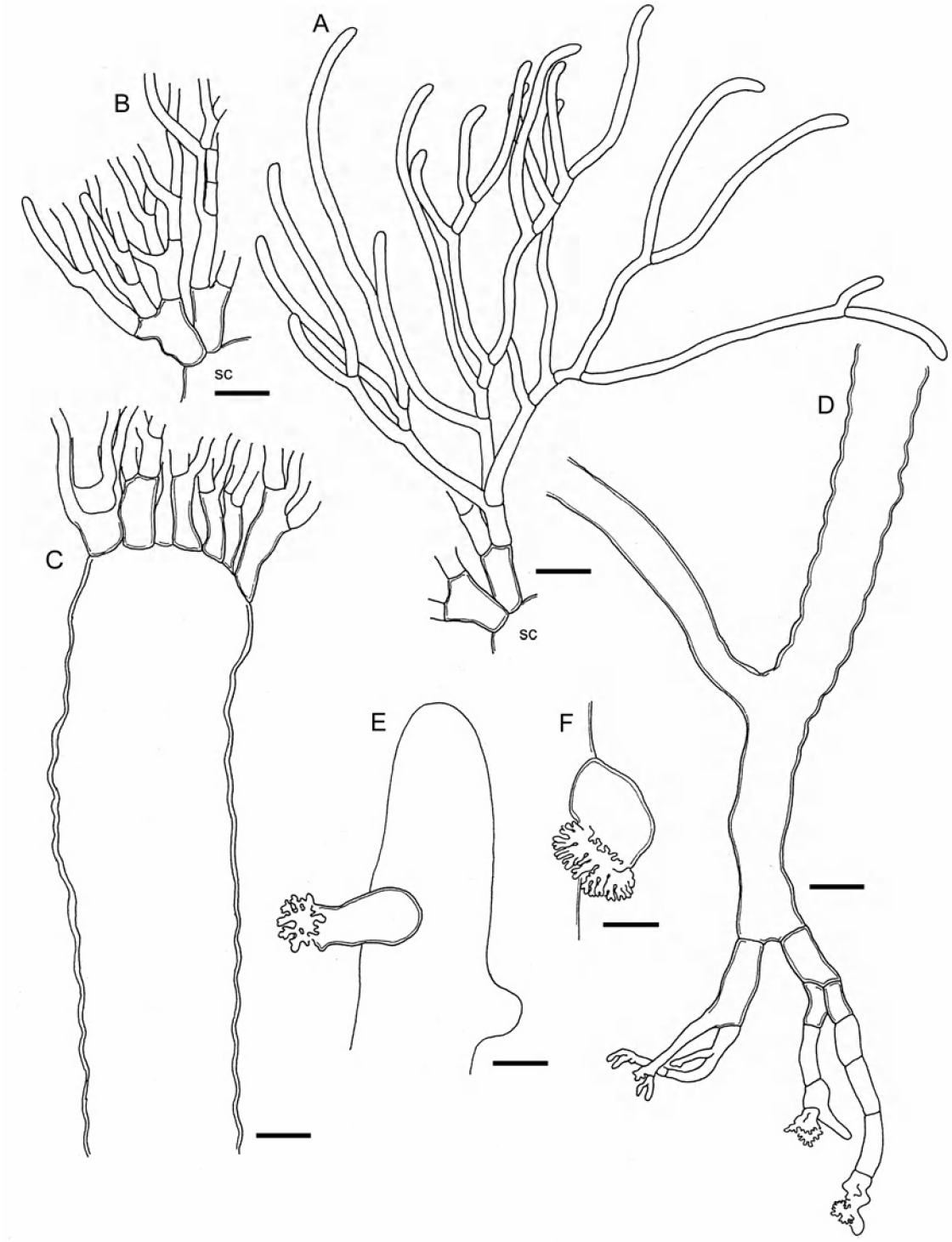


Fig. 72. *Cladophoropsis delphinii*. **A.** Unilaterally branched capitulum filaments; **B.** Basal branches of the capitulum; **C.** Distal end of annulated stipe without superimposed cells and producing the capitulum filaments; **D.** Proximal pole of branched, annulated stipe; septate type-1 rhizoids developing from the base; **E-F.** Type-3 tenacular cells. Scale bars: A-D = 500 µm; E-F = 50 µm. SC = stipe cell.

Cladophoropsis arbuscula Leliaert & Coppejans, nom. nov. prov. Figs 73, 74

Chamaedoris orientalis Okamura & Higashi, *in* Okamura, 1931: 98, pl. 10 [Type locality: Island of Kôtôsho (Botel Tobago), east of southern extremity of Taiwan, leg. Segawa. The location of the type material is uncertain, and is possibly present in the Imperial Fisheries Institute, Tokyo].

Description

Thallus yellowish green, erect, forming stipitate capitula, 5-20 cm high, attached to the substratum by branched, multicellular rhizoids arising from the lower pole of the stipe cells (Fig. 73A, C-D); rhizoids giving rise to new stipe cells. Stipes single to densely clustered (up to 20), single-celled, subcylindrical, with annular constrictions over the entire length, generally unbranched. Capitulum oblong, obovate, pyriform, or globose, diameter 2-4 cm, 2.5-10 cm high.

Young stipes gradually becoming annularly constricted from the base upwards. When fully grown, 14 to 28 small cells are formed at the swollen apex of the stipe cell (probably by segregative cell division), later becoming the central axis of the capitulum. Capitulum filaments arising in whorls of 3-6 from the swollen distal end of the stipe cell and cells of the central axis (Fig. 73B). Cell division of the capitulum filaments by centripetal invagination of the cell walls or by segregative cell division. Growth of the capitulum mainly by division of the apical cells, followed by cell-elongation. Each new cell, after being divided from the apical cell, giving off one lateral at its apical pole; lower down a second lateral may be produced (Fig. 74A-B). Cross wall formation of the branches delayed; l/w ratio of laterals in open connection with the mother cell, up to 8. In older cells, cross walls are steeply inclined to the parent cell. Branching of the capitulum filaments up to the 4th order. The diameter of the basal capitulum cells 1.4-2.2 times that of the apical cells. Angle of ramification 25°-65°.

Structural reinforcement of the capitulum by loosely entangling of the filaments and by occasional anastomosis of adjacent filaments by type-3 tenacular cells, laterally or (sub)terminally placed, 80-100 µm in diameter, 85-250 µm long (Fig. 74C-F).

Apical cells of the capitulum filaments 320-480 µm in diameter, 2500-8800 µm long; cells of the main capitulum filaments 330-490 µm in diameter, 2000-4500 µm long; basal capitulum cells 520-680 µm in diameter, 900-1300 µm long. Cells of the central axis 600-800 µm in diameter, 650-1900 µm long. Stipe cells 900-1500 µm in diameter in the middle part, slightly tapering towards both extremities, 4-7 cm long. Tenacular cells 80-100 µm in diameter, 150-250 µm long.

Cell wall thickness of the capitulum filaments increasing from 2-7 µm in the terminal branch systems to 6-40 µm in the basal filaments. Cell walls of the stipe markedly stratified, up to 60 µm thick.

Chloroplasts were not well preserved in the herbarium material and therefore their morphology could not be examined.

Prismatic calcium oxalate crystals abundant in the capitulum filaments (over 200 per cell) but absent in the stipe cell, needle-shaped, 10-30 µm long, ca. 0.5-1.5 µm wide. Protein crystals absent.

Ecology: Shallow subtidal (down to 6 m depth), epilithic on horizontal rock substratum.

Geographic distribution: *C. arbuscula* seems to be restricted to the tropical West Pacific Ocean. The species has been recorded from Taiwan (type locality), Ryukyu, Japan (Yamada 1934), Micronesia (Itono & Tsuda 1980; Tsuda 1981) and the Philippines (Gilbert & Doty 1969; Cordero 1977).

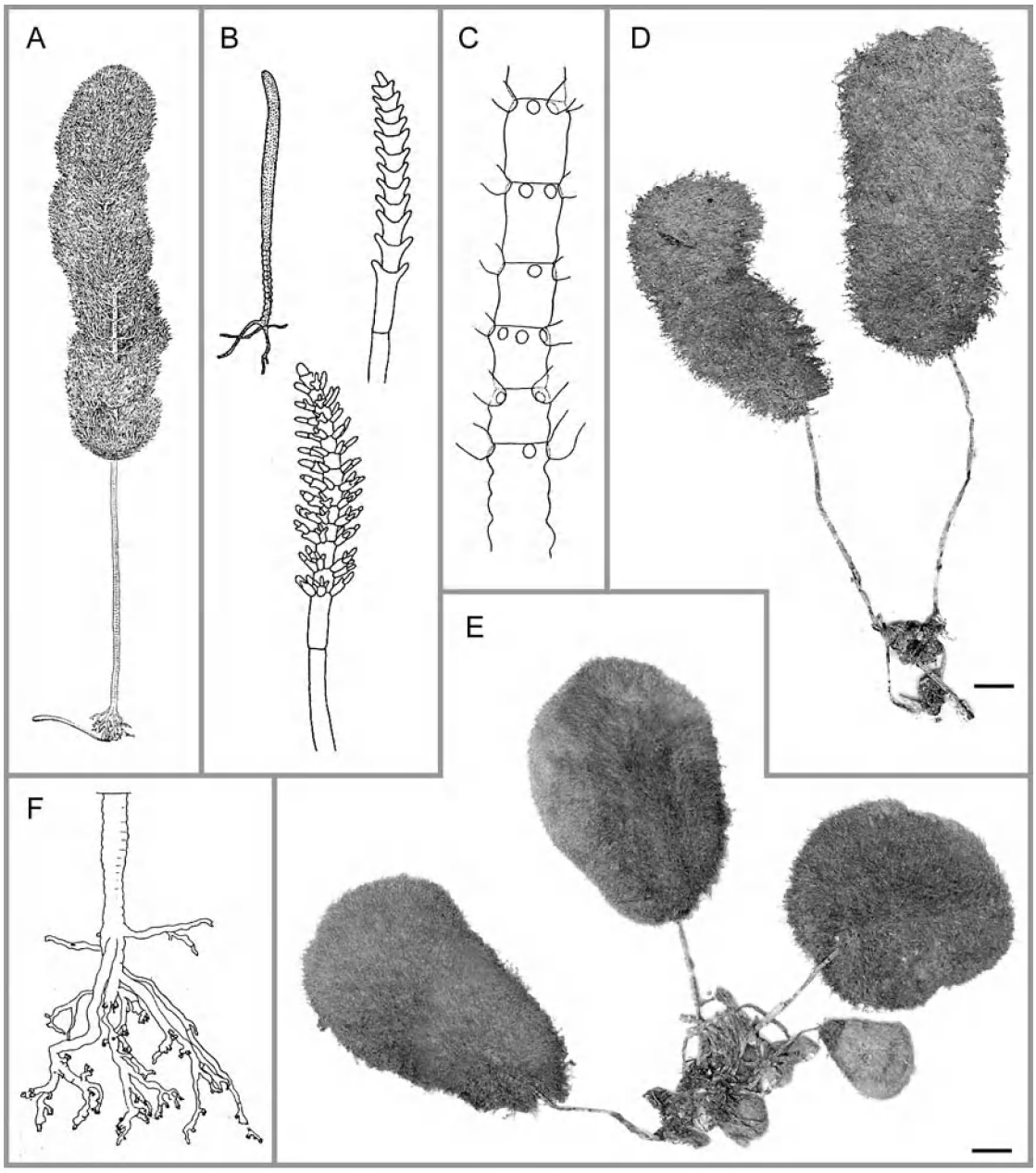


Fig. 73. *Cladophoropsis arbuscula*. **A.** Habit; some capitulum filaments removed, displaying the central axis; **B**. Early stages of thallus development: young cylindrical stipe with basal annular constrictions; apical division of the stipe cell into a large number of cells; each cell initially producing an opposite pair of laterals; later up to six laterals are formed per cell; **C.** Distal end of annulated stipe cell and cells of the central axis, producing whorls of capitulum filaments; **D, E.** Habit (HEC 12301: Philippines); **F.** Attachment to the substratum by rhizoids sprouting from the base of the stipe cell. [A: reproduced from Yamada (1934); B: reproduced from Hori (1994); C & F: reproduced from Okamura (1932)]. Scale bars = 1 cm.

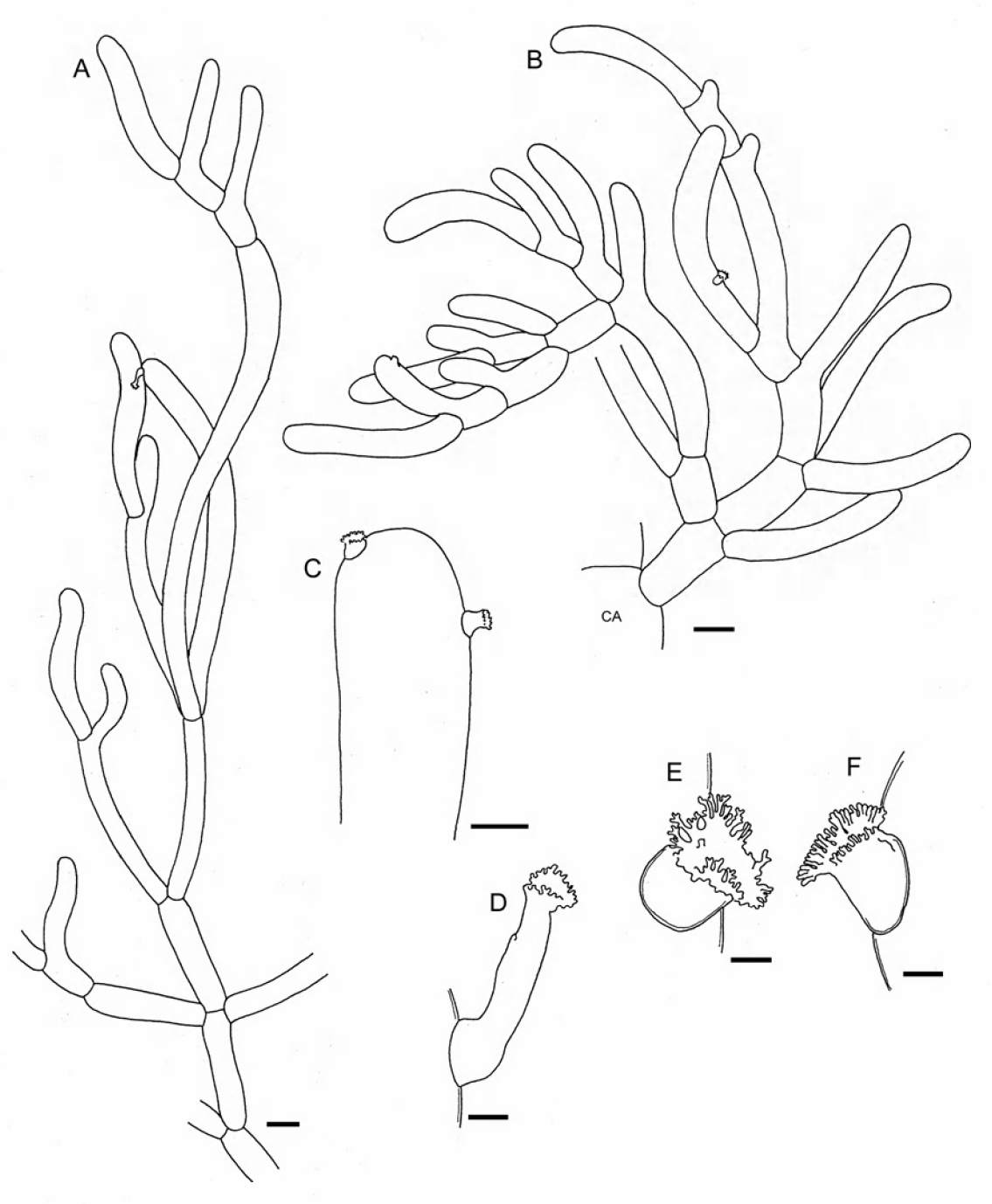


Fig. 74. *Cladophoropsis arbuscula* (HEC 12301). **A-B.** Capitulum filaments; ultimate branchlets unilateral, older cells producing a second, opposite lateral; **C-F.** Type-3 tenacular cells. Scale bars: A-B = 500 µm; C = 200 µm; D-F = 50 µm. CA = central axis.

Specimens examined: Pacific Ocean: Japan. Yonakuni Island, Ryukyu, (unknown collector, 15.iv.1935, NY); Yonakuni-jima, Ryukyu, (leg. Yamada s.n., 15.iv.1935, S); The Philippines. Dancalan, Bulusan, Sorsogon Province, (leg. Coppejans, 21.iv.1998, HEC 12289); Dapdap, Bulusan, Sorsogon Province, shallow subtidal, 6 m deep, epilithic on horizontal rock substratum of lagoon, (leg. Coppejans, 22.iv.1998, HEC 12301).

Notes:
In transferring *Chamaedoris orientalis* Okamura & Higashi to *Cladophoropsis*, a new epithet has to be chosen because of the older basionym of *Cladophoropsis orientalis* (A. Gepp & E. Gepp) Leliaert & Coppejans (= *Struvea orientalis* A. Gepp & E. Gepp 1908). We propose the name *C. arbuscula* based on the typical tree-like habit of the stipitate capitula.

C. arbuscula can be easily distinguished from the other species in the section by the generally oblong (sometimes globose) capitulum and the coarse capitulum filaments. Okamura (1932: 69) argues that the number of cells composing the central axis of the capitulum is always 14, regardless of the size (age) of the capitulum. Yamada (1934) however counted 28 cells in the central axis and argues that the number of cells is proportional to the length of the capitulum.

The diplohaplontic and isomorphic sexual life cycle of *C. arbuscula* has been studied and illustrated by Enomoto (*in* Hori 1994). It is remarkable that the early stages of thallus development, characterized by regular opposite laterals (Fig. 73B), are very similar to the sections *Phyllodictyon* and *Struvea*, while the branching patterns in mature thalli are typically unilateral and similar to some species in the section *Cladophoropsis*.

General references. As *Chamaedoris orientalis* Okamura & Higashi: Okamura (1932: 68, pl. 284, figs 8-15); Yamada (1934: 48-50, fig. 11).

Cladophoropsis peniculum (Ellis & Solander) Leliaert & Coppejans, comb. nov. prov.
Figs 75, 76

Corallina peniculum Ellis & Solander, 1786: 127, pl. 7, figs 5-8, pl. 25, fig. 1 [Syntypes: "American seas", particularly Bahama Islands, leg. Ellis. The collections of Ellis are considered lost according to Dixon (1960: 28-31). Since the illustrations, given with the original description, are of good quality and adequate for identification, it is proposed to designate the illustration as the nomenclatural type of *C. peniculum*].

Penicillus annulatus Lamarck, 1813: 299 (nom. illeg.) [This name is based on the original description and illustrations of *Corallina peniculum*. It is unclear why Lamarck changed the species epithet; possibly to avoid the formation of what he perceived to be a tautonym. The change is illegitimate, however, since the eschewed binomial does not fit the definition of a tautonym given in Article 23 (International Code for Botanical Nomenclature 2000)].

Nesaea annulata (Lamarck) Lamouroux, 1816: 256 ("*Nesea*") (nom. illeg.).

Scopularia annulata (Lamarck) Chauvin, 1842: 122 (nom. illeg.).

Chamaedoris annulata (Lamarck) Montagne, 1842: 261 (nom. illeg.).

Corallocephalus peniculum (Ellis & Solander) Kützing, 1843: 311.

Chamaedoris peniculum (Ellis & Solander) Kuntze, 1898: 400.

Description:
Thallus bright yellow green, forming erect, stipitate capitula, 2-10 (-14) cm high, attached to the substratum by branching, multicellular rhizoids arising from the lower pole of the stipe cells (Fig. 76D); rhizoids giving rise to new stipe cells. Stipes unbranched, single-celled, with annular constrictions over the entire length, single or densely clustered. Capitulum oval, cup-shaped to flattened, or nearly ball-shaped, diameter 1-10 cm, about 4-8 mm thick (Fig. 75).

