

Morphological re-assessment of the *Boodlea composita*–*Phyllocladion anastomosans* species complex (Siphonocladales: Chlorophyta)

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Abstract. *Boodlea composita* (Harvey) F. Brand and *Phyllocladion anastomosans* (Harvey) Kraft & M.J. Wynne, two widespread tropical siphonocladalean green algae, have had a long and confusing history because of the vague taxonomic boundaries between the two species. Molecular phylogenetic studies on the basis of nuclear-encoded rDNA sequences have resolved these indistinct species boundaries and suggest these taxa are part of a species complex. Detailed morphological investigations in combination with field and culture observations show that the concept of traditionally recognised taxa in this species complex is clouded by an ecologically induced phenotypic plasticity and developmental variability. Examination of a large number of specimens of *B. composita*, *P. anastomosans* and morphologically allied taxa including *Boodlea siamensis* Reinbold, *Boodlea montagnei* (Harvey ex J.E. Gray) Egerod, *Nereodictyon imitans* Gerloff and *Struveopsis siamensis* (Egerod) P. C. Silva, worldwide, including types, shows a wide morphological variety. We recognise seven more or less distinct morphological entities based on differences in thallus architectures, branching systems, cell dimensions and tenacular cell types. Awaiting the recovery of the true nature of the defined entities in this species complex (different species or growth forms of the same species), they are referred to as morphotypes, i.e. making no assumptions as to which taxonomic level they best apply.

Introduction

Boodlea composita (Harvey) F. Brand and *Phyllocladion anastomosans* (Harvey) Kraft & M.J. Wynne, two of the most abundant and wide-spread tropical siphonocladalean taxa, were described by Harvey from both sides of the Indian Ocean: *Conferva composita* was based on a cushion-like specimen from Mauritius (Harvey 1834), whereas *Cladophora anastomosans* was described from Western Australia as having stipitate blades with branch systems confined to a single plane (Harvey 1859).

Numerous *Boodlea* and *Phyllocladion* (as *Struvea*) species and varieties have been distinguished from *B. composita* and *P. anastomosans* based on small, often trifling differences in branching patterns, cell dimensions and blade sizes (*B. coacta* (Dickie) Murray & DeToni, *B. siamensis* Reinbold, *S. delicatula* Kützing, *S. multipartita* Pilger and *S. tenuis* Zanardini). Most of these taxa were later reduced to synonyms of either *B. composita* or *P. anastomosans*, depending on their thallus form: cushion-like thalli composed of three-dimensional branch systems, or unistratose blades with stipes, respectively (Murray and Boodle 1888; Børgesen 1946; Egerod 1952; Cribb 1960; Steentoft 1967). This distinction in growth form has been widely adopted to distinguish both taxa (e.g. Womersley and Bailey 1970; Tseng 1984; Abbott 1989; Sartoni 1992; Wynne 1993, 1995; Leliaert *et al.* 1998; Littler and Littler 2000, 2003; Coppejans *et al.* 2001, 2004; Abbott and Huisman 2004; N'Yeurt and Payri, in press).

Several authors, however, commented on the extreme variability of both species and the resultingly vague boundaries between the two taxa (Egerod 1975; Kooistra *et al.* 1993;

Leliaert *et al.* 1998). In fact, in 1859, Harvey mentioned that, 'the nature and ramification of the filaments are very similar in *Cladophora anastomosans* to what they are in *Cladophora composita*, and several other undoubted species of that genus'. Egerod (l.c.) noticed that the early developmental stages of *B. composita* and *P. anastomosans* are nearly identical, and hypothesised that both taxa might represent growth forms of the same species. Strangely enough, she described a new genus and species in the same paper, *Pseudostruvea siamensis*, based on two characters that she previously recognised to be variable (presence of annular constrictions and the absence of tenacular cells). Moreover, she stated that *P. siamensis* is indistinguishable from *B. composita* or *P. anastomosans* in the initial stages of thallus development.

The close relationship between *Boodlea composita*, *Phyllocladion anastomosans* and morphologically allied taxa has been confirmed by molecular data. Partial large subunit (LSU) nrDNA sequences of *B. composita*, *B. siamensis*, *B. montagnei*, *P. anastomosans* and *Struveopsis siamensis* have been found to be nearly identical (maximum pairwise sequence divergence of 1.2%) (Leliaert *et al.* 2003). This level of divergence is comparable to those found within other siphonocladalean species (e.g. *Valoniopsis pachynema*: 1.4% divergence, *Cladophora catenata*: 1.6% divergence and *Dictyosphaeria cavernosa* 4.3% divergence), and is therefore indicative of a species complex.

In the current study the morphological variety within the *Boodlea composita*–*Phyllocladion anastomosans* species complex is examined on the basis of historical collections,

including type specimens, as well as recently collected samples from various regions of the tropical and subtropical Indo-Pacific and Atlantic Ocean. With this study we aim to provide a firm morphological framework for further molecular phylogenetic studies.

Material and methods

Extensive field collections were made by Eric Copejans and co-workers of the Phycology Research Group (Ghent, Belgium) in various regions of the (sub)tropical Indo-West Pacific from 1980 onwards; specimens with these herbarium numbers are deposited in GENT and are prefixed by 'Copp & PvR' (seaweeds from Papua New Guinea, collected by Eric Copejans and Willem Prud'homme van Reine), 'FL' (collections of Frederik Leliaert), 'HEC' (herbarium Eric Copejans), 'HOD' (herbarium Olivier Dargent); 'KZN' (collections from KwaZulu-Natal, South Africa), 'ODC' (collections of Olivier De Clerck), 'PH' (Philippine collections of Leliaert, Liao and Dargent), 'SEY' (Seychelles collection of Copejans, Kooistra and Audiffred), '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 B, BM, BR, L, M, MEL, NY, PC, S and UC (herbarium abbreviations follow Holmgren *et al.* 1990). All specimens examined in this study, ranged per morphotype (i.e. morphological entity), are listed in the supplementary material, which are available as accessory publications on the web.

Liquid-preserved material, herbarium specimens and culture isolates were examined with a light microscope after portions were prepared on glass microscopic slides and stained with 1% methylene blue. Herbarium specimens were first rehydrated in 5% formalin-seawater for 24 h, placed in 10% sodium hypochlorite for 5 min (dissolving the cell contents) and rinsed in distilled water. Drawings were made with a camera lucida on a Leitz-Dioplan (Wetzlar, Germany) brightfield light microscope. Photographs were taken with an Olympus-DP50 (Tokyo, Japan) digital camera mounted on the microscope. Cells were also examined for crystalline inclusions using differential interference contrast (Nomarski), as the presence and morphologies of these structures have been found to be species-specific in several siphonocladalean algae (Leliaert and Copejans 2004).

Results

The ambiguous distinction between *Phyllocladion anastomosans* and *Boodlea composita* can, paradoxically enough, be shown by the authentic material of *P. anastomosans*, which consists of four cushion-like specimens with branch systems growing in three directions. Only one of the specimens (designated as lectotype in this paper, Fig. 1) partially consists of stipitate blades, and it is presumably upon this fragment that Harvey (1859) based the original description. This find leads one to suspect that the blade-like morphology of *Phyllocladion anastomosans* is merely a juvenile stage of a cushion-like *Boodlea composita*.

On the basis of apparent morphological similarities, several other species in *Boodlea* and *Phyllocladion*, as well as *Struveopsis* are here considered to fall within the circumscription