Young stipes cylindrical, gradually becoming annularly constricted from the base upwards. When fully grown, one to three small cells may be formed at the swollen apex of the stipe cell by segregative cell division, followed by the formation of the capitulum. Capitulum filaments arising in whorls from the swollen apex of the stipe cell and from the small cells formed at the top of the stipe, if present (Fig. 76C). Cell division of the capitulum filaments by centripetal invagination of the cell walls or by segregative cell division. Growth of the capitulum mainly by division of the apical cells, followed by cell-elongation. Each new cell, after being divided from the apical cell, producing one lateral at its apical pole; laterals generally curved or sinuous (Fig. 76A). Basal cells of the capitulum occasionally forming a second lateral. Cross wall formation at the base of the laterals markedly delayed; l/w ratio of laterals in open connection with the mother cell up to 55. Branching of the capitulum filaments up to the 5th order. The diameter of the basal capitulum cells 1-2.3 times that of the apical cells. Angle of ramification 25°-85°.
Structural reinforcement of the capitulum mainly achieved by entanglement of the filaments (facilitated by the curved or sinuous filaments), also by anastomosis of capitulum filaments by type-3 tenacular cells (Fig. 76E-G).
Apical cells (80-) 100-170 µm in diameter, 600-7500 µm in length; main filaments 90-175 µm in diameter, 200-5000 µm in length; basal cells 180-250 µm in diameter, 220-850 µm in length. Stipe cells up to 1.5 mm in diameter, up to 5 (-11) cm long. Tenacular cells 45-55 µm in diameter, 80-90 µm in length.
Cell wall thickness of the capitulum filaments increasing from 2-10 µm in the terminal branch systems to 15 µm in the basal filaments. Cell walls of the stipe cell markedly stratified, up to 65 µm thick.
Chloroplasts rounded, 2.4-3.8 µm in diameter, forming an open to relatively closed parietal network. Most chloroplasts containing a single pyrenoid, ca. 1.2 µm in diameter.
Prismatic calcium oxalate crystals only present (but rare) in the capitulum filaments, diamond shaped, 15-30 µm in diameter. Protein crystals absent.

Ecology: Subtidal (down to 50 m depth), epilithic. Deep water forms presenting large flat capitula. Stipes often epiphytised by crustose coralline rhodophytes [e.g. *Fosliella chamaedoris* (Foslie & M. Howe) M. Howe] (Littler & Littler 2000: 330).

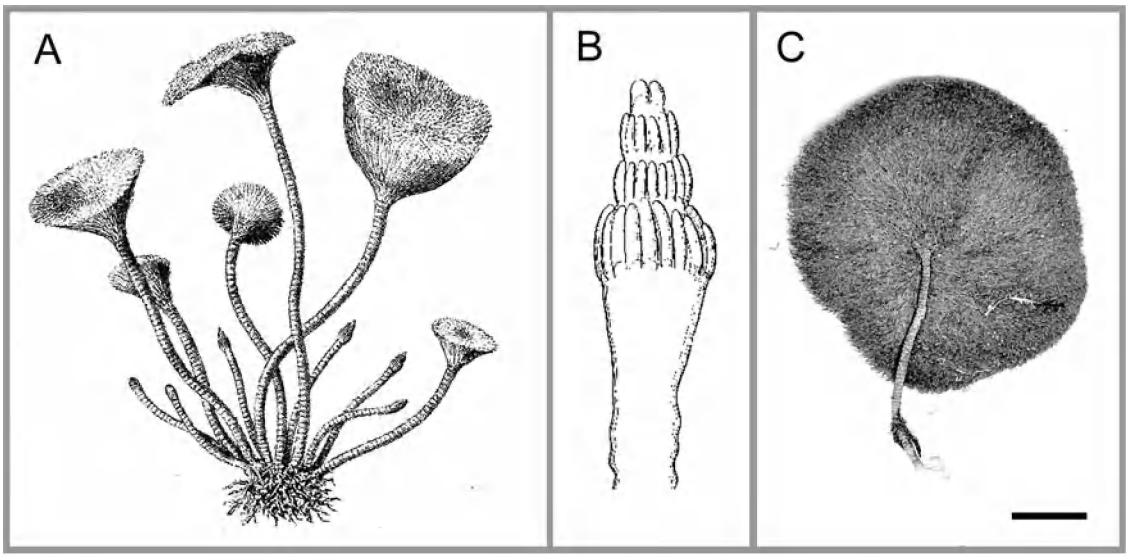


Fig. 75. *Cladophoropsis peniculum*. **A.** Habit; **B.** Stipe and four superimposed cells producing whorls of capitulum filaments; **C.** Habit. [A: reproduced from Børgesen (1913); B: HOD RD2-02-45]. Scale bar = 1 cm.

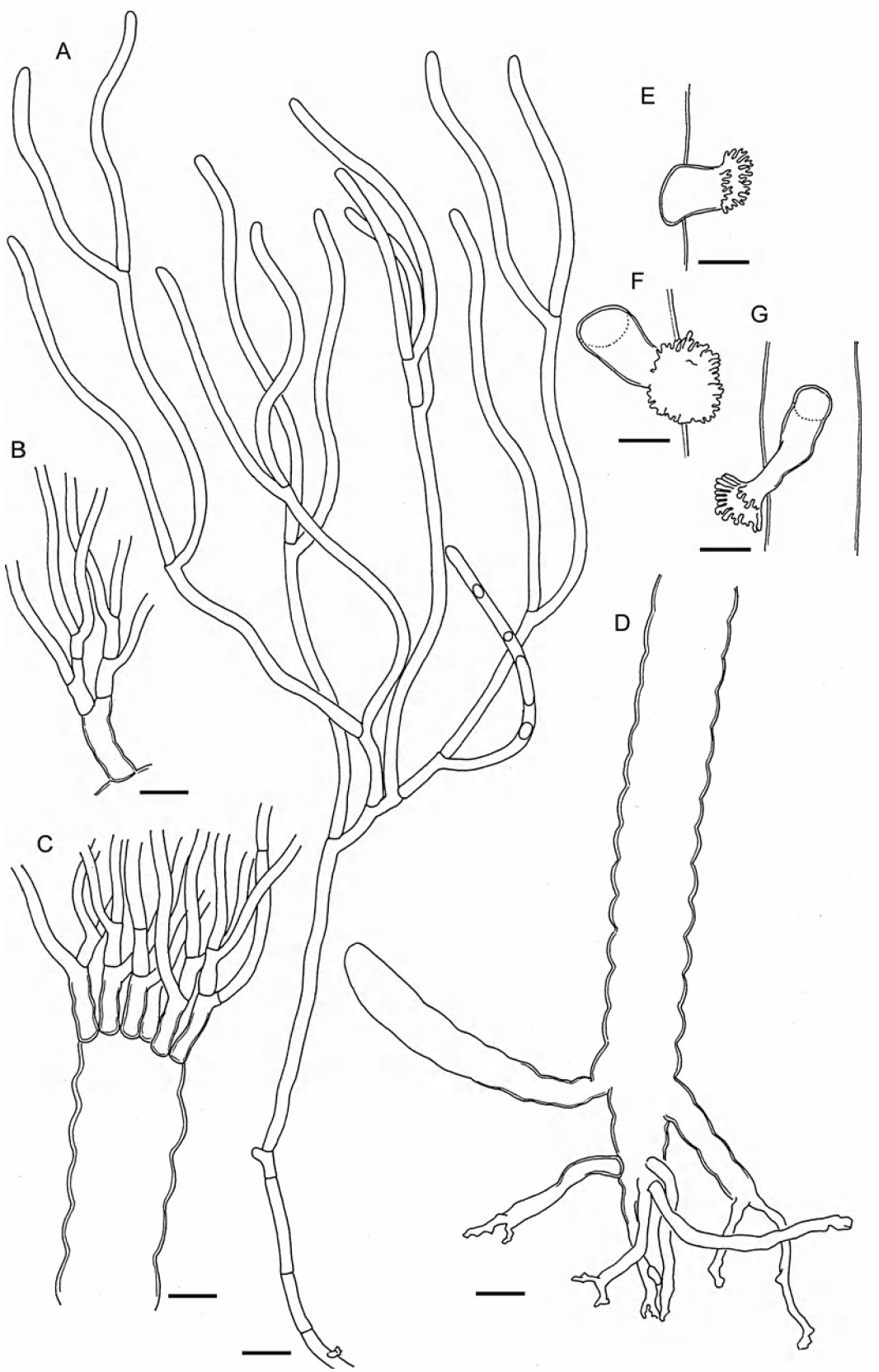


Fig. 76. *Cladophoropsis peniculum* (HOD RD2-02-45). **A.** Unilaterally branching capitulum filaments; **B.** Basal branches of capitulum; **C.** Distal pole of stipe without superimposed cells and producing capitulum filaments; **D.** Proximal pole of annulated stipe, producing a new stipe and type-1 rhizoids at the base; **E-G.** Type-3 tenacular cells. Scale bars: A-D = 500 µm; E-G = 50 µm.

Geographic distribution: Atlantic Ocean: Brasil; Caribbean Sea: Florida, Bahamas, Greater Antilles, Lesser Antilles, Southern Caribbean (Littler & Littler 2000: 330); North East Herald Cay, Coral Sea, South Pacific (Millar 1999: 66). Records from South Africa are misapplied names according to Børgesen (1940) and Papenfuss (1952).

Specimens examined: **Atlantic Ocean: Brasil**. Pernambuco, (unknown collector, 1844-1845, S); **Carribean Sea: Bahamas**. Cave Cays, under rock overhang at low tide mark, (leg. Howe 4005, 28.iii.1903, NY); Stella Maris Estate, Long Island, (leg. Coppejans, 20.viii.1982, HEC 5032); **Barbados**. Bath, (leg. Vickers 34, 13.ii.1899, NY; leg. Vickers s.n., 24.i.1899, BR); Bathsheba, W coast of Barbados, (leg. Diaz-Piferrer 17537, 26.x.1966, NY); Kendal Point, (leg. Vickers s.n., ii.1899, BR); unknown locality, (leg. Vickers 34, L 937 183 160; leg. Vickers s.n., ii.1899, L 937 183 163); **Curaçao**. Boca Ascension, low intertidal, under overhanging rock, (leg. Vroman s.n., 23.iv.1958, L 7665); Dominican Republic; Puerto Plata, infralittoral fringe, epilithic, (leg. Dargent & Bel, 8.ii.2002, HOD RD 2-02-45); Rio San Juan, Laguna Gri-Gri, infralittoral fringe, epilithic, (leg. Dargent & Bel, 13.ii.2002, HOD RD 08-02-16); **Jamaica**. Marant Bay, (leg. Pease & Butler s.n., vii.1894, NY); Port Antonio, (leg. Pease & Butler s.n., vii.1894, NY); Pt. Morant, drift, (leg. Howe 6154, 8.iii.1909, NY); **Puerto Rico**. E of Guanica Harbour, dredged 40-50 m deep, (leg. Howe 7091, 28.iii.1903, NY); Guanica, epilithic, 4.5 m deep, (leg. Almodovar 4454, 28.iii.1962, NY); Muertos Island, (leg. Howe 7530, 8.vii.1915, BR); San Juan, drift, (leg. Howe 2218, 28.iii.1903, NY; leg. Howe 4430, 25.iii.1906, NY); **Santo Domingo**. Bahia Escosesa, Nagua, (leg. Almodovar 7481, 10.vi.1976, NY); **St. Croix**. The Beach of White Bay, (leg. Børgesen 1575, 9.ii.1906, NY); White Bay, (leg. Børgesen 1530, 7.ii.1906, L 937 183 187; leg. Børgesen 1575, L 937 183 180); **St. Jan**. Cruz Bay, (leg. Børgesen 2155, 26.iii.1906, NY); **Gulf of Mexico: USA**. Key West, Florida, (leg. Hall 626, v.1897, NY; leg. Hall 629, iv.1897, BR); Key West, Florida, (leg. Howe 1650, 8.xi.1902, NY); Loggerhead Key, Dry Tortugas, Florida, (leg. Taylor 83, 7.xii.1924, NY).

Notes:

The nomenclatural history of this species is somewhat confusing, mainly because Lamarck (1813) changed the species epithet without an obvious reason. This results in the impression that *Chamaedoris annulata* and *Chamaedoris peniculum* are heterotypic. Only when reading Lamarck's (1813) diagnosis it becomes clear that *Penicillus annulatus* is based on the original description of *Corallina peniculum*, and that both species should be regarded as homotypic synonyms. Consequently the monospecific genus *Scopularia*, based on *Penicillus annulatus* (= *Corallina peniculum*), is to be regarded as a synonym of *Chamaedoris* (now *Cladophoropsis*).

In the SW Indian Ocean, *C. annulata* has been misapplied for *C. delphinii* several times according to Børgesen (1940) and Papenfuss (1952) (see Silva *et al.* 1996).

C. peniculum often forms plane capitula and can therefore be confused with *C. auriculata*. *C. peniculum* can be distinguished by the capitulum being cup-shaped with the stipe being centrally inserted, while in *C. auriculata* the plane capitula are auriculate with an eccentrically inserted stipe.

General references: Børgesen (1912: 270-273, figs 16, 17; 1913: 56-60, figs 40-43; 1940: 16-20, footnote on p. 20-21, fig. 5); Taylor (1960: 115, pl. 5, fig. 2); Littler & Littler (2000: 330, fig. on pp. 25, 331).

8. Doubtful taxa, species of uncertain systematic affinity and species excluded from *Cladophoropsis*

8.1. Doubtful taxa

The type material of the names listed below was untraceable and the original descriptions are too vague to permit a conclusion as to their identity.

Cladophoropsis psyttaliensis (Schmitz) Wille, *in* Engler & Prantl, 1910: 116. *Siphonocladus psyttaliensis* Schmitz, 1879: 20 (Holotype: Psyttalia Island, Gulf of Athens, Greece; paratypes: Gulf of Saronikos, Greece and Gulf of Napels, Italy; leg. probably F. Schmitz]. The type material is untraceable, possibly destroyed in B. As far as we know this species has only been mentioned once after its original description (Gerloff & Geissler 1974).

Struveopsis chagoensis Rhyne & H. Robinson, 1968: 469, figs 1-3 [Holotype: Diego Garcia Atoll, Chagos Archipelago, lagoon side of West Island, in shallow *Cymodocea* bed in 0.3-0.7 m of water, epiphytic on *Cymodocea*, leg. Rhyne 421, 16.vi.1967, USNM].
The description of *S. chagoensis* is based on small specimens and this species possibly represents a-typical, juvenile plants of *Struveopsis siamensis* (here regarded as the *struveopsis* phenodeme of the *C. composita* complex).

Struvea enomotoi Chihara (nom. nud.).
Yoshida (1998: 83) included *S. enomotoi* in expectation that this name would be published validly before the appearance of his book. Chihara is preparing a paper on this species, and the name must still be treated as a nomen nudum (Tadao Yoshida pers. comm.).

8.2. Species of uncertain systematic affinity

Cladophoropsis brachyartrus (Svedelius) Wille, 1910: 116. *Siphonocladus brachyartrus* Svedelius, 1900: 304-311, pl. 16: figs 2, 3; pl. 18; text fig. 3 [Holotype: Puerto Angosto, Isla Desolacion, Chile, leg. P. Dusén. The Dusén collection is usually to be found in S or UPS but in both herbaria specimens of *S. brachyartrus* were untraceable].
According to Hylmö (1938) and Papenfuss (1964) this species has an Antarctic to subantarctic distribution. We have not seen the type material nor other material but the original description and illustration of this species suggest a close relationship of with *C. rigida*. Since all other representatives of *Cladophoropsis* have a tropical to subtropical geographical distribution, the affinity of this Antarctic species with *Cladophoropsis* remains questionable.

Cladophoropsis gracillima Dawson, 1950: 149, figs 12, 13 [Holotype: Punta Palmilla, Baja California Sur, Mexico, leg. Dawson 3233, 7.xi.1946, AHFH 36937; isotype in NY!].
The systematic position of this species is uncertain due to the absence of calcium oxalate crystals and the chloroplasts containing up to four pyrenoids. A description and illustrations of *C. gracillima* are provided in the appendix.

Siphonocladus voluticola Hariot, 1887: 56, fig. 1 (misspelled "*voluticula*", correct in caption to fig.) [Holotype: on rejected shells of *Voluta magellanica*, Orange Bay, Tierra del Feugo, Chile, leg. M.P. Hariot, s.n., PC!]. *Cladophoropsis voluticola* (Hariot) Wille, *in* Engler & Prantl, 1910: 116.
The cell dimensions of this minute filamentous species (cell diameter 6-8 μm) are so small

that its taxonomic position in the Cladophorophyceae is questionable. The type material consists of some shells with green crusts but no filaments could be observed.

8.3. Species excluded from *Cladophoropsis*

Aegagropila javanica Kützing, 1847: 773 [Holotype: Java, Indonesia, leg. Zollinger 2379, L! 937.276.41; isotypes in NY! and PC!]. *Cladophora zollingeri* Kützing, 1849: 415. *Aegagropila zollingeri* (Kützing) Kützing, 1854: 14, pl. 64: fig. II. *Siphonocladus zollingeri* (Kützing) Bornet ex De Toni, 1889: 359. *Cladophoropsis zollingeri* (Kützing) Reinbold, 1905: 147. *Cladophoropsis javanica* (Kützing) P. Silva, *in* Silva *et al.*, 1996: 792.
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Boodlea vanbosseae Reinbold, 1905: 148 [Lectotype: Lucipara Island, Indonesia, leg. Weber-van Bosse, Siboga expedition s.n., Herbarium Reinbold 1915, M!]
This species fits morphologically in the *Cladophora* section *Boodleoides* as circumscribed by van den Hoek (1963, 1982a) and van den Hoek & Chihara (2000). See the appendix for a description and discussion on this species.

Cladophora lyallii Harvey, 1855a: 262, pl. CXXI, C [Holotype: Lyall, South Island, New Zealand, collector unknown, BM]. *Cladophoropsis lyallii* (Harvey) V.J. Chapman, 1956: 471.
This species was moved to *Wittrockiella* by van den Hoek, Ducker & Womersley (1984: 45).

Cladophora modonensis Kützing, 1849: 416 [Type: Modon, Morea Peninsula, Peloponnesos, Greece, leg. Bory St. Vincent. Specimen dedit amic. Lenormand No. 61; the location of the type material could not be found]. *Cladophora* (*aegagropila*) *modonensis* Kützing, 1854: 14, Tab 68A. *Siphonocladus modonensis* (Kützing) Bornet, *in* De Toni, 1889: 359. *Cladophoropsis modonensis* (Kützing) Reinbold, 1905: 147.
According to Reinbold (1905: 147) the cell dimensions of *C. modonensis* fall within the limits of *C. sundanensis* but the species differs in forming tufts and being flaccid. We examined one specimen identified as *C. modonensis* from the type locality (leg. J.M. Despréaux, BR). This specimen and the drawings based on the authentic material by Kützing (1854: 14, Tab. 68A) demonstrate that *C. modonensis* is characterized by septate laterals and rhizoids developing from the proximal pole of numerous cells, even in the apical regions of the thallus. This suggests that the species should be replaced in *Cladophora*. Based on cell dimensions, we consider *C. modonensis* conspecific with *Cladophora coelothrix* Kützing.

Cladophoropsis adhaerens Gilbert, 1962: 136, fig. 2 [Holotype: between Natatorium & Elks Club, Waikiki, Honolulu, Oahu, Hawaii, leg. W.J. Gilbert 9410, 9.iv.1959, MICH!].
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Cladophoropsis bulbosa Womersley, 1955: 391, figs 8, 9 [Holotype: Queenscliff, Victoria, Australia, leg. Sonder 3; MEL!]; *Chlorodesmis bulbosa* (Womersley) Ducker, 1965: 149, figs 1-4.
This species was moved to *Chlorodesmis* by Ducker (l.c.) and later reduced to a synonym of *Chlorodesmis baculifera* (Ducker 1966).

Cladophoropsis corallinicola Kajimura, 1987: 178, figs 1-6 [Holotype: off Tsudo, Oki Island, Japan, leg. Kajimura, 31.v.1985, OS 9900, TNS)].
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Cladophoropsis coriacea Yendo, 1920: 1 [Lectotype: Osezaki, Goto Islands, Nagasaki Prefecture, Japan, collector unknown, 6.viii.1916, TI in SAP; syntype[1]: Kojima, Tamanoura, Goto Islands, Nagasaki Prefecture, collector unknown, 8.viii.1916, TI in SAP].
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Cladophoropsis fallax Schiffner, 1933: 304, figs 10-19 [Holotype: Lacroma Island, near Ragusa (Dubrovnic), South Dalmatia, Croatia, leg. F. Berger, Schiffner Algae Marinae no. 964, NY!; isotype in MICH!].
C. fallax is considered as a synonym of *Cladophora coelothrix* Kützing from which it is morphologically indistinguishable.

Cladophoropsis howensis Lucas, 1935: 197 [Holotype: Lord Howe Island, leg. Lucas, vi.1933, NSW! 416126].
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Cladophoropsis infestans Setchell, 1924: 177, fig. 41 [Holotype: Tutuila Island, Samoa, leg. Setchell 1134, NY!].
The holotype is morphologically indistinguishable from *Cladophora socialis* Kützing.

Cladophoropsis limicola Setchell, 1924: 176, fig. 40 [Holotype locality: Tutuila Island, Samoa, leg. Setchell 1167, NY!].
This mud-inhabiting, estuarine species is referable to *Cladophora coelothrix* as was already suggested by Cribb (1960: 10). *C. coelothrix* is often found in sheltered inner bays or estuaries where it can grow on muddy substratum (van den Hoek 1963: 42; 1982a: 48).

Cladophoropsis luxurians Gilbert, 1962: 136, fig. 3 [Holotype: shore of Molokai opposite Mokuhooniki Island, Hawaii, leg. W.J. Gilbert, 10077, 6.vi.1959; MICH!]. *Cladophora luxurians* (Gilbert) Abbott & Huisman, 2003: 275-285.
The type specimen and two specimens from Hawaii (Herb. U.S. S. Pacific Exploring Expedition, 1838-42, Wilkes, s.n., NY! and L! 01757), identified as *C. luxurians* by Gilbert and Tsuda respectively are indistinguishable from *Cladophora catenata* (Linnaeus) Kützing.

Cladophoropsis pallida Baardseth, 1941: 13, fig. 3G, 4A [Holotype: between North Point and Blenden Hall, Inaccessible Island, South Atlantic, leg. Baardseth 354, station 137, 19.ii.1938, O!; paratype: Julia Point, Tristan da Cunha, leg. Baardseth 122, station 23, 24.xii.1937, O!].
The specimen denoted "Type specimen" by Baardseth (from station 137, Inaccessible) is the one that is illustrated in his fig. 4A. Another sheet gives the specimens from stat. No. 23; no collections seem to have been made from stat. Nos. 37 and 76 (Per Sunding, pers. comm.). Both specimens most likely belong to *Cladophora albida* (Hudson) Kützing as described by van den Hoek (1963, 1982a).

Cladophoropsis peruviana Howe, 1914: 30, pl. 2, figs 1-9 [Holotype: La Palisada, Peru, leg. Coker, 370, p.p., NY!].
This mud-inhabiting species is referable to *Cladophora coelothrix* as already suggested by Cribb (1960: 10).

Cladophoropsis robusta Setchell & Gardner, 1924: 714-715, pl. 13: fig. 16 [Holotype: Isla Tortuga, Baja California Sur, Mexico, leg. I.M. Johnston 135, CAS in UC 1330].
Pseudostruvea robusta (Setchell & Gardner) Egerod, 1975: 47. *Struveopsis robusta* (Setchell & Gardner) Rhyne & H. Robinson, 1968: 470.
The original description and illustration of this species does not correspond with the holotype

[1] See footnote on p. 144.

material which is referable to *Valoniopsis pachynema* (G. Martens) Børgesen (see note under *Cladophoropsis mexicana*).

Conferva herpestica Montagne, 1842: 15 [Lectotype: New Zealand, leg. Hombron s.n., PC! herbier général, folder 48; isotype in NY!]. *Cladophora herpestica* (Montagne) Kützing, 1849: 415. *Aegagropila herpestica* (Montagne) Kützing, 1854: 14. *Cladophoropsis herpestica* (Montagne) Howe, 1914: 31.
Molecular and morphological evidence (Leliaert *et al.* 2003 and Leliaert & Coppejans 2004) demonstrate that *C. herpestica* belongs to the *Cladophora* section *Longi-articulatae* (see 3.3.1. Circumscription of *Cladophoropsis* to date). Description and illustrations of this species are provided in the appendix.

Microdictyon mutabile Dellow, 1950: 3, figs 1-4 [Holotype: Leigh, North Auckland, New Zealand, leg. U.V. Dellow 618, 7.ix.1949, Herb. U.V. Dellow, AK!; paratype: same locality, No. 307, Fasc. XIII Herb. V.W. Lindauer as *M. umbilicatum*, AKU! VWL 307]. *Boodlea mutabile* (Dellow) Adams, 1994: 39, pl. 8.
This species is characterized by sponge-like thalli composed of branching filaments forming a three-dimensional reticulum, attached to the substratum by rhizoids sprouting from the proximal pole of cells in any part of the thallus (type-2 rhizoids). Anastomosis of adjacent cells is accomplished by type-1 tenacular cells (annular adhesion pads formed distally on apical cells). Cells lack calcium oxalate crystals. Adams (1994) transferred *M. mutabile* to *Boodlea* on account of the sponge-like thallus morphology. Thallus morphology, however, cannot be used to distinguish the two genera. Based on the mode of anastomosis (only by type-1 tenacular cells), and the absence of calcium oxalate crystals, this species should be returned to its original genus, *Microdictyon*.

Siphonocladus concrescens Reinbold, 1898: (88) [Lectotype: Rhodos Island, Greece, leg. J. Nemetz 46, M! 0066781]. *Cladophoropsis concrescens* (Reinbold) Wille, *in* Engler & Prantl, 1910: 116.
The lectotype of this species is referable to *Cladophora coelothrix*.

Siphonocladus exiguus Möbius, 1893: 129, pl. 9: figs 9a-d [Type: Coast of Semarang, Java, Indonesia, leg. F. Benecke, the location of the type material could not be retrieved]. *Cladophoropsis exiguus* (Möbius) Wille, *in* A. Engler & K. Prantl, 1910: 116.
This taxon is regarded as a synonym of *Cladophora herpestica* (see appendix).

Siphonocladus rhodensis Reinbold, 1898: 88 [Holotype: harbour of Rhodos, Greece, leg. J. Nemetz, 50, M! 0066782; isotypes in BR! and NY!]. *Cladophoropsis rhodensis* (Reinbold) Wille, *in* A. Engler & K. Prantl 1910: 116.
The holotype represents reduced thalli of *Cladophora laetevirens* (Dillwyn) Kützing.

Struvea scoparia Kützing, 1863: 12 [Holotype: Ile de Pin, New Caledonia, leg. Vieillard s.n., L! 937 183 105].
This species was excluded from *Struvea* and reduced to a synonym of *Apjohnia laetevirens* Harvey by Murray & Boodle (1888b: 266). See Kützing (1866: 1, tab. 1), Papenfuss & Chihara (1975: 309-316, figs 4-11) and Womersley (1984: 180, fig. 59A, B) for detailed descriptions and illustrations of this species.

Appendix: descriptions of *Cladophoropsis gracillima* (uncertain systematic affinity) and the excluded species *Cladophora herpestica* and *Boodlea vanbosseae*

Cladophoropsis gracillima Dawson

Figs 77, 78

Cladophoropsis gracillima Dawson, 1950: 149, figs 12, 13 [Holotype: Punta Palmilla, Baja California Sur, Mexico, leg. Dawson 3233, 7.xi.1946, AHFH 36937; isotype in NY!].

Description:
Thallus forming radiating, supple tufts of sparsely branched filaments, 2-4 cm across, up to 3 cm high; ultimate branches light to medium green, basal branches and rhizoids dark green to blackish.
Cell division by centripetal invagination of the cell walls. Growth by apical and intercalary cell division; subsequent cell elongation without cell enlargement (the diameter of the filaments even decreasing towards the base of the thallus). Diameter of the thickest part of the main axes about 0.5-1.3 times that of apical cells. Newly formed cells in the terminal part of the thallus each producing one lateral at their apical pole; branches generally unilaterally arranged. Cells in the basal part of the thallus generally failing to produce laterals, resulting in long unbranched basal filaments. Cross walls at the base of the laterals absent. Laterals not displacing the main axes. Branch systems generally restricted to the first order.
Attachment to the substratum by branching, multicellular rhizoids, arising from the proximal pole of the basal cells (type-1 rhizoids). Structural reinforcement of the thallus achieved by interweaving of filaments and by rhizoids sprouting from the proximal pole of numerous cells in the central and upper parts of the thallus (type-2 rhizoids).
Apical cells and cells of the ultimate branch systems cylindrical and extremely elongated, straight, or faintly curved or sinuous, (60-) 80-120 (-135) µm in diameter, up to 15 mm long, l/w ratio 30-100. Main filaments cylindrical, straight or slightly sinuous, 50-120 (-130) µm in diameter; diameter decreasing towards the base of the thallus. Basal cells and rhizoids slightly torulose (Fig. 77F, arrowheads). Basal branches 50-160 µm in diameter. Rhizoids sprouting from the proximal pole of the cells, 50-80 µm in diameter at their base, attenuating towards their tips to 40-60 µm, up to 3 mm long. Cell walls thin, less than 2 µm in the cells of the ultimate and basal branch systems.
Chloroplasts rounded to elongated, 2.5-4.5 µm broad, up to 14 µm long, forming a dense to slightly open parietal reticulum. Plasts containing 1-4 pyrenoids; in elongated chloroplasts the pyrenoids are linearly organized with one large central pyrenoid flanked by two or three smaller ones; in rounded chloroplasts the pyrenoids are irregularly organized (Fig. 78A-C) and of similar size.
The dark coloured basal cells and rhizoids are densely packed with starch grains (colouring dark blue with Lugol's iodine), (4-) 6-12 (-15) µm in diameter (Fig. 78D-I). Cells lacking crystalline cell inclusions.

Ecology: Growing epilithic in intertidal rock pools; entangled with other filamentous algae.

Geographical distribution: The records from *C. gracillima* outside the type locality remain uncertain and are possibly misapplied names for *C. sundanensis*: Micronesia (Dawson 1956), N-Australia (Lewis 1987), Philippines (Silva *et al.* 1987), Japan (Tsuda 1968), Pitcairn Islands (Tsuda 1976), Mariana Islands (Tsuda & Tobias 1977).

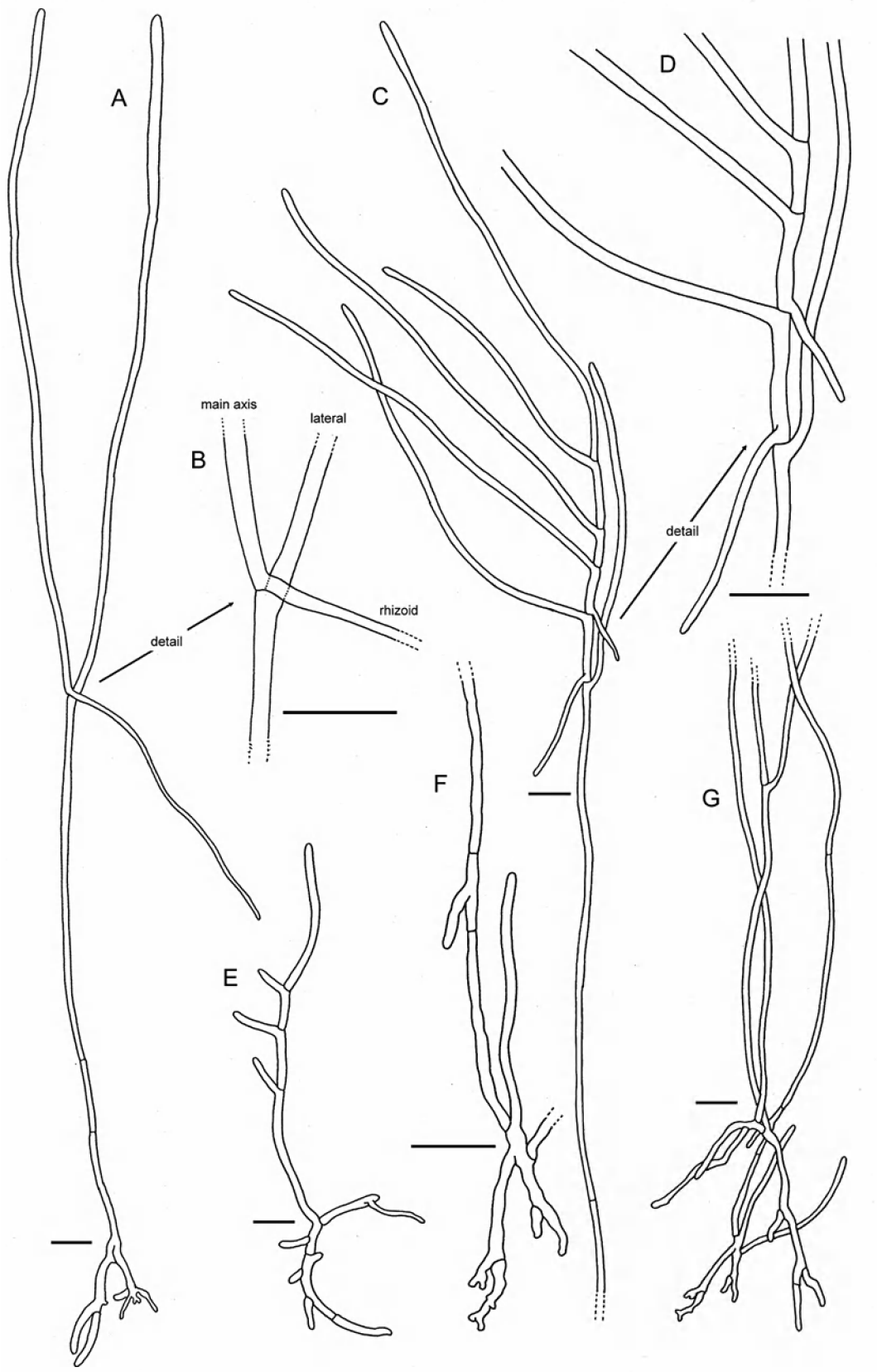


Fig. 77. *Cladophoropsis gracillima* (isotype, Dawson 3233, NY). **A, C, E, G.** Thallus composed of unilateral branch systems with type-2 rhizoids produced from the proximal poles of the cells and attached by branched type-1 rhizoids arising from the proximal poles of the basal cells; **B.** Type-2 rhizoid; **D.** Ultimate branch systems; **F.** Detail of torulose basal branches and rhizoids. Scale bars: A, C-G = 500 μm, B = 200 μm.

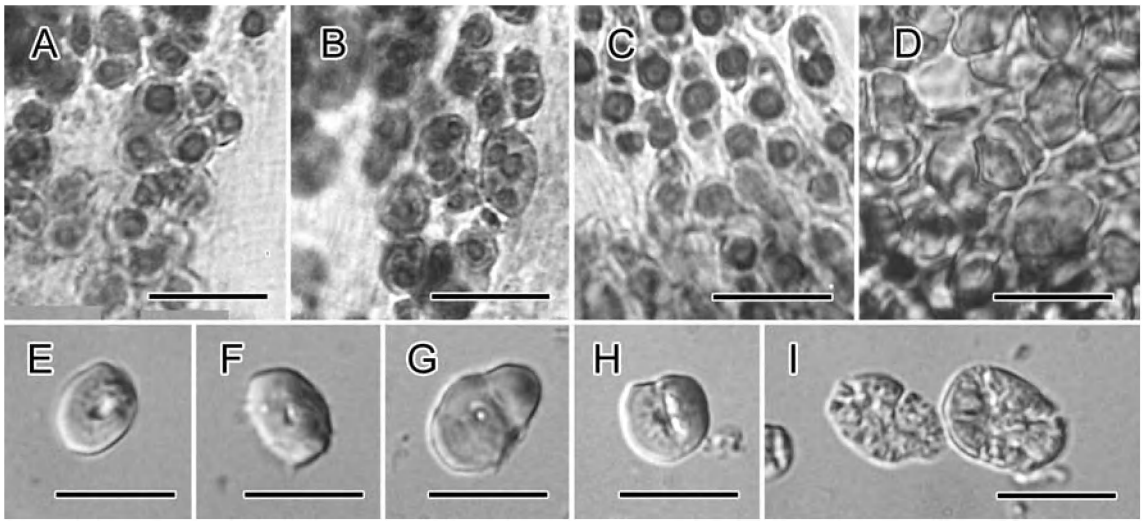


Fig. 78. *Cladophoropsis gracillima* (isotype, Dawson 3233, NY). **A.** Round chloroplasts, each containing a single pyrenoid; **B.** Oval chloroplasts containing one to four pyrenoids; **C.** Elongate chloroplasts with a single large central pyrenoid flanked by two or three smaller ones; **D.** Densely packed starch grains in the basal cells; **E-I.** Details of starch grains with a central pit; older starch grains with cracks. Scale bars = 10 μm.

Specimen examined: Punta Palmilla, near San Jose del Cabo, Baja California, Mexico: intertidal reef pools, (leg. Dawson 3233, 7.xi.1946, NY, s.n., isotype).

Notes:

C. gracillima resembles *C. sundanensis* in branching pattern and cell diameter but differs from it by forming erect tufts instead of spongy cushions, the extreme long apical cells, the presence of rhizoids sprouting from the proximal pole of cells in the terminal branch systems, the absence of calcium oxalate crystals and the number of pyrenoids per chloroplast.

The systematic position of *C. gracillima* is uncertain, mainly because of the lack of crystalline cell inclusions and the absence of tenacular cells. The species shows morphologic affinity with the *Cladophora* section *Repentes* (especially with *C. coelothrix* Kützing) with the exception that cross wall at the base of *C. gracillima* are always absent (whereas in *C. coelothrix* the cross wall formation is only delayed to some extent). Up to know members of the Cladophorophyceae were thought to have chloroplasts with maximum one pyrenoid. In *C. gracillima* many chloroplasts were found with two to four pyrenoids, resulting in an even more doubtful systematic position of this species.

Cladophora herpestica (Montagne) Kützing Figs 80, 81

Conferva herpestica Montagne, 1842: 15 [Lectotype: New Zealand, leg. Hombron s.n., PC! herbier général, folder 48; isotype in NY!].
Cladophora herpestica (Montagne) Kützing, 1849: 415.
Aegagropila herpestica (Montagne) Kützing, 1854: 14.
Cladophoropsis herpestica (Montagne) Howe, 1914: 31.
Aegagropila javanica Kützing, 1847: 773 [Holotype: Java, Indonesia, leg. Zollinger 2379, L! 937.276.41; isotypes in NY! and PC!].
Cladophora zollingeri Kützing, 1849: 415 [On transferring *Aegagropila javanica* to *Cladophora*, Kützing had to change the epithet because of the existence of *Cladophora javanica* Kützing (1847: 773), a freshwater species also collected by Zollinger (no. 2479a) (Silva *et al*. 1996: 792-793)].
Aegagropila zollingeri (Kützing) Kützing, 1854: 14, pl. 64: fig. II.
Siphonocladus zollingeri (Kützing) Bornet ex De Toni, 1889: 359.
Cladophoropsis zollingeri (Kützing) Reinbold, 1905: 147.
Cladophoropsis javanica (Kützing) P.C. Silva, *in* Silva *et al*., 1996: 792.
Valonia rhizophora Piccone & Grunow, *in* Piccone, 1884a: 293, pl. VII: fig. 10 [Syntypes: Suakin and Baja d'Assab, Red Sea, leg. A. Issel s.n., probably VER].
Siphonocladus exiguus Möbius, 1893: 129, pl. 9: figs 9a-d [Type: Coast of Semarang, Java, Indonesia, leg. F. Benecke, the location of type material could not be retrieved].
Cladophoropsis exiguus (Möbius) Wille, *in* A. Engler & K. Prantl, 1910: 116.
Cladophoropsis coriacea Yendo, 1920: 1 [Lectotype: Osezaki, Goto Islands, Nagasaki Prefecture, Japan, collector unknown, 6.viii.1916, TI in SAP; syntype (see footnote on p. 144): Kojima, Tamanoura, Goto Islands, Nagasaki Prefecture, collector unknown, 8.viii.1916, TI in SAP].
Cladophoropsis howensis Lucas, 1935: 197 [Holotype: Lord Howe Island, leg. Lucas, vi.1933, NSW! 416126].
Cladophoropsis adhaerens Gilbert, 1962: 136, fig. 2 [Holotype: between Natatorium & Elks Club, Waikiki, Honolulu, Oahu, Hawaii, leg. W.J. Gilbert 9410, 9.iv.1959, MICH!], non *C. adhaerens* Pham-Hoàng, 1969: 447, fig. 4.51-4.52 (possibly a synonym of *C. sundanensis*).
Cladophoropsis corallinicola Kajimura, 1987: 178, figs 1-6 [Holotype: off Tsudo, Oki Island, Japan, leg. Kajimura, 31.v.1985, OS 9900, TNS)].

Description:
Thallus medium to dark green, forming compact cushions or moss-like mats, firmly attached to the substratum, often sand-trapping, 2-20 cm across and 1-2 cm thick, composed of stiff, strongly entangled, often curved or sinuous branch systems with a vaguely acropetal organization.
Cell division by centripetal invagination of the cell walls. Growth mainly by elongation and subsequent division of apical cells. Cut off cells not elongating nor enlarging; the cells gradually becoming shorter and narrower towards the base of the thallus. The diameter of the thickest part of the main axes about 0.7-2.6 times that of the apical cells.
Newly formed subapical cell generally each producing a single lateral at their apical pole, mostly unilaterally placed. At increasing distance from the apex a cell may give off a second branch. Occasionally thalli are characterized by proliferations of up to 7 laterals produced from a single cell, probably as a wounding response (Fig. 80C). Cross wall formation at the base of the laterals markedly delayed; cross walls only occurring infrequently in the basal regions (and very rarely in apical regions) of the thallus. Older laterals eventually displacing the main axes,

which then appear as lateral appendages (Fig. 80F, arrowheads). Thallus generally branching to the 1st or 2nd order.

Attachment to the substratum by basal hapteroid rhizoids (Type-1 rhizoids, Fig. 80G), and by rhizoids sprouting from the proximal pole of cells in any part of the thallus including the apical cells (Type-2 rhizoids, Fig. 80E). Type-2 rhizoids septate or aseptate, sometimes branched (Fig. 80B). Structural reinforcement of the thallus achieved by spirally entangling of the filaments and rhizoids.

Apical cells and cells of the terminal branch systems subcylindrical, generally curved or sinuous, (100-) 140-400 (-540) µm in diameter, up to 10 mm long, l/w ratio 8-30. Basal cells subcylindrical, straight or slightly curved, (70-) 120-370 (-500) µm in diameter, 500 µm - 5 mm long, l/w ratio 2-20. Type-2 rhizoids 80-300 µm in diameter at the proximal part, attenuating to 40-160 µm, up to 10 mm long. Cell walls ca. 5 µm thick in young cells, up to 80 (-110) µm thick in the basal cells, coarsely striated longitudinally (Fig. 80D).

Chloroplasts round, 6-14 µm in diameter, forming a dense parietal reticulum. Chloroplasts each containing one large pyrenoid, 3.5-6.4 µm in diameter (Fig. 81A).

Tetrahedral, proteinaceous cell inclusions present in most cells of the thallus, up to 40 µm in diameter (Figs 81B-E).

Ecology: *C. herpestica* grows epilithic on horizontal to vertical substrata, in shaded to sun-exposed locations, frequently in the supralittoral fringe and in the intertidal to shallow subtidal, occasionally collected down to 40m depth.

Geographical distribution: *C. herpestica* is widely distributed in the tropical to subtropical Indo-Pacific as far east as Hawaii (Womersley 1984, Sartoni 1992, Hodgson & Abbott 1992). *C. herpestica* has only been recorded sporadically along the South American west coast [Peru (Howe 1914) and Chile (Hoffmann & Santelices 1997)]. The occurrence of this species in the Mediterranean Sea (as *Cladophoropsis zollingeri* in Egypt and the Levant States by Gallardo *et al.* 1993: 408) has not been investigated.

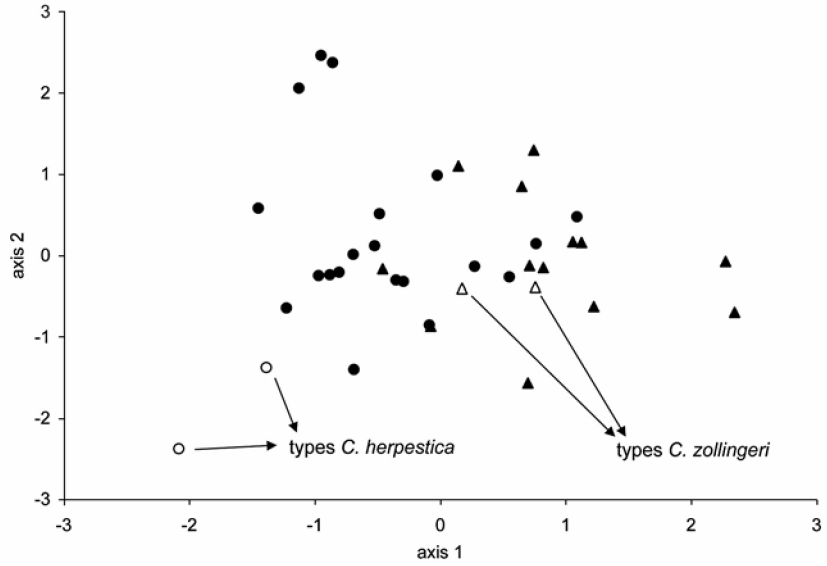


Fig. 79. First two ordination axes of a PCA of *Cladophora herpestica* specimens (eigenvalue axis 1: 0.7125, axis 2: 0.1041). Specimens initially identified as *C. herpestica* are indicated as black circles; *C. javanica* specimens are indicated as black triangles; type specimens are in gray symbols.

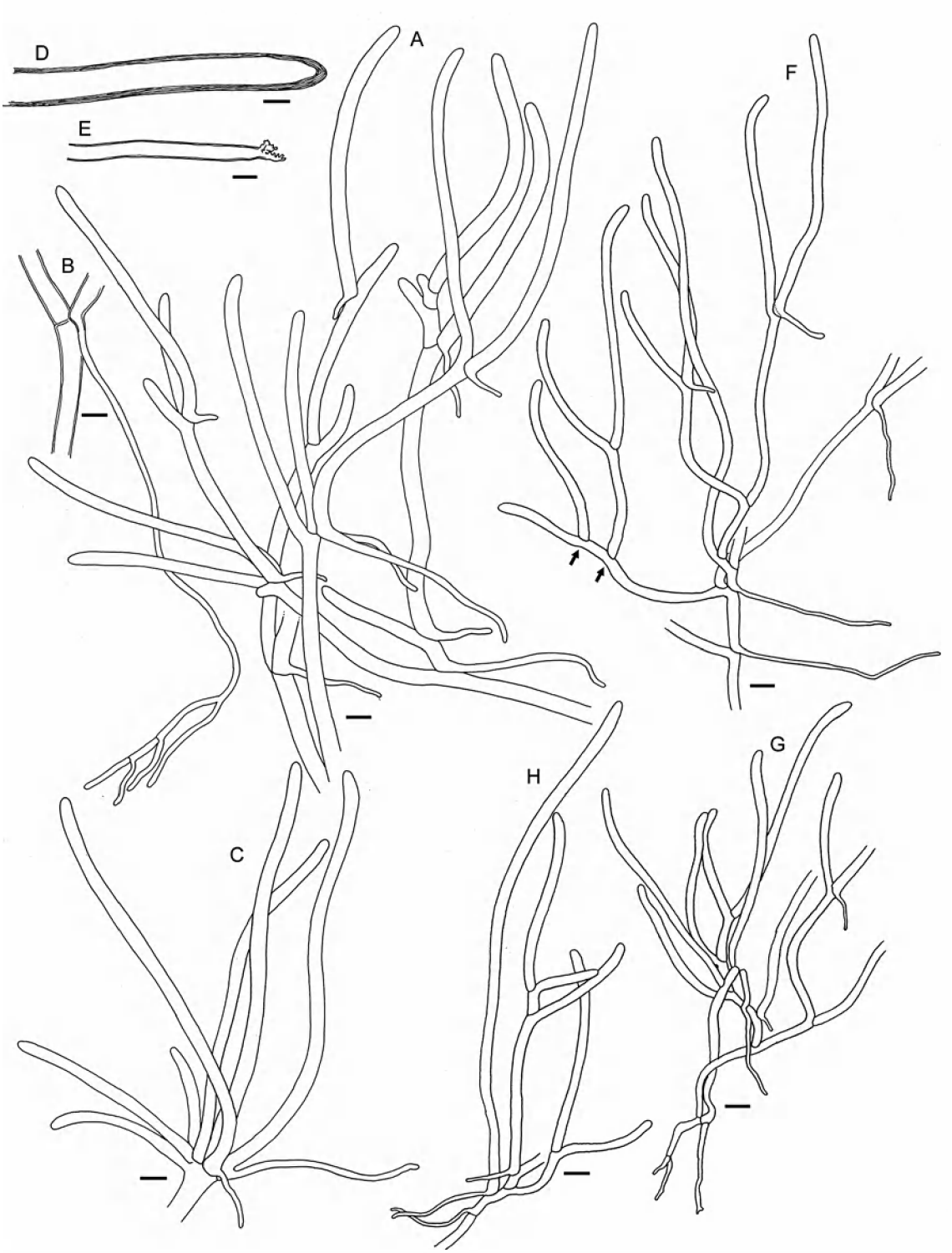


Fig. 80. *Cladophora herpestica*. **A.** Terminal branches with rhizoids sprouting from the basal poles of most cells; **B.** Branched type-2 rhizoid; **C.** High number of laterals produced from a single cell; **D.** Detail of an apical cell showing the thick, lamellate cell wall; **E.** Type-2 rhizoid with a hapteroidal tip; **F.** Terminal branch systems with rhizoids sprouting from the basal poles of most cells; arrows indicate older laterals displacing the main axes and appearing as lateral appendages; **G.** Portion of a thallus showing terminal and basal branches; **H.** Terminal branches. (A, B, D-F: lectotype of *Conferva herpestica*, PC; C: isotype of *C. herpestica*, Hombron s.n., NY; F-H: holotype of *Aegagropila javanica*, L). Scale bars: A-C, F-H = 500 µm; D-E = 200 µm.

Specimens examined: **Indian Ocean: Australia**. Hopetown, Western Australia, (leg. Woelkerling 1655, 20.vi.1968, MEL 699017); **Indonesia**. Java, (leg. Zollinger 2379, L 937.276.41, holotype of *Aegagropila javanica*; PC and NY, isotypes); **Kenya**. Mc Kenzie Point, Mombasa, (leg. Coppejans, i.1986, HEC 6001); Mc Kenzie Point, Mombasa: high intertidal rock pools, under the overhanging cliff wall, epilithic, (leg. Coppejans *et al.*, 12.ix.1992, HEC 9408); **Oman**. Shaghaf Island, Masirah Island: high intertidal, epiphytic on *Laurencia papillosa*, (leg. Schils, MAS 190); mangroves of Shaghaf Island, Masirah Island: mid intertidal, (leg. Schils, MAS 464); Barr al Hickman, Masirah Island: shallow subtidal, - 4 m, (leg. Schils, MAS 93); **Rodrigues**. Petite Butte: mid intertidal, epilithic, (leg. Coppejans, 21.ix.2001, HEC 14724 and HEC 14727); Ile Hermitage: tide channel, on coral rubble, (leg. Coppejans, 27.ix.2001, HEC 14823); **Seychelles**. Pointe du Sel, Ile Sourie, Mahé Island: lagoon, reef pools, (leg. Coppejans *et al.*, 10.xii.1992, SEY 16); Aride Island, south coast: subtidal, epilithic on dead coral surface, (leg. Coppejans *et al.*, 18.xii.1992, SEY 151); Ile Seche, Beacon Islet: supralittoral fringe, vertical granite rocks, (leg. Coppejans *et al.*, 25.xii.1992, SEY 393); **South Africa**. Port O'Call, Trafalgar, (leg. Leliaert, 21.iii.1997, FL 253); Treasure Beach, The Bluff, Durban, KwaZulu-Natal, (leg. Coppejans *et al.*, 3.viii.1999, KZN 0072b); The Bluff, Durban, KwaZulu-Natal: high intertidal, epilithic on horizontal rock substratum, (leg. Coppejans *et al.*, 4.viii.1999, KZN 167); Sodwana Bay, KwaZulu-Natal: mid to lower intertidal rock pools, (leg. Coppejans *et al.*, 8.viii.1999, KZN 232); **Tanzania**. Mbudya Island: mid intertidal rock pool, epilithic, (leg. Leliaert & Coppejans, 11.vii.2001, FL 909); Mbudya Island: high intertidal, epilithic vertical fossil coral cliff wall, (leg. Coppejans & De Clerck, 18.i.1996, HEC 11339); Mana Hawanja Island, Mnazi Bay, Mtwara area: low intertidal reef flat, epilithic on shaded vertical substratum, (leg. Coppejans *et al.*, 30.vii.2000, HEC 12994); mangrove tide channel, Chwaka, Zanzibar: high intertidal rock pool, epilithic, (leg. Leliaert, 31.vii.1997, FL 721); Mnemba Atol, Zanzibar: subtidal reef, 22 m deep, on sponge, (leg. Leliaert & Coppejans, 15.vii.2001, FL 937); Matemwe, Zanzibar: supralittoral fringe, epilithic on vertical shaded fossil cliff wall, (leg. Coppejans, 4.viii.1993, HEC 9911); seaward side of Juani Island, Mafia Island: high intertidal, epilithic on horizontal rock, under overhanging fossil coral cliff, (leg. Coppejans & De Clerck, 11.i.1996, HEC 11210); Vitongoji (Watangme Beach), E coast of Pemba Island: infralittoral fringe, strongly exposed to surf, epilithic horizontal coral substratum, (leg. Coppejans & De Clerck, 23.i.1996, HEC 11415). **Pacific Ocean: Australia**. Arrawarra Headland (30 km N of Coffs Harbour): low intertidal rock pools, (leg. Coppejans, 12.ix.1998, HEC 12432); Clarence Heads, New South Wales, (collector unknown 25, MEL 3008); Clarence Heads, New South Wales, (leg. Mueller s.n., MEL 3009); Kissing Point, Townsville, Queensland, (leg. Price IRP 2399, 5.vii.1978, MEL 665993); New South Wales, (collector unknown, MEL 699008); Elliston, South Australia: lower intertidal, shaded inner reef, (leg. Womersley s.n., 15.i.1951, NY); Elliston, South Australia: lower intertidal, sheltered inner reef, (leg. Womersley 234, 15.i.1951, MEL 3010); **Hawaii**. Oahu, (leg. Wilkes 1838-42, 1838-42, NY); between Natatorium and Elks Club, Waikiki Beach, Honolulu, Oahu: epilithic, (leg. Gilbert 9410, 9.iv.1959, MICH, holotype of *C. adhaerens*); **Lord Howe Island**: unkown locality, (leg. Lucas, vi.1933, NSW 416126, photograph); **Japan**. Sesoko, Okinawa: subtidal, (leg. Coppejans, 7.ix.1993, HEC 9985); Seto, Kii Province, (leg. Okamura s.n., NY); Tokyo, Hachijyo Island, Yaene: lower intertidal zone, (leg. Tanaka 84, 11.v.1990, L 993 356 458); Marshall Islands; Bikini Atoll, Romurikku Island, (leg. Taylor 46-287, 14.v.1946, NY); **New Zealand**. unknown locality, (leg. Hombron 3, 1841, PC, lectotype of *Conferva herpestica*); unknown locality, (leg. Hombron s.n., NY, isotype of *C. herpestica*); Motu Archia, Bay of Islands, (leg. Jones, South Pacific Plants, second series, 423, 21.i.1935, NY); **Tahiti**. On reef at Punaruu Pass, (leg. Setchell & Parks A, 11.vi.1922, UC 261240); Punaruu Pass, (leg. Setchell & Parks 5258, vii.1922, UC 261290).

Notes:

The close morphological similarity between *Cladophoropsis herpestica* and *C. javanica* (*C. zollingeri*) was already noted by Weber-van Bosse (1913: 76). Howe (1914) distinguished the two species on differences in cell diameter and cell wall thickness. Howe (l.c.) based his observations solely on the type material of both species without consideration of a possible morphological continuum between the two. Later, Cribb (1960) argued that cell-wall thickness is too variable to be taxonomically significant. Based on the similarities in thallus morphology and overlapping cell dimensions he considered it improbable that the two species were distinct from one another. Cribb's view is confirmed by a Principal Component Analysis (PCA) carried out using 38 specimens identified as *C. herpestica* or *C. zollingeri* (including the type material of both species) and measurements of apical, basal cell and rhizoid diameters, and cell wall thickness. The PCA ordination diagram (Fig. 79) shows a gradual transition of specimens between both species. The type specimens of *C. zollingeri* are found to have intermediate cell dimensions, while the type of *C. herpestica* is positioned at the extreme left of the ordination diagram (large cell diameter and thick cell walls). These extreme large cell dimensions in the authentic material of *C. herpestica* probably accounts for the separation of the two species by many authors (e.g. Kützing 1849 and Howe 1914).

The original description and illustrations of *Valonia rhizophora* (plant with filaments 150-200 µm in diameter and descending rhizoids from the base of the cells) leaves not much doubt that this species is conspecific with *C. herpestica*.

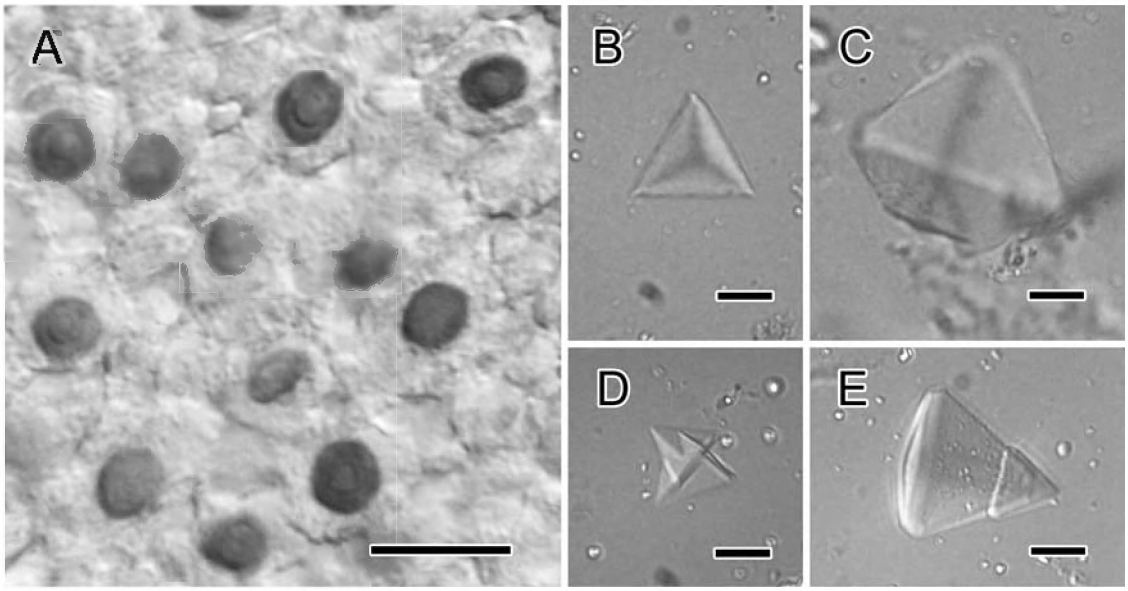


Fig. 81. *Cladophora herpestica*. **A.** Chloroplasts with large pyrenoids forming a dense parietal network; **B-E.** Tetrahedral, proteinaceous cell inclusions. (A: FL 909; B-E: HEC 6001). Scale bars = 10 µm.

The description of *C. exiguus* is based on juvenile thalli. Branching pattern and the presence of descending rhizoids sprouting from the proximal pole of most cells indicates that this species most likely belongs to *C. herpestica*.

Yendo (1920) distinguished his new species, *Cladophoropsis coriacea*, on the basis of the thick cell walls (up to 40 µm thick). Okamura (1921: 76), who examined the authentic material, argued that cell wall thickness is too variable (even within a single specimen) to have a taxonomic significance. Moreover he found similar cell wall dimensions in *C. coriacea* and *C. herpestica* (as *C. fasciculatus*, misapplied name) and therefore considered the two species conspecific. This viewpoint was later followed by Yamada (1944: 11) and Yoshida (1998: 87).

Cladophoropsis howensis is morphologically indistinguishable from *C. herpestica* and is therefore regarded as a synonym of *C. herpestica* by Womersley (1956: 377), Cribb (1960) and Kraft (2000).

Gilbert (1962) distinguished his new species *Cladophoropsis adhaerens* by its preference for shaded habitats, which he considered to be unique in the genus. *C. adhaerens* however is morphologically indistinguishable from *C. herpestica*. Moreover shaded localities fall within the ecological range of *C. herpestica*.

Apart from the aberrant ecology of *C. corallinicola* (growing in deep water, down to a depth of 40 m, on crustose coralline rhodophytes) it is morphologically indistinguishable from *Cladophora herpestica*.

Siphonocladus fasciculatus was treated as a taxonomic synonym of *Cladophoropsis zollingeri* by Yoshida *et al.* (1990: 272). The holotype of this species however corresponds to *C. sundanensis* (see there).

Dixit (1968: 13) states without providing firm evidence that *Chaetomorpha prostrata* Anand and *Rhizoclonium grande* Børgesen apply to the basal perennial portion of *Cladophoropsis*

zollingeri ("*zoolengeri*"). This viewpoint is refuted by the SSU rRNA phylogeny of Hanyuda *et al.* (2002), demonstrating *R. grande* to be unrelated to *C. zollingeri*. Examination of the original description of *R. grande* and numerous specimens from the African east coast, shows that this species differs from *C. herpestica* in a number of characters. Most obviously, *R. grande* is unbranched and does not show any remains of branches. Furthermore, unlike *C. herpestica*, the cells of *R. grande* do not contain protein crystals, and the chloroplast morphology is also different (large chloroplasts containing pyrenoids surrounded by smaller plasts lacking pyrenoids). We therefore consider *R. grande* as a distinct species.

General references. As *Cladophoropsis herpestica*: Montagne (1845: 6); Setchell (1926: 77, pl. 8, figs 1-3); Chapman (1956: 470, fig. 130); Cribb (1960: 10, pl. 4, figs 5-6); Egerod (1971: 123, figs 1-9); Womersley (1984: 184-185, figs 58B, 59C); Sartoni (1986: 365, fig. 6A; 1992: 311); Kraft (2000: 575, fig. 25E, F); Leliaert & Coppejans (2004: figs 39, 40). As *Cladophoropsis javanica* (*C. zollingeri*): Børgesen (1933: 1-3, figs 1a-e); Anand (1940: 6-7, 46-47, fig. 24); Basson (1979: 51, pl. II: fig. 9); Teo & Wee (1983: 45, fig. 41); Chowdary & Singh (1984: 178-180, 182, figs 8, 8a); Al-Hasan & Jones (1989: 294: pl. 2: fig. 17); Chaugule, Quadri, & Goswamy (1989: 113, figs 47-50); Wynne (1995: 332). As *Cladophoropsis fasciculatus* (missaplied name): Okamura (1921: 75-77, pl. 164, figs 1-7).

Boodlea vanbosseae Reinbold

Figs 82, 83

Boodlea vanbosseae Reinbold, 1905: 148 ("*van Bossei*") [Lectotype: Lucipara Island, Indonesia, leg. Weber-van Bosse, Siboga expedition s.n., Herbarium Reinbold 1915, M!. Various localities in Indonesia (including Rotti reef and Lucipara Island) were indicated in the original prologue. Only a single specimen, collected by Weber-van Bosse from Lucipara Island, and identified by Reinbold and labeled in his hand "*Boodlea van Bossei* Rbd", was found in M and is indicated as lectotype].

Description:
Thallus dark green, forming dense, matted cushions up to 8 cm across, composed of densely branched, entangled filaments. Attachment and reinforcement of the thallus mainly by unbranched, septate or aseptate rhizoids sprouting from the tips of apical cells and distal pole of intercalary cells (type-2 and -3 rhizoids) and by type-1 tenacular cells; type-3 tenacular cells rare or absent.
Growth of the thallus by apical and intercalary cell divisions (by centripetal wall ingrowths); newly formed cells producing a single lateral; older cells occasionally producing a second lateral. Cross wall formation almost immediately after lateral initiation; branches laterally inserted with a steeply inclined cross wall. Some terminal branch systems composed of cells which are markedly smaller cells than in the rest of the thallus. Branching irregular, three-dimensional. Angle of ramification 40°-90°.
Apical cells 150-240 µm in diameter, l/w ratio 2-4; in some terminal branch systems 72-90 µm in diameter, l/w ratio 1-3.5. Cells of the main axes 190-340 µm in diameter, l/w ratio 1.4-4.2. Rhizoidal cells 70-100 µm in diameter, up to 4200 µm long.
Cells invariably infected with a fungus (Ascomycota), growing on the distal face of the cross walls. Fungal thalli growing up to 800 µm high, hyphae 8-12 µm in diameter (Fig. 83).
Cell walls ca. 5 µm thick in the apical cells, up to 16 µm thick in the main axes.
Calcium oxalate crystals absent.

Ecology and geographical distribution: *B. vanbosseae* has a disjunct distribution in the tropical Indo-West Pacific (Diego Garcia, Seychelles, Indonesia and the Solomon Islands). The species grows epilithic, from the mid intertidal to subtidal, down to 10 m depth.

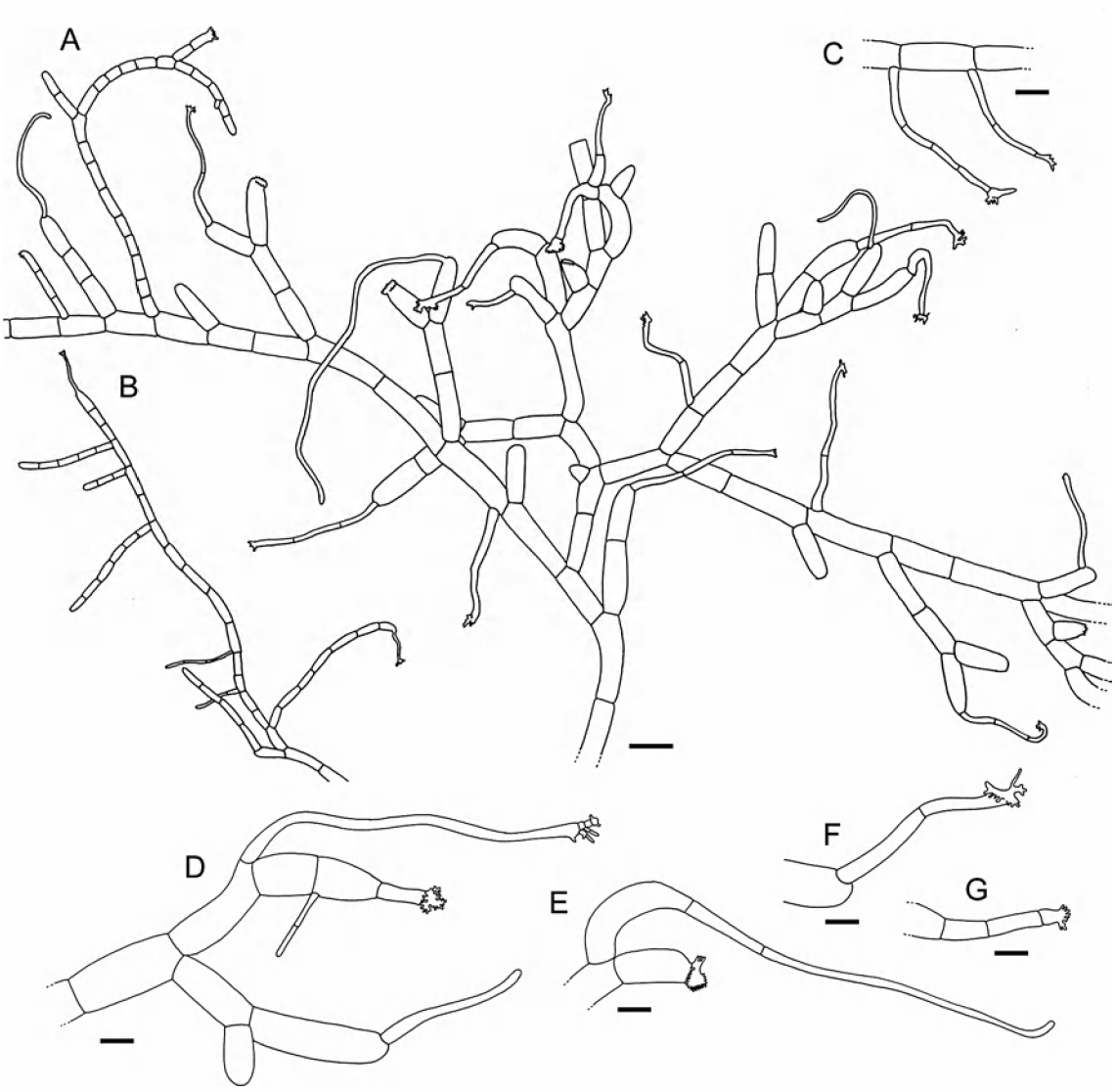


Fig. 82. *Boodlea vanbosseae* (lectotype, M). **A-B.** Unilateral or pseudodichotomous branches; numerous terminal branch systems composed of cells which are markedly narrower than in the rest of the thallus; **C.** Type-2 rhizoids produced from the proximal pole of the cells; **D-F.** Rhizoids (type-3), tenacular cells (type-1 or -3), or intermediate forms. Scale bars: A-B = 500 µm; C-F = 200 µm.

Specimens examined: Indian Ocean: Diego Garcia. unknown locality, (B 09457, B 09453); **Seychelles.** Bird Island, East coast, epilithic on coral boulders, (leg. Coppejans, Kooistra & Audiffred, 20.xii.1992, SEY 221); Plate Island, NW side, subtidal, 15 m depth, (leg. Coppejans, Kooistra & Audiffred, 7.i.1993, SEY 752); Poivre Island, NW side, epilithic on shallow limestone platform, (leg. Coppejans, Kooistra & Audiffred, 31.xii.1992, SEY 603); St. Joseph Atoll, subtidal, 2-10 m depth, (leg. Coppejans, Kooistra & Audiffred, 26.xii.1992, SEY 409; 28.xii.1992, SEY 460; 29.xii.1992, SEY 501); **Pacific Ocean: Indonesia.** Banda reef, (leg. Weber-van Bosse, Siboga expedition s.n., L 936 181 362); E of Melolo, Sumba, intertidal reef flat, (leg. Coppejans, Prud'homme van Reine & Heijs, 14.ix.1984, Snellius-II 10442); Kaledupa reef, Tukang Besi Islands, Banda Sea, subtidal, (leg. Coppejans, Prud'homme van Reine & Heijs, 9.ix.1984, Snellius-II 10260; 10.ix.1984, Snellius-II 10292); Kawa Ceram, (leg. Weber-van Bosse, Siboga expedition s.n., 3.ix.1899, L 936 181 363); Liroeng, (leg. Weber-van Bosse, Siboga expedition s.n., L 936 181 350); Lucipara Eiland, (leg. Weber-van Bosse s.n., M: lectotype of *B. vanbosseae*); Maisel Island, Banda Sea, (leg. Coppejans, Prud'homme van Reine & Heijs, 5.ix.1984, Snellius-II 10421; 7.ix.1984, Snellius-II 10117); Maisel Island, Banda Sea, intertidal reef flat, (leg. Coppejans, Prud'homme van Reine & Heijs, 5.ix.1984, Snellius-II 10404; 7.ix.1984, Snellius-II 10383; Snellius-II 10390); Maisel Island, Banda Sea, low intertidal, (leg. Coppejans, Prud'homme van Reine & Heijs, 7.ix.1984, Snellius-II 10113); NE Taka Bone Rate, S of Tarupa Kecil, in seagrass meadow, (leg. Coppejans, Prud'homme van Reine & Heijs, 17.x.1984, Snellius-II 11216); Rotti reef, (leg. Weber-van Bosse, Siboga expedition s.n., L 936 181 364); **Solomon Islands.** New Georgia, Matiu Island, mid intertidal, (leg. Womersley & Bailey 436, 30.viii.1965, L 211507).

Notes: *B. vanbosseae* morphologically fits in the *Cladophora* section *Boodleoides* as circumscribed by van den Hoek (1963, 1982a) and van den Hoek & Chihara (2000). This section (along with the section *Repentes*) is found to be more closely related to siphonocladalean genera (possibly with *Microdictyon* and *Anadyomene*) than to *Cladophora* s.s. (as specified by van den Hoek & Chihara 2000: 22) (Leliaert *et al.* 2003). We therefore await the making of a new combination until the taxonomy of this particular group is resolved.

In all specimens examined, cells were infected by an endoparasitic or -symbiotic fungus (Ascomycota) which could not be identified since no fruitbodies have been observed (Van Ryckegem, pers. comm.). About 40 marine parasitic or symbiotic fungi have been described in seaweeds, mainly in Phaeophyta; endoparasitic or endosymbiotic fungi in green algae are relatively ill known (Kohlmeyer & Kohlmeyer 1979; Hyde & Pointing 2000).

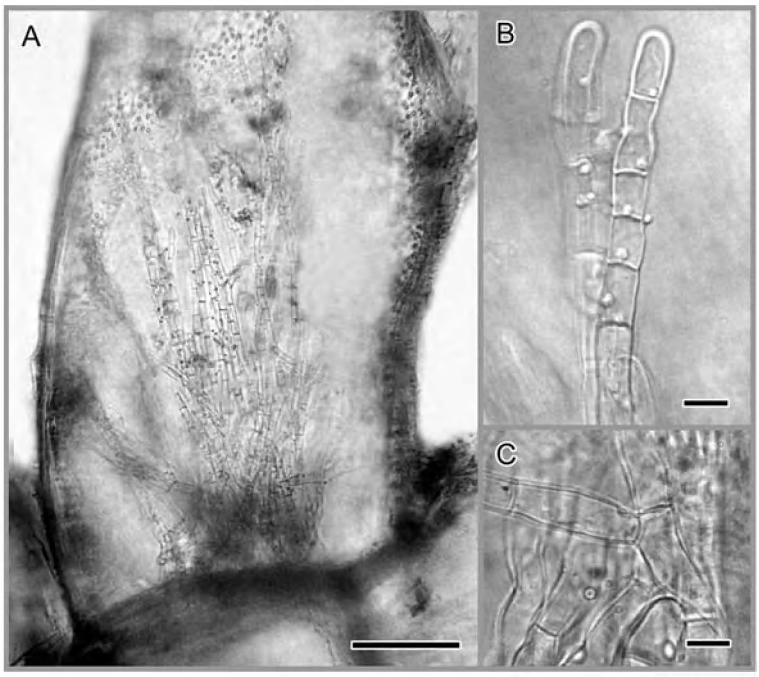


Fig. 83. Endophytic fungus (Ascomycota) in the cells of *Boodlea vanbosseae* (Snellius-II 10117). **A.** Fungal hyphae attached on the distal face of a cross-wall; **B.** Distal end of the hyphae; **C.** Basal branch. Scale bars: A = 100 µm; B-C = 10 µm.

General reference: Weber-van Bosse (1913: 70-71, fig. 12).

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Chapter 6

Synthesis and perspectives

In this thesis the taxonomy and evolutionary relationships of species and genera in the Cladophorophyceae nom. nud. (van den Hoek *et al.* 1995) are evaluated, based on morphology and molecular data. One of the main conclusions of this study is that the molecular phylogeny of the class differs considerably from the traditional classification based on the morphological characters which were previously assumed to be taxonomically significant. This incongruence between traditional classification and phylogeny can be largely attributed to morphological homoplasy caused by convergence, parallel evolution and secondary reduction. This does not imply that morphological characters are completely useless. A number of characters (e.g. some types of tenacular cells, and crystalline cell inclusions) are diagnostic for certain monophyletic groups. A detailed morphological study, in combination with available molecular data has led to the lumping of 6 genera into a single genus.

Linnaean classification and phylogenetic systematics: can they go together?

Classification is a very broad term which simply means organizing information by grouping similar things in classes. This definition is necessarily vague: there are many reasonable ways of defining similarity, and hence many alternative classifications for the same things but there is no "right way" to classify things. Classifying is one of the most basic activities of any science, because it is easier to think about a few groups of things than about numerous separate things. Human beings classify things spontaneously. For example, after seeing enough examples of a chair, we form a classification in which any given object is either a chair or a non-chair. Given a new object, we do remarkably well at deciding whether it is a chair (in essence, whether or not it is practical and socially acceptable to sit on it) (Olsen, unpublished).

The naming and classification of living organisms has been developing for over 2000 years and the true father of *biological classification* is considered to be Aristotle who arranged all animals into a single graded *scala naturae* utilising their level of perfection as a yardstick. The starting point for the modern classification of plants and animals are the comprehensive works of Linnaeus (1753, 1758). The so called Linnaean system of classification has served biologists for more than two centuries. Originally designed to catalogue diverse works of the Creator, the hierarchical categories in this ordering scheme later became interpretable as natural outcomes of the nested branching structures in evolutionary trees. Yet most classification in current use go on grouping species according to some unspecified mix of (an intuitive sense of) similarity by resemblance (phenetic clades) and similarity by descent (phyletic clades) (Avise & Johns 1999). A primary limitation of conventional taxonomy is that extant taxa, placed at the same Linnaean rank are not necessarily equivalent in age, diversity, disparity or any other consistent property of their biology or evolutionary histories. Although there is no absolute rule for designing a classification of living organisms (we can classify species by any criterion we choose), there are however a number of practical questions: Is there a preferred classification of organisms from which we can learn more than we can from alternative classifications? How practical or useful is it? (Olsen, unpublished).

Darwin (1859) referred to a classification based on evolutionary history as a natural system. In recognizing the parallel between phylogenetic closeness and species similarity, Darwin explained why the Linnaean system had been so successful for flowering plants and animals: they had been placed into the hierarchical groups of the Linnaean classification on the basis of similarities, and because these similarities reflected the evolutionary closeness of the respective species, the classification tended to reflect their historical relationships. In general, when

similarities due to common ancestry are easy to recognize and measure, a classification of the organisms tends to approximate a natural system. This, however, is not true for most organismal groups, especially those with either few morphological characters or with morphological characters with a high degree of homoplasy.

A new rigorous taxonomic approach, termed cladistics, was proposed by Hennig (1966), and uses evolutionary descent as the sole criterion for classification. Classifications based on the relationships of organisms have more predictive potential than does an arbitrary classification. Hennig (1966) called for disbanding the use of so-called grade taxa with their paraphyletic groupings and instead calls for strictly genealogical (cladistic) classifications that depict sister-group relationships. Furthermore, Hennig (1966) reasoned that the optimal yardstick for measuring which clades are equivalent is the absolute age of origin of the clades, i.e. the taxa assigned the same rank should represent clades of about the same absolute age. Hennig's (1966) suggestion that the categorical rank of any taxon should denote its geological age has been neglected, perhaps because of a widespread perception that the nodes in evolutionary trees cannot be dated with reasonable assurance (de Queiroz & Gauthier 1992, Avise & Johns 1999). Molecular phylogenetic investigations have provided tools (including gene-specific molecular clocks) along with those of paleontological investigations for dating branch-points in phylogeny and thus for constructing phylogenetic classifications in which taxa at the same rank represent clades of equivalent age (Goodman, unpublished; Goodman *et al.* 1998). The potential exists from the combined tools of molecular phylogenetics and paleontology for eventually extending a temporal scheme of biological classification to all living phyla (above the level of species) (Avise and Johns 1999). A universal time-based taxonomy would prompt and facilitate comparative evolutionary studies. Also, the ago-old issue of whether to split or lump supraspecific taxa would vanish because the ratified standards in the temporal-banding convention would be the final arbiter.

Changes in the methodologies of systematics have brought a number of revolutionary proposals about the mechanisms of classification. The claim has been that the principles of phylogenetic classification (or phylogenetic nomenclature, systematics or taxonomy) will produce stability in classification (de Queiroz & Gauthier 1992, 1994). The principles for a reformed classification have been developed into a new code of practice, the so called PhyloCode (Forey 2001, Cantino & de Queiroz 2001). These proposals of phylogenetic classification are meant to translate cladistic phylogenies directly into classifications, and to define taxon names in terms of clades.

According to Mayr (1982), biological classifications should have two functions: practical (to serve as a universal reference system) and universal (evolutionary). The relative importance of these two functions has waxed and waved through time. Benton (2000) argues that phylogenetic classification is based on a fundamental misunderstanding of the difference between a phylogeny [which is real: there is a single evolutionary tree linking all organisms living and extinct (Darwin 1859)] and a classification (which is utilitarian). Biological classifications are entirely human constructs; there is no single, true classification inherited in nature that is there to be discovered. Moreover, it is a general misconception that traditional classification which follows the Linnaean hierarchy and the rules of the international codes for nomenclature would be incompatible with (molecular) phylogenetic studies. Linnaean classifications are not as rigid and conservative as some authors (e.g. Tautz *et al.* 2003, Cantino *et al.* 1999, de Queiroz & Gauthier 1990, 1992) might claim, and they have been modified several times in the past 200 years (e.g. exclusion of polyphyletic and paraphyletic taxa and inclusion of fossil taxa). These modifications have shared a common principle: classifications should adhere ever closer to current knowledge of phylogeny, while at the same time remaining conservative.

To answer the question "do Linnaean classification and phylogenetic systematics go together?", I principally follow Benton (2000), for pragmatic reasons. He argues that we should be able to accept pluralism: "the search to identify the one true phylogeny, and the acceptance of classifications that reflect that phylogeny, but which retain utilitarian properties (e.g. the use of species binomina, ranks and flexible clade definitions)". In other words, biological classifications are meant to represent the best current estimate of phylogeny, but, for the sake of utility, they should not drift and evolve slavishly in response to every newly proposed phylogeny.

Is the classification of the Cladophorophyceae in need of revision?

In the past, classifications have tended to change only after some major landmark studies that lay out universally convincing evidence that the previous notion of phylogeny was in error. The present molecular phylogenetic study (see chapter 3 of this thesis, Leliaert *et al.* 2003) and the studies of Bakker *et al.* (1994) and Hanyuda *et al.* (2002), in combination with a re-evaluation of morphological data have indeed shown that the traditional classification of the Cladophorophyceae is in need of revision. The molecular phylogeny of the Cladophorophyceae differs considerably from the traditional classification based on thallus architecture and mode of cell division. However, the current phylogenetic hypothesis of this class is far from complete. Before undertaking radical taxonomic and nomenclatural changes, further morphological and molecular research is needed. The molecular phylogenies have until now only been based on the small and large subunit of the nuclear rDNA. Additional, independent markers (preferably also including chloroplast and mitochondrial encoded genes) are needed to confirm (or contradict) the present phylogenies and/or to resolve some presently unresolved lineages. The reliability of a phylogenetic hypothesis increases when different trees, based on independent markers or genes from different organelles, are congruent (Page & Holmes 1998). Furthermore, the number of species and strains investigated by molecular methods is far too limited to permit a sound classification based on phylogeny. The different genera should preferably be represented by additional species, preferably also including their type species. This is essential because the simple morphological characters that determine the generic concept in the class can easily have evolved multiple times. This has been demonstrated for the morphological genera *Cladophora*, *Chaetomorpha* and *Cladophoropsis* and the same could easily be true (although less likely) for other genera like *Anadyomene*, *Microdictyon* and *Valonia*. Finally, a new classification should preferably be based on time-dated phylogenies, applying a temporal banding approach, at least within the class (Hennig 1966, Avise & Johns 1999). However, a time-based phylogeny for the Cladophorophyceae is not yet available and will be difficult to obtain, mainly due to the lack of fossils in this group.

In the following paragraphs some possible revised classification schemes for the Cladophorophyceae are suggested, based on the phylogenetic information available to date (Fig. 1, Table 1). Some of these schemes illustrate how new classifications, based on monophyletic groups, can become impractical due to a senseless inflation of taxa (families in this case) which cannot be characterized by morphological characters. Classification schemes with few families are believed to be more practical and are here considered to be the most elegant (provisional) solution. Since the traditional taxon circumscriptions (families in particular) are very vague and variable, they do not contribute to a stable classification and are therefore not utilitarian (see chapter 1, Table 1). Therefore, any new phylogenetic classification could in principle be considered "better" than the traditional classifications. In general, the essential difficulty arising from reforming the cladophorophycean taxonomy is finding **apomorphic morphological**

characters for the monophyletic groups. Ultrastructural and chemical studies might provide useful characters to delimit natural groups in the Cladophorophyceae.

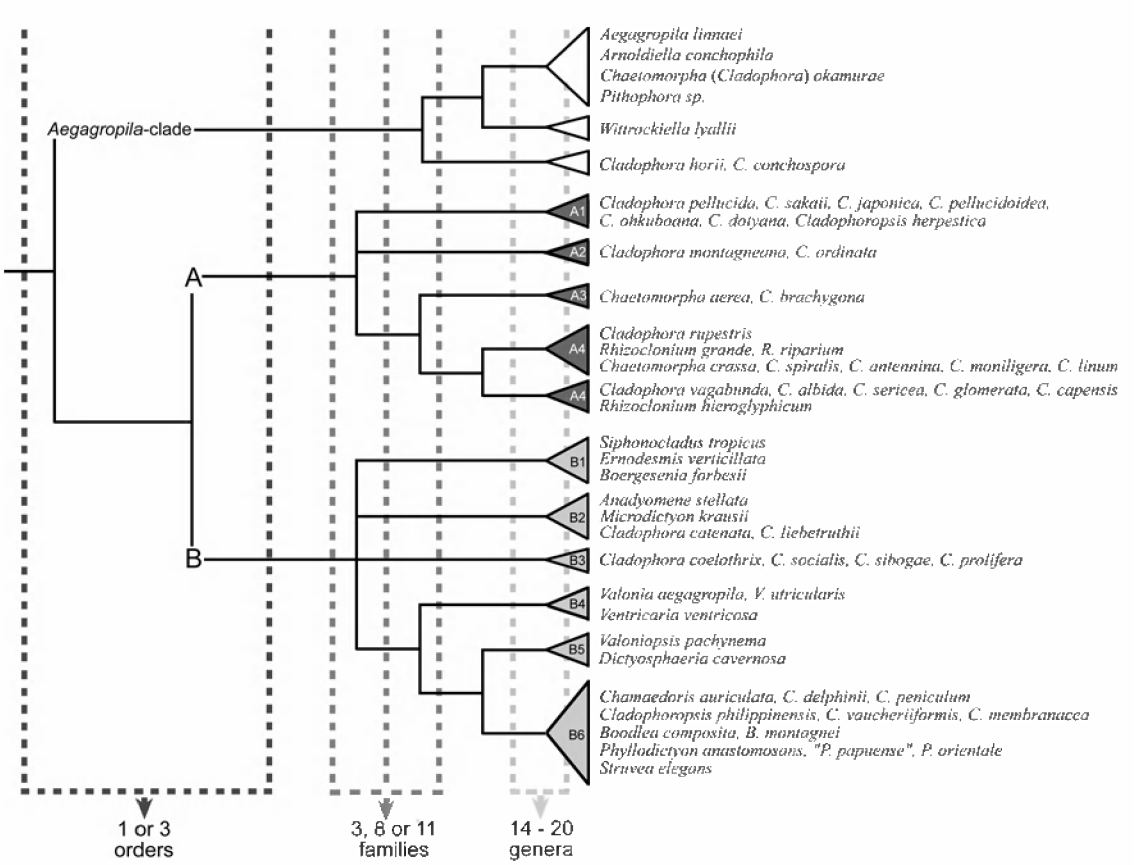

Fig. 1. Hypothetical cladogram combining the SSU nrDNA phylogenies of Bakker *et al.* (1994) and Hanyuda *et al.* (2002), and the partial LSU nrDNA phylogeny presented in this study. Clade numbers correspond to Fig. 4 of chapter 3. Taxa in clade B6 are lumped in a single genus, *Cladophoropsis* s.l., in chapter 5.

One or three orders

Within the Cladophorophyceae either a single order (Cladophorales or Siphonocladales s.l.) or three separate orders could be recognized. Since all siphonocladalean taxa (excluding part of *Cladophoropsis* and including some *Cladophora* species) are grouped in a single lineage (B), the second option is supported in the 3rd chapter of this thesis. In order to avoid the creation of paraphyletic taxa, a new order would have to be proposed for the species in the *Aegagropila*-clade. A nomenclatural difficulty which arises is the uncertain affinity of the type species of *Cladophora* [*Cladophora oligoclona* (Kützing) Kützing, a taxonomic synonym of *C. rivularis* (Linneaus) van den Hoek]. Depending on the phylogenetic position of this species, one of the orders should be named Cladophorales. The first order contains marine and freshwater representatives of *Cladophora* and the related genera *Aegagropila*, *Arnoldiella*, *Chaetomorpha*, *Pithophora* and *Wittrockiella*, all characterized by similar and relatively simple thallus architectures[1]. The second order ("Cladophorales", clade A) includes most species with a

[1] The genus *Aegagropila* has previously been reduced to a section of *Cladophora* by van den Hoek (1963). The species in the genus *Wittrockiella* much resemble those of the *Cladophora* section *Aegagropila* and this would possibly justify the inclusion of *Wittrockiella* in the morphological genus *Cladophora* (van den Hoek *et* al. 1984; Burrows 1991). *Pithophora* differs from *Cladophora* only by the formation of akinetes as overwintering spores (Wittrock 1877).

Cladophora-type thallus architecture and several species with a reduced thallus architecture. The third order ("Siphonocladales", clade B) comprises taxa with specialized morphologies and a few *Cladophora* species with some unique characters (e.g. rhizoids in the apical regions of the thallus) not found in the species of the second order. Hanyuda *et al.* (2002) indicated that the *Aegagropila*-clade could possibly be characterized by some ultrastructural and chemical characteristics (Table 2) but clear-cut synapomorphies for the three orders are yet to be discovered.

Table 1. A possible new ordinal and familial classification scheme of the Cladophorophyceae with 8 to 11 families.

Orders	Families
A new order[1] would have to be proposed for *Cladophora horii* and its relatives ("*Aegagropila*-clade")	**One or two new families** [possibly named Wittrockiellaceae (Wille 1909), Pitophoraceae (Wittrock 1877) or Cladophoraceae (Wille, *in* Warming 1884)[1]] would have to be proposed for *Cladophora horii*, *C. conchospora*, *Aegagropila linnaei*, *Arnoldiella conchophila* and *Chaetomorpha okamurae*.
A second order **"Cladophorales"**[1]	**A new family**[1] would have to be proposed for *Cladophoropsis herpestica* and the *Cladophora* species in clade A1. **A new family**[1] would have to be proposed for the *Cladophora* species in clade A2 **One or two new families**[1] would have to be proposed for the *Cladophora*, *Chaetomorpha* and *Rhizoclonium* species in the clades A3 and A4
A third order **"Siphonocladales"**[1]	**Siphonocladaceae** (Schmitz 1879) including *Siphonocladus*, *Boergesenia* and *Ernodesmis* (clade B1) **Anadyomenaceae** (Kützing 1843) including *Anadyomene*, *Microdictyon* and the Cladophora species, *C. catenata* and *C. liebetruthii* (clade B2) **A new family**[1] would have to be proposed for the *Cladophora* species in clade B3 **One family (Valoniaceae s.l.)** including clades B4, B5 and B6 ***or* two families:** **Valoniaceae** (Kützing 1849) including *Valonia* and *Ventricaria* (clade B4) **Dictyosphaeriaceae**[3] (Kützing 1849) including *Valoniopsis* and *Dictyosphaeria* (clade B5), and *Cladophoropsis* s.l.[2] (clade B6)

[1] Depending on the phylogenetic position of the type species of *Cladophora* [*Cladophora oligoclona* (= *C. rivularis*)], one of these orders would be named **Cladophorales**, one of the families **Cladophoraceae** and one of the genera ***Cladophora***.
[2] See chapter 5 for the circumscription of *Cladophoropsis* s.l.
[3] Dictyosphaeriaceae (Kützing 1849) would have priority over Boodleaceae (Børgesen 1925), in accordance with ICBN, art. 11, 14.4 and 14.5.

Table 2. Comparison of pyrenoid structure, carotenoid composition and cell wall composition between the *Aegagropila*-clade and clades A & B (see Fig. 1) (After Hanyuda *et al.* 2002).

Character	*Aegagropila*-clade	clades A & B
Pyrenoid structure	Polypyramidal	Bilenticular, rarely polypyramidal
Carotenoid composition	Loroxanthin type	Lutein type, loroxanthin type or siphonoxanthin type
Cell wall composition	Cellulose-I and chitin (*Pithophora*)	Cellulose-I

Many small families

Depending on the level of division, 8 to 11 families could be recognized; a difficulty being that these families would be largely based on unresolved clades (basal polytomies in lineages A and B) (Fig. 1, Table 1). None of the four or five traditional family definitions (see chapter 1) would be left untouched. The traditional "Cladophoraceae" would have to be split up into at least 5 families; the old family names Wittrockiellaceae and Pitophoraceae could then be resurrected (see Table 1, footnote). Also, taxa traditionally belonging to the Siphonocladaceae would have to be placed in 3 different families. The Siphonocladaceae s.s. would then only include *Siphonocladus*, *Boergesenia* and *Ernodesmis*. The Anadyomenaceae, traditionally only including *Anadyomene* and *Microdictyon*, would also have to include the *Cladophora* species, *C. catenata* and *C. liebetruthii*. A possible relationship between *C. liebetruthii* and the genus *Microdictyon* based on morphology was already suggested by van den Hoek (1984). *C. catenata* however, is morphologically very distinct from either *Anadyomene* or *Microdictyon*. One or two families could be recognized for the clades B4, B5 and B6. In the first option, the Valoniaceae s.l. would include *Valonia*, *Ventricaria*, *Valoniopsis*, *Dictyosphaeria* and *Cladophoropsis* s.l. In the second option (two families), the circumscription of the Valoniaceae would have to be narrowed down on the one hand by excluding a number of taxa with inflated cells (e.g. *Ernodesmis* and *Valoniopsis*). On the other hand it would have to be extended by including *Ventricaria*, characterized by segregative cell division. A second family (which would have to be named Dictyosphaeriaceae, based on priority) would then include *Dictyosphaeria*, *Valoniopsis* and *Cladophoropsis* s.l.

A few small families

The above family classification is undesirable for two main reasons: firstly because it is largely based on unresolved clades, secondly because of the senseless inflation of the number of families without any (apparent) apomorphic morphological characters. An alternative to the classification in Table 1, is the recognition of a single order and three families, or three monotypic orders. Such a classification would not only be more simple (and therefore more practical), it would also be based on resolved and well supported clades.

How many genera?

Similar to the number of recognized families, 14-20 genera could be recognized, depending on the level of division. Each of the clades (triangles) illustrated in Fig. 1 could be considered as a single genus, or alternatively, each clade could be further subdivided. For example *Siphonocladus tropicus*, *Ernodesmis verticillata* and *Boergesenia forbesii* (clade B1) could either be lumped into a single genus (*Siphonocladus* would have priority), or kept in three separate genera. The first option could be morphologically supported since the three species are all characterized by inflated, club-shaped cells with basal annular constrictions. The differences in thallus architecture between *Siphonocladus*, *Ernodesmis* and *Boergesenia* are merely a result of their different mode of cell division. *Ernodesmis verticillata* forms spherical thalli composed of cells with verticillate, apical clusters of branches formed by lenticular cell division (modified segregative cell division occurs only occasionally). The branches in *Siphonocladus tropicus* are formed by segregative cell division s.s. and radiate laterally from the club-shaped main axes. In *Boergesenia forbesii* the club-shaped cells remain unbranched and cell division occurs by modified segregative cell division.

The independent recognition of the traditional genera in clade B6 is more problematic because non-monophyly has been demonstrated for a number of included genera (*Boodlea*,

Phyllodictyon and *Cladophoropsis*). The clustering of these genera in a well supported monophyletic group, the non-monophyly of a number of included genera, in combination with the fuzzy morphological boundaries and the presence of a number of morphological synapomophies supports the recognition of a single genus (see chapter 5).

Table 3. Comparison of morphological characters of genera within the family Dictyosphaeriaceae: *Dictyosphaeria*, *Valoniopsis* and *Cladophoropsis* s.l.

	Dictyosphaeria	*Valoniopsis*	*Cladophoropsis* s.l.
Thallus filamentous		✓	✓
Thallus parenchymatic	✓		
Cell division by centripetal wall ingrowths			most species
Segregative cell division	✓		some species
Lenticular cell division		✓	
Tenacular cells type-1			✓
Tenacular cells type-2	✓		
Tenacular cells type-3			✓
Tenacular cells type-4			some species
Inflation of cells (diameter of cells in µm)	300-4000	1000-1500	40-5000
Calcium oxalate crystals type-1			some species
Calcium oxalate crystals type-3	some species		
Calcium oxalate crystals type-4		✓	

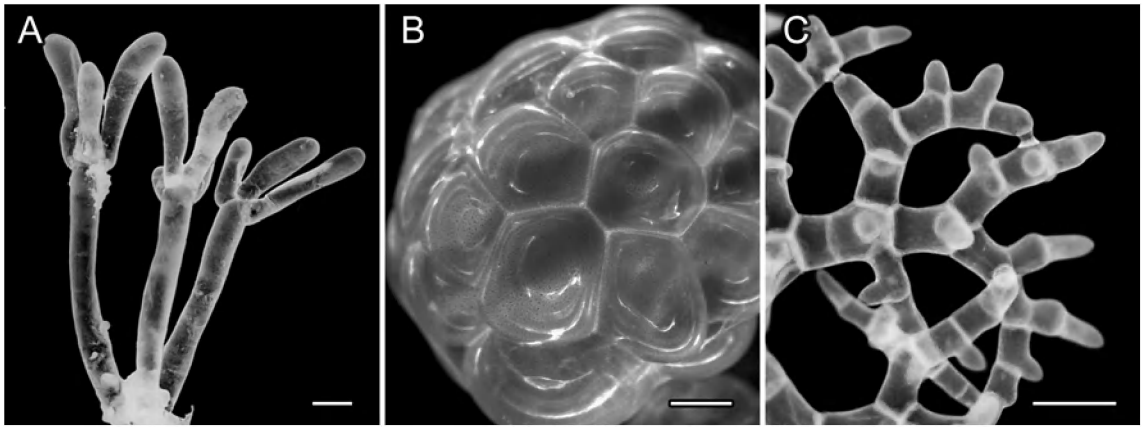

Fig. 2. Comparison of the thallus architecture of three closely related genera. **A.** *Valoniopsis pachynema* (FL 681: Paje, Zanzibar); **B.** *Dictyosphaeria cavernosa* (UTEX #2365: Amami Island, Japan); **C.** *Cladophoropsis* (*Boodlea*) *composita* (FL 958: Chwaka Bay, Zanzibar). Scale bars: A, B = 1 mm, C = 200 µm.

The main difficulty with any revised classification based on phylogeny, is the incongruity with morphological characters. On the one hand, morphologically similar species end up in different genera, families or even orders. For example *Cladophora horii* and *C. prolifera* share a relatively large number of characters (thallus forming dense spreading tufts, acropetally organized branch systems, attachment by descending rhizoids produced by cells in the basal part of the thallus, dark green thalli), and have therefore been placed in the same *Cladophora* section *Rugulosae* (van den Hoek & Chihara 2000). In the new classification the two species would be placed in two different orders with the sole morphological criterion being the structure of the pyrenoids. On the other hand species with distinct characters, sharing little or no morphological

characters, would be placed in a single genus (e.g. *Dictyosphaeria* and *Valoniopsis*) or family (e.g. *Dictyosphaeria*, *Valoniopsis* and *Cladophoropsis* s.l.) (Table 3, Fig. 2).

Species concepts in the *Cladophoropsis composita* complex

"The literature about species concepts might be larger than that about any other subject in evolutionary biology, but the issue of empirically testing species boundaries has been given little attention relative to seemingly endless debates over what species are" (Sites & Marshall 2003).

Morphological as well as molecular studies confirm the indistinct boundaries between *Boodlea composita*, *Phyllodictyon anastomosans* and *Struveopsis siamensis*. Phylogenetic studies based on ITS sequences have demonstrated that thallus morphology is incongruous with the evolutionary history within this complex (Wysor 2002), indicating that the different thallus morphologies could have evolved several times independently. Alternatively, the different architectural types could be ecologically determined, or represent different developmental stages of the same species. Morphological examination of a large number of specimens worldwide of *B. composita* and morphological allied taxa, demonstrates a wide variety in thallus architecture, branching systems, cell dimensions and tenacular cell types. Based on these characters, six more or less distinct morphological entities can be recognized. Awaiting the true nature of these entities (separate species or growth forms of the same species), the different morphological types have been provisionally referred to as phenodemes (i.e. groups of morphologically allied individuals) of a single species, *Cladophoropsis composita*.

A better insight into the species concept of this group could be gained by an integrated approach of phylogenetic, reproductive and morphological criteria. Different empirical methods for delimiting species have been recently described (Sites & Marshall 2003). In one of these methodologies, termed the exclusivity criterion, phylogenetic species are delimited, using genealogical concordance of multiple independent loci (Dettman *et al.* 2003). With this method, species are delimited based on two requirements: species are exclusive groups (those in which all members are more closely related to each other than to any organism outside of the group) and species reside at the boundary between reticulate and divergent genealogy, where unlinked genes should have concordant genealogical histories (Sites & Marshall 2003). Within single interbreeding species (or in case of hybridisation between lineages), the mixing effects of recombination between genes would cause unlinked loci to have different genealogies, but between genetically isolated species, the extinction of ancestral alleles by genetic drift would lead to the congruence of genealogies. Hence, the transition between deep genealogical concordance and shallow genealogical discordance can be used to recognize phylogenetic species (Taylor *et al.* 2000; Dettman *et al.* 2003).

Crossing experiments could be carried out to test sexual compatibility within and between the circumscribed phylogenetic and morphological species. A diplohaplontic, isomorphic life cycle has been demonstrated in "*Boodlea composita*", based on cultural and karyological evidence (Bodenbender *et al.* 1988, Kapraun & Nguyen 1994). The haploid gametophytes produce biflagellate gametes while the diploid sporophytes produce quadriflagellate meiospores as well as asexual, biflagellate (diploid) zoospores. A difficulty will be the identification of the morphological identical generations and the different types of zoospores. This could be solved by the use of cytophotometry using the DNA-localizing fluorochrome DAPI. With this technique haploid and diploid thalli or spores can be distinguished by differences in fluorescence intensity (Kapraun & Nguyen 1994).

Taxonomic and phylogenetic studies in the Cladophorophyceae (Chlorophyta)

The Cladophorophyceae (including both orders Cladophorales and Siphonocladales) form a class of siphonocladous green algae with a worldwide distribution in tropical to arctic marine and freshwater environments. Thallus organization in the class ranges from branched or unbranched uniseriate filaments to more complex architectural types such as parenchymatic thalli, thalli composed of inflated cells, stipitate plants, blade-like thalli, and reticulate plants composed of anastomosing filaments. Two main modes of cell division have been distinguished in the Cladophorophyceae. In most taxa, including all *Cladophora* species, cells divide by centripetal invagination of the cell wall. A number of other taxa are characterized by a peculiar way of cell division termed "segregative cell division" in which the protoplast is cleaved into several rounded and walled portions, later expanding into new cells and even branches. Historically, phycological systematists have hypothesized many alternative classifications and phylogenies, which were all mainly based on thallus organization and mode of cell division. Most of the taxonomic controversy has centered on whether or not the two orders, Siphonocladales and Cladophorales, need separate recognition. The general consensus to date is to combine both orders to a single order within the class Cladophorophyceae. Within *Cladophora*, the largest genus of the class, a number of different architectural types can be distinguished, representing the sections of the genus. Based on comparison of morphology, van den Hoek (1984) hypothesized that numerous reduction and specialization events have occurred independently several times in *Cladophora* sections, resulting in the various reduced (cladophoralean) and specialized (siphonocladalean) morphologies (genera). A historical taxonomic overview of the orders Cladophorales and Siphonocladales and the current circumscription of the class Cladophorophyceae is presented in chapter 1.

The present study investigates the taxonomy and evolutionary relationships of species and genera in the Cladophorophyceae, with emphasis on tropical marine representatives. With the advent of formal cladistic methods and comparative DNA sequence data in the last decennia, opportunities for more accurate investigation of phylogenies became possible. Although the class is believed to be an originally tropical clade, it is mainly the temperate taxa that have previously been investigated in detail, both in taxonomic and phylogenetic studies.

Chapter 2 reports on a taxonomic study of the genus *Cladophora* along the subtropical South African East Coast. This genus has been well investigated in the northern Atlantic Ocean, Southern Australia and Japan by van den Hoek during the last 40 years; however, the tropical Indian Ocean representatives remain relatively understudied. Twelve *Cladophora* species, representing seven morphological sections of the genus, occur along the South African East Coast and detailed descriptions and illustrations are presented. Four species are recorded for the first time in South Africa: *C. catenata*, *C. vagabunda*, *C. horii* and *C. dotyana*; the last two are also new records for the Indian Ocean. A comparison of the South African *C. rugulosa* specimens with those of *C. prolifera* from South Africa and other regions demonstrates that these species are not synonymous as previously considered, leading to the resurrection of *C. rugulosa* which is probably a South African endemic. Although the newly described Japanese species *C. horii* (van den Hoek & Chihara 2000) has been placed in the section *Rugulosae* (together with *C. prolifera*), its systematic position remained uncertain, primarily because of its abberant pyrenoid morphology (polypyramidal as opposed to bilenticular in the rest of the genus and class). As will be demonstrated by LSU nrRNA sequence analyses in chapter 3, *C. horii* falls within a separate, sister clade of the Cladophorophyceae and is more closely related to some genera with a deviant *Cladophora*-type morphology (including *Wittrockiella*, *Pithophora* and *Arnoldiella*) than to other species in the "main *Cladophora*-clade". Previous SSU rRNA

phylogenies and the present LSU phylogeny also demonstrates that a number of other *Cladophora* species (including the South African *C. catenata*, *C. coelothrix*, *C. liebetruthii* and *C. socialis*) are located in the "*Siphonocladales*-clade" and possibly closely related to the genera *Anadyomene* and *Microdictyon*. These *Cladophora* species are all characterized by rhizoids sprouting from cells in any part of the thallus, a feature not shared with the species of the "main *Cladophora*-clade". Intercalary rhizoids promote the formation of dense tufts loaded with sand that are unattractive to herbivores and might be considered as an adaptation to the high grazing pressure in tropical and subtropical marine environments. Seven distribution groups of the genus *Cladophora* have been distinguished, based on the species' northern and southern boundaries in combination with winter and summer isotherms of the sea surface. The 11 species identified along the South African East Coast fall into three biogeographical categories: two species belong to the strictly tropical distribution group and have their southernmost boundary in northern KwaZulu-Natal (*C. catenata* and *C. horii*), eight species (*C. coelothrix* Kützing, *C. socialis*, *C. liebetruthii* Grunow, *C. prolifera*, *C. dotyana*, *C. flagelliformis*, *C. vagabunda*, *C. ordinata*) belong to the tropical to warm temperate distribution group, and *C. rugulosa* seems to be restricted to the cooler South and East Coast of South Africa.

In chapter 3, phylogenetic relationships within the Cladophorophyceae are inferred from partial LSU nrRNA gene sequence. This study extends the SSU nrRNA phylogenies of Bakker *et al.* (1994) and Hanyuda *et al.* (2002) mainly with representatives of species traditionally ascribed to the Siphonocladales s.s., including 37 species in 18 genera. The genus *Cladophora* is represented by 10 species, belonging to six sections. Because certain parts of the sequences are highly divergent, the secondary structure of the RNA molecule had to be taken into account for the alignment. The partial LSU rRNA sequences contain the appropriate amount of variation to resolve the basal divergences within the Cladophorophyceae. The present study in combination with previously published SSU nrRNA phylogenies reveals three lineages within the class: one sister clade comprising taxa with a *Cladophora*-type architecture, and two main lineages. The first main lineage (A) includes most *Cladophora* species and several taxa with a reduced thallus architecture. The second main lineage (lineage B) comprises taxa with specialized (siphonocladalean) morphologies and a few *Cladophora* species with some unique characters (e.g. intercalary rhizoids) not found in the species of lineage A. The sister clade comprising *Cladophora horii* suggests that the siphonocladalean morphologies arose as specialized forms from a *Cladophora*-like ancestor. The present study partly confirms van den Hoek's (1984) hypothesis: different reduction events occurred several times independently. All taxa with specialized thalli however, are grouped in one lineage, with the first divergences being unresolved. This either indicates a single evolution event of an ancestor with a *Cladophora*-type architecture to the siphonocladalean taxa, or a number of independent evolution events which took place in a relative short period of time and therefore cannot be revealed in the present phylogeny. The grouping of all siphonocladalean taxa (excluding part of *Cladophoropsis* and including some *Cladophora* species) in one lineage, separated by long branches from the cladophoralean lineages, clearly supports the recognition of a separate order Siphonocladales, with the Cladophorales (s.s.) remaining paraphyletic. Traditionally four or five families are recognized within the Cladophorophyceae, mainly based on differences in thallus architecture. The family circumscriptions are rather vague and variable, and consequently the included genera have changed frequently in the course of time. The present phylogeny indicates that the traditional family-level classification is untenable since all families (except for the Anadyomenaceae, consisting only of *Anadyomene* and *Microdictyon*) are found to be polyphyletic.

In chapter 4, the morphological variety and taxonomic significance of crystalline cell inclusions are investigated in the Cladophorophyceae. A wide variety of crystalline structures (including calcium oxalate crystals, calcium carbonate cystoliths and silica bodies) has been observed in vascular plants but they have long been neglected in macro-algae. Both the morphology and distribution of calcium oxalate (CaOx) crystals within vascular plants exhibit species-specific patterns. In macroalgae, CaOx crystals have only rarely been recorded, but the reports that do exist represent a broad sample of algae (Pueschel 2001). Protein crystals have been reported in a wide range of Rhodophyta and some Phaeophyta (Pueschel 1992). In Chlorophyta, and in particular the Cladophorophyceae, reports of crystalline cell inclusions are sparse. The cell contents of 66 species of Cladophorophyceae were screened, and 45 species were found to possess some kind of crystalline cell inclusion. The crystals can be classified into eight morphological types, including needle-shaped, prismatic, octahedral, tetrahedral, cubical or globular, and they were found to occur as single crystals or in clusters. In addition to the different morphological types, the crystals are characterized by different chemical composition. Chemical tests distinguished the crystals as being composed of calcium oxalate, calcium carbonate, proteins or silica. The diversity of crystal types raises the possibility of these structures having systematic value. The occurrence of crystalline structures is compared with the LSU phylogeny of the Cladophorophyceae. Only prismatic CaOx crystals are characteristic for a single clade (see below). The other types either occur in two or more separate lineages, or are only represented by a single taxon in the cladogram. Crystalline cell inclusions may provide useful diagnostic characters to distinguish between species characterized by similar thallus architectures (e.g. *Cladophoropsis sundanensis* and *Cladophora coelothrix*).

In chapter 5, a taxonomic re-assessment of the genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis* is presented. The extreme close relationship between these genera has been confirmed by phenetic as well as molecular evidence (Olsen-Stojkovich 1986; Kooistra *et al.* 1993; this study). The genus complex can be characterized by a number of shared derived morphological characters: the thalli are composed of branched, entangled filaments, often forming a two- or three-dimensional reticulum; thallus reinforcement is generally achieved by type-3 tenacular cells (with the exception of some species where this feature may have been lost secondarily); prismatic calcium oxalate crystals are found in the cells of most taxa; laterals are produced singly or in opposite pairs, almost immediately after cell division; cross walls at the base of the laterals are absent or the formation is markedly delayed; segregative cell division, either organized or through cell wounding has been documented in most representatives. The clustering of *Struvea*, *Phyllodictyon*, *Boodlea*, *Struveopsis*, *Chamaedoris* and *Cladophoropsis* in a well supported monophyletic group, the non-monophyly of a number of included genera, in combination with the fuzzy morphological boundaries and the presence of a number of synapomorphic morphological characters supports the recognition of a single genus. In order to avoid disadvantageous nomenclatural changes the name *Cladophoropsis* is preferred over *Chamaedoris*, and this name would then have to be proposed for conservation against *Chamaedoris*, *Struvea*, *Phyllodictyon*, *Boodlea*, *Nereodictyon*, *Spongodendron*, *Struveopsis* and *Pseudostruvea*. Given the apparent morphological variety in the newly defined genus *Cladophoropsis*, six sections are distinguished, based on morphological and molecular evidence. These sections only partly correspond with the circumscriptions of the former genera. The application of the morphological species concept in the group is often problematic because of the limited number of morphological characters and the considerable phenotypic plasticity. Therefore a good understanding of this morphological variability (which is possible through the examination of a large number of specimens) is essential for establishing reliable (morphological) species circumscriptions. Detailed descriptions and illustrations are provided for the 20 recognized

species, including two new species *C. kenyensis* and *C. papuensis*. Lectotypification of 15 taxa (including many synonyms) is made in this paper. In order to avoid nomenclatural confusion, the new species, new combinations and new sections are indicated as provisional names.

Morphological as well as molecular studies confirm the indistinct boundaries between *Boodlea composita*, *Phyllodictyon anastomosans* and *Struveopsis siamensis*. Partial LSU rRNA sequences of these taxa are nearly identical, indicating that they might represent growth forms of a single species. Phylogenetic studies based on ITS sequences have demonstrated that thallus morphology is incongruous with the evolutionary history within this complex (Wysor 2002), indicating that the different thallus morphologies could have evolved several times independently. Alternatively, the different architectural types could be ecologically determined, or represent different developmental stages of the same species. Morphological examination of a large number of specimens worldwide of *B. composita* and morphological allied taxa, demonstrates a wide variety in thallus architecture, branching systems, cell dimensions and tenacular cell types. Based on these characters six more or less distinct morphological entities can be recognized. Awaiting the true nature of these entities (separate species or growth forms of the same species), the different morphological types are provisionally referred to as phenodemes (i.e. groups of morphologically allied individuals) of a single species, *Cladophoropsis composita*.

Samenvatting

Taxonomische en fylogenetische studies in de Cladophorophyceae (Chlorophyta)

De Cladophorophyceae vormen een klasse van meercellige wieren behorende tot de Chlorophyta (groenwieren) en worden voornamelijk gekenmerkt door de coenocytische thallusbouw (thallus samengesteld uit meerkernige cellen). De klasse bevat een dertigtal genera en een driehondertal soorten die verspreid zijn van tropische tot artische gebieden. Het merendeel van de soorten is marien, maar enkelen hebben zich succesvol aangepast aan zoetwater en zelfs aan terrestrische biotopen. De thallusarchitectuur in de groep varieert van onvertakte of vertakte filamenten tot meer complexe structuren zoals bladvormige of parenchymatische thalli. Enkele genera hebben bijzondere kenmerken zoals sterk opgezwollen cellen met diameters van enkele millimeters of zelfs centimeters (bv *Ventricaria*), intercalaire rhizoiden, speciale vasthechtingstructuren (tenacula) of steelcellen met ringvormige vernauwingen. De taxonomische geschiedenis van de groep is lang en complex; de grootste controverse draaide rond het al dan niet erkennen van twee afzonderlijke ordes, Siphonocladales en Cladophorales. Het voornaamste argument om alle genera in één orde te plaatsen is de klaarblijkelijke homogeniteit in chloroplastmorfologie, celwandstructuur en thallusbouw (coenocytisch). Anderzijds was de erkenning van twee afzonderlijke ordes hoofdzakelijk gebaseerd op verschillen in thalluscomplexiteit: de Cladophorales omvatten de genera met een eenvoudige thallusarchitectuur (onvertakte of vertakte uniseriate filamenten, bv *Cladophora*); de Siphonocladales bevatten de genera met een meer complexe thallusarchitectuur of met bijzondere kenmerken (bv opgezwollen cellen of tenacula). Enkele auteurs beschouwen segregatieve celdeling (een bijzondere manier van celdeling waarbij de meerkernige protoplast opgedeeld wordt in verschillende sferische dochterprotoplasten die nadien omringd worden door een celwand en daarna opzwellen) als het voornaamste kenmerk van de Siphonocladales. Het soortenrijkste genus binnen de klasse is *Cladophora* en wordt gekenmerkt door thalli opgebouwd uit vertakte, uniseriate filamenten. Ondanks de eenvoudige thallusbouw, worden binnen het genus een elftal architecturale types (morfologische secties) onderscheiden. Gebaseerd op een vergelijkende morfologische studie, werd door van den Hoek (1984) de hypothese opgesteld dat verscheidene, onafhankelijke evolutielijnen, vertrekkende uit de verschillende *Cladophora* secties, onstaan hebben gegeven aan de verschillende genera in zowel de Cladophorales als Siphonocladales. Deze evolutielijnen zijn zowel gekenmerkt door reductiegebeurtenissen (vereenvoudiging van de thallusbouw, bv verlies van takken) als door specialisatiegebeurtenissen (bv vorming van bladachtige structuren). Hoofdstuk 1 geeft een historisch en taxonomisch overzicht van de ordes Cladophorales en Siphonocladales en verduidelijkt de huidige omschrijving van de klasse Cladophorophyceae.

De huidige studie heeft tot doel de evolutionaire verwantschappen tussen soorten en genera in de Cladophorophyceae te onderzoeken, na te gaan welke morfologische kenmerken congruent zijn met de moleculaire fylogenieën (evolutionaire geschiedenis), en de taxonomie van enkele groepen in detail te bestuderen. De nadruk van dit proefschrift ligt voornamelijk op de tropische mariene vertegenwoordigers van de klasse.

Hoofdstuk 2 behelst een studie van het genus *Cladophora* langs de subtropische oostkust van Zuid-Afrika. Dit genus werd taxonomisch grondig bestudeerd door van den Hoek die zich voornamelijk toelegde op de soorten van de Noord-Atlantische Oceaan, Zuid Australië en Japan. De tropische soorten zijn echter veel minder goed gekend. Twaalf *Cladophora* soorten uit zeven morfologische secties komen voor langs de Zuid-Afrikaanse oostkust. Vier daarvan worden voor de eerste keer vermeld voor Zuid-Afrika: *C. catenata*, *C. vagabunda*, *C. horii* en *C. dotyana*; de laatste twee zijn tevens nieuwe waarnemingen voor de Indische Oceaan. Een vergelijkende morfologische studie van de Zuid-Afrikaanse *C. rugulosa* met specimens van *C.*

prolifera toont aan dat deze soorten geen synoniemen zijn zoals eerder werd verondersteld. *C. prolifera* kent een wijde verspreiding in tropische en subtropische zeëen terwijl de verspreiding van *C. rugulosa* waarschijnlijk beperkt is tot Zuid-Afrika. De systematische positie van de recent beschreven Japanse *C. horii* (van den Hoek & Chihara 2000) is onzeker door de afwijkende pyrenoïde structuur. Een moleculaire fylogenie (zie volgende hoofdstuk) toont inderdaad aan dat deze soort niet verwant is aan de meeste andere *Cladophora* soorten, maar tot een zuster clade van de Cladophorophyceae behoort. Ook de in Zuid-Afrika voorkomende *C. catenata*, *C. coelothrix*, *C. liebetruthii* and *C. socialis* blijken onverwant te zijn met de rest van de *Cladophora* soorten maar behoren tot de evolutielijn van Siphonocladales. Deze vier *Cladophora* soorten worden gekenmerkt door kussenvormige thalli met intercalaire rhizoiden die zand kunnen vasthouden en zo onaantrekkelijk worden voor herbivoren. Intercalaire rhizoiden kenmerken ook tal van andere tropische Siphonocladales soorten en kunnen beschouwd worden als een adaptatie aan de hoge begrazingsdruk in tropische mariene habitats.

Hoofdstuk 3 is gericht op de fylogenetische verwantschappen binnen de Cladophorophyceae. Betrouwbaar onderzoek naar evolutionaire verwantschappen tussen organismen werd de laatste decennia mogelijk met de opkomst van formele fylogenetische methoden en de mogelijkheid tot het vergelijken van DNA-sequenties. Deze studie is gebaseerd op gedeeltelijke LSU nrRNA sequenties (grote subeenheid van het nucleair ribosomaal RNA) en is een uitbreiding van twee eerder gepubliceerde fylogenieën die gebaseerd waren op het meer conservatieve SSU nrRNA (kleine subeenheid van het nucleair ribosomaal RNA) (Bakker *et al.* 1994 en Hanyuda *et al.* 2002). 37 soorten, behorend tot 18 genera, werden geanalyseerd; het genus *Cladophora* werd vertegenwoordigd door 10 soorten, behorend to 6 morfologische secties. De hier voorgestelde fylogenie is congruent met de eerder gepubliceerde SSU fylogenieën en bestaat uit één zuster clade en twee hoofdevolutielijnen. De zuster clade bevat een aantal *Cladophora* soorten (o.a. *C. horii*) en enkele andere genera die gekenmerkt worden door een eenvoudige, *Cladophora*-achtige thallusarchitectuur. Een eerste hoofdevolutielijn omvat de meeste *Cladophora* soorten en verschillende taxa met een gereduceerde thallusbouw. De tweede evolutielijn bevat voornamelijk tropische vertegenwoordigers die traditioneel in de Siphonocladales werden geplaatst en enkele *Cladophora* soorten met een meer complexe of gespecialiseerde thallusbouw. De positie van *Cladophora horii* in de zuster clade van de klasse suggereert dat de Siphonocladales geëvolueerd zijn uit een *Cladophora*-achtige voorouder. De huidige studie bevestigt ten dele de hypothese van van den Hoek (1984). Verschillende reducties zijn inderdaad verschillende keren onafhankelijk van elkaar opgetreden. Daarentegen zijn alle soorten met gespecialiseerde thallusbouw gegroepeerd in één, duidelijk afzonderlijke clade, wat de erkenning van de orde Siphonocladales bekrachtigd. De basale divergenties in deze clade zijn echter onopgelost. Dit kan enerzijds betekenen dat een *Cladophora*-achtige voorouder éénmalig ontstaan heeft gegeven aan alle gespecialiseerde vormen. Ofwel zijn meerdere, onafhankelijke evolutionaire gebeurtenissen in een relatief korte periode opgetreden waardoor deze niet worden weerspiegeld in de huidige fylogenie.

Traditioneel worden vier of vijf families onderscheidden in de Cladophorophyceae die voornamelijk gebaseerd zijn op verschillen in thallusarchitectuur. De omschrijving van deze families is altijd vaag gebleven en is bovendien in de loop der tijd vaak aangepast. De huidige fylogenie wijst aan dat de klassieke familieclassificatie niet overeenkomt met de evolutionaire geschiedenis en dus onhoudbaar is.

In hoofdstuk 4 wordt de morfologische variatie en systematische bruikbaarheid van intracellulaire kristallen in de Cladophorophyceae onderzocht. Een grote verscheidenheid van kristalachtige structuren (waaronder calcium oxalaat kristallen, calcium carbonaat cystolieten en silica structuren) is gekend bij hogere planten en maar in macrowieren zijn ze lange tijd

onbestudeerd gebleven. In de deze studie werd de celinhoud van 66 soorten Cladophorophyceae onderzocht op de aanwezigheid van kristalstructuren. Daarvan werd in de cellen van 45 soorten één of ander kristaltype aangetroffen. De kristallen kunnen onderverdeeld worden in acht morfologische groepen (waaronder naaldvormige, prismatische, tetrahedrische en cubische) en worden gekenmerkt door verschillende chemische samenstelling (calcium oxalaat, calcium carbonaat, proteïnen en silica). De grote diversiteit doet de vraag rijzen of deze kristallen een systematische waarde hebben. Het voorkomen van kristallen in soorten werd vergeleken met de LSU fylogenie van de Cladophorophyceae. Enkel prismatische calcium oxalaat kristallen zijn kenmerkend voor één enkele clade terwijl de andere types blijkbaar meerdere malen onafhankelijk van elkaar zijn geëvolueerd. Kristallen zijn vooral bruikbaar als determinatiekenmerk tussen onverwante soorten met een gelijkaardige thallusbouw, bijvoorbeeld *Cladophoropsis sundanensis* and *Cladophora coelothrix*.

Hoofdstuk 5 omvat een taxonomische revisie van de genera *Boodlea*, *Chamaedoris*, *Cladophoropsis*, *Phyllodictyon*, *Struvea* and *Struveopsis*. De nauwe verwantschappen tussen deze genera werden reeds geopperd op basis van fenetische en moleculaire gegevens (Olsen-Stojkovich 1986; Kooistra *et al*. 1993) en worden in deze studie bevestigd. De genetische variatie van de partiële LSU rRNA sequenties tussen vertegenwoordigers van deze genera is vergelijkbaar met die tussen twee isolaten van éénzelfde soort *Cladophora* (*Cladophora dotyana*) en is beduidend kleiner dan tussen alle soorten van *Cladophora* s.s. (omschreven door van den Hoek & Chihara 2000). Het genus complex wordt bovendien gekenmerkt door een aantal gemeenschappelijk afgeleide morfologische kenmerken: thalli samengesteld uit vertakte en verweefde filamenten die vaak twee- of driedimensionele netvormige planten vormen; versteviging van de thallus door type-3 tenacula; aanwezigheid van prismatische calcium oxalaat kristallen; celdeling wordt snel opgevolgd door de vorming van één of twee zijtakken; uitstel van ontwikkeling van dwarswanden aan de basis van de zijtakken; en segregative celdeling is bij de meeste vertegenwoordigers vastgesteld, al dan niet als een reactie op celbeschadiging. De groepering van de genera in één clade, het feit dat enkele van de genera polyfyletisch zijn en de zeer nauwe genetische verwantschappen tussen de soorten van het genuscomplex en, in combinatie met de vage morfologische grenzen en de aanwezigheid van een aantal gemeenschappelijk afgeleide morfologische kenmerken staven de erkenning van één enkel genus: *Cladophoropsis*. De twintig onderscheiden soorten, waaronder twee nieuwe voor de wetenschap (*C. kenyensis* en *C. papuensis*), worden nauwkeurig beschreven en geïllustreerd.

Glossary

Some of the terms below may have a broader meaning when applied in a different context. The definitions therefore only apply to their use in the Cladophorophyceae. For terms related to molecular phylogeny we refer to Page & Holmes (1998).

Acropetal thallus organization: thallus with branching system in which the laterals are produced in acropetal succession, i.e. with the youngest and shortest laterals closest to the apex [e.g. *Cladophora vagabunda*: chapter 2, Fig. 15].

Anastomosis: attachment or connection of two cells by tenacular or rhizoidal cells [e.g. *Cladophoropsis composita*: chapter 5, Fig. 27C, D].

Apex: the tip or point of a structure.

Apical cell: the cell at the tip of a filament or branch. The apical cell is often meristematic and responsible for apical growth.

Axis: central filament(s) on which higher order laterals are arranged.

Basipetal: developing in succession from apex to base.

Biflagellate: with two flagella.

Bilenticular pyrenoid: pyrenoid consisting of two hemispheres, separated by a single thylakoid and each hemisphere capped by a bowl-shaped starch grain [e.g. *Cladophoropsis macromeres*, chapter 5, Fig. 5A].

Calcium oxalate (CaOx): monoclinic, organic mineral with chemical formula: CaC_2O_4; insoluble in water. Two forms of CaOx crystals are found in biological systems: di-hydrated CaOx (mineralogical name: Weddellite) and mono-hydrated CaOx (mineralogical name: Whewellite) [see chapter 4].

Capitulum: three-dimensional (globose to flattened) terminal thallus part situated on top of the stipe and composed of branching, entangling and anastomosing filaments [in species of *Chamaedoris* (genus or section of *Cladophoropsis*): chapter 5, Figs 68, 71, 73 and 75].

Clavate: club-shaped [e.g. *Cladophora dotyana*, cells of the basal branches: chapter 2, Fig. 11].

Coenocytic: see siphonocladous.

Conspecific: of the same species.

Crenate: margins with shallow rounded or blunt teeth [e.g. *Cladophoropsis plumosa*: chapter 5, Fig. 66].

Cryptic species: genetically distinct species that cannot be distinguished using morphological characters alone.

Cupiform: barrel-shaped [e.g. *Cladophoropsis elegans*, cell of the terminal branch systems: Fig. 58 (p. 200)].

Cytokinesis: division of the cytoplasm.

Decumbent: lying flat on the substratum.

Deme: any assemblage of taxonomically closely related individuals [see chapter 5, p. 129-132].

Diploid: with two homologous sets of chromosomes.

Diplohaplontic: life cycle with separate multicellular diploid sporophytes and haploid gametophytes.

Distal: remote from place of attachment.

Epilithic: growing attached to rocks or stones.

Epiphytic: growing attached to other plants (seaweeds or seagrasses), but not parasitizing them.

Epizoic: growing attached to animals.

Eurythermal: organisms adaptable to a wide range of temperature.

Falcate: (branch systems) curved like a sickle [e.g. *Cladophora vagabunda*: chapter 2, Fig. 15].

Fasciculate: with clustered branches or filaments [e.g. *Cladophora rugulosa*: chapter 2, Fig. 6E].

Fastigiate: with clustered branches or filaments, parallel and erect [e.g. *Cladophoropsis auriculata*: chapter 5, Fig. 69B].

Filament: a line of connected cells.

Flabellate: fan-shaped [e.g. branches of *Cladophora ordinata*: chapter 2, Fig. 14].

Flagelliform: long, sparsely branched or unbranched (whip-shaped) filaments [e.g. *Cladophora flagelliformis*: chapter 2, Fig. 13C].

Gamete: a haploid reproductive cell produced by sexually reproducing organisms which fuses with another gamete of opposite sex or mating type to produce a diploid zygote.

Gametophyte: the haploid, gamete-producing phase of the life cycle.

Globose: spherical.

Haploid: with one set of chromosomes and therefore with a single genome.

Hapteroidal rhizoid: rhizoids ending in a disc-like or crenulate attachment structure [e.g. *Cladophoropsis vaucheriiformis*: chapter 5, Fig. 40F-H].

Holotype: the single specimen on which an author based the description of a new species.

Infralittoral fringe: zone between mean and spring low tide.

Intercalary cell: cells of a filament which are not the apical nor the basal cell.

Intercalary growth: growth of a thallus by division of intercalary cells.

Intertidal: the region of the shore between mean low and high tide.

Isolectotype: duplicate specimen of the lectotype.

Isotype: duplicate specimen of the holotype.

Lamellate cell wall: cell wall made up of thin plates (lamellae); each lamella is composed of cellulose microfibrils, arranged parallel to each other [e.g. *Cladophoropsis vaucheriiformis*: chapter 5, Fig. 39H].

Lamina: blade.

Lateral: side-branch.

Lectotype: a specimen or illustration designated from the original material as the nomenclatural type if no holotype was indicated at the time of publication, or if it is missing, or if it is found to belong to more than one taxon (ICBN, Art. 9.2).

Lenticular cell division: cell division in which a round, convex septal disc is developed along the cell wall of an inflated cell, followed by elongation and formation of a branch.

Meiosis: nuclear division in which the chromosome number is reduced from 2n to n.

Mitosis: the process of nuclear division that results in both daughter nuclei receiving identical sets of chromosomes, following replication of the chromosomes during the preceding cycle.

Monophyletic: descended from a single ancestor.

Multinucleate: (cell) containing two or more nuclei.

Oblong: being longer than wide.

Obovate: inversely ovate, i.e. ovate with the narrow end downward.

Obtuse: with a blunt apex.

Pantropical: distributed throughout the tropics.

Paraphyletic: a group descending from a single ancestor, but not containing all the descendants of the most recent ancestor.

Parallel evolution: evolution of similar traits, in two or more non-related groups.

Paratype: specimen cited in the prologue of a new species that is neither the holotype nor an isotype (ICBN, Art. 9.5).

Parenchymatic: tissue consisting of a homogeneous mass of isodiametric cells, derived by cell divisions in different planes (e.g. *Dictyosphaeria*).

Penicillate: tufted like an artist's brush [e.g. *Cladophoropsis delphinii*, capitulum: chapter 5, Fig. 71].

Phenodeme: group of morphologically allied individuals [see chapter 5, p. 129-132].

Polyphyletic: descended from several different ancestors.

Polypyramidal pyrenoid: radially subdivided pyrenoid covered by a number of radially arranged starch grains.

Prostrate: lying flat on the substratum.

Proximal: nearest to the axis or basal part of the thallus.

Pseudodichotomy: a false dichotomy. One lateral arising as a side branch from the main axis; the apparently equal dichotomy arises as a result of subsequent equal development of the main axis and the side branch.

Pseudoparenchymatic: tissue composed of closely appressed filaments of cells, which resembles a parenchyma.

Pyriform: pear-shaped.

Quadriflagellate: with four flagella.

Refracto-falcate: branch systems recurved like a sickle.

Reticulate: forming a two- or three-dimensional network of branching, anastomosing filaments.

Rhizoid: unicellular or multicellular filament, involved in attachment or entanglement.

Segregative cell division: a form of cell division in which a multinucleate protoplast divides into several, rounded daughter protoplasts, which subsequently become surrounded by a wall. The newly formed cells are either released after rupture of the mother cell (*Ventricaria*), remain in situ and form parenchymatic thalli (*Dictyosphaeria*), or rupture old parental walls and form laterals (*Struvea*, *Siphonocladus*).

Sinuous: (filaments) curving in and out [e.g. *Cladophoropsis peniculum*: chapter 5, Fig. 76A].

Siphonocladous thallus organization: septated thallus composed of multinucleate cells.

Siphonous thallus organization: thallus formed of multinucleate tubular cells (siphons) without septa (or cross walls).

Sporophyte: the diploid phase of the life cycle in which meiospores are produced.

Stenothermal: organisms adaptable to only slight variations in temperature.

Stipe: stalk; basal cell of the thallus which is conspicuously larger than the other cells in the upper parts of the thallus, and attaching to the substratum by rhizoids sprouting from the base of the cell or by a hapteroid disc [e.g. *Cladophoropsis orientalis*: chapter 5, Fig. 51].

Stipitate: with a stipe.

Stolon: creeping filaments, often with intercalary rhizoids [e.g. *Cladophora socialis*, stolon-like filaments: chapter 2, Fig. 3A].

Subtidal: region below spring low tide; continuously submerged.

Supralittoral: the area above mean high water mark, or the 'splash' or 'spray' zone.

Supralittoral fringe: zone between mean and spring high tide.

Synonym: a superseded name, replaced by the correct name. Taxonomic (heterotypic) synonyms apply to names with different types; nomenclatural (homotypic) synonyms are based on the same type.

Syntype: any one of two or more specimens cited in the prologue when no holotype was designated or any one of two or more specimens simultaneously designated as type (ICBN, Art. 9.4).

Tapering: gradually narrowing toward a point [e.g. *Cladophora ordinata*, apical cells: Fig. 14F (p. 47)].

Taxon: a group of organisms at any level in the classification of living organisms.

Tenacular cell: specialized cell achieving attachment (anastomosis) with adjacent cells or filaments. Four types have been distinguished by Olsen-Stojkovich [p. 9, 53, 101; chapter 5, Fig. 2].

Thallus: the relatively simple plant body of a non-vascular plant.

Thylakoid: a membrane vesicle, numbers of which are stacked up to form the grana of chloroplasts.

Torulose: filament with bulges or constrictions at irregular intervals [e.g. *Cladophoropsis gracillima*: chapter 5, Fig. 77F].

Unilateral: (branches) arranged on one side only [e.g. *Cladophoropsis sundanensis*: chapter 5, Fig. 14C].

Uniseriate: (filament) with a single, linear row of cells.

Verticillate: (branches) arranged in one or more whorls [e.g. *Cladophoropsis arbuscula*: chapter 5, Fig. 73B].

Zoid: a reproductive cell that bears flagella and is hence free-swimming.

Zoidangium: a cell whose contents divides up to produce zoids. The zoids remain enclosed within the zoidangium for a short time before release.

Zonate pyrenoid: a variant of bilenticular pyrenoid with two intrapyrenoidal thylakoids.

Zoospore: a flagellate spore.

Symbols and abbreviations

!	seen and examined by the author.
µm	micrometer (10^{-6} m).
CaOx	calcium oxalate.
CI	cell division by centripetal invagination of the cell wall.
comb. prov.	*combinatio provisoria*: provisional combination.
diam.	diameter.
ICBN	International Code of Botanical Nomenclature.
INA	Index Nominum Algarum (compiled by P. Silva and available on the internet).
l/w ratio	length/width ratio.
LSU rRNA	large subunit of the ribosomal RNA.
LC	lenticular cell type of cell division (sensu Olsen-Stojkovich 1986).
leg.	*legit*: collected by.
ML	maximum likelihood.
MP	maximum parsimony.
ms.	manuscript
nom. cons.	*nomen conservandum*: conserved name (ICBN).
nom. illeg.	*nomen illegitimum*: illegitimate name (ICBN).
nom. inval.	*nomen invalidum*: invalidly published name (ICBN).
nom. nud.	*nomen nudum*: name without a description (ICBN).
nom. prov.	*nomen provisorium*: provisional name.
nrRNA	nuclear ribosomal RNA.
p.p.	*pro parte*: partly.
rRNA	ribosomal RNA.
s.l.	*sensu lato*: in a broad sense.
s.n.	*sine numero*: without a number.
s.s.	*sensu stricto*: in a narrow sense.
SDM	modified type of segregative cell division (sensu Olsen-Stojkovich 1986).
SDSS	segregative cell division s.s. (sensu Olsen-Stojkovich 1986).
sp.	species
stat. prov.	*status provisorius*: provisional status.

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Page references in bold refer to the main pages of treatment or to pages where a specific taxon is illustrated.
Note: due to some last minute changes, some taxa may have shifted one or two pages.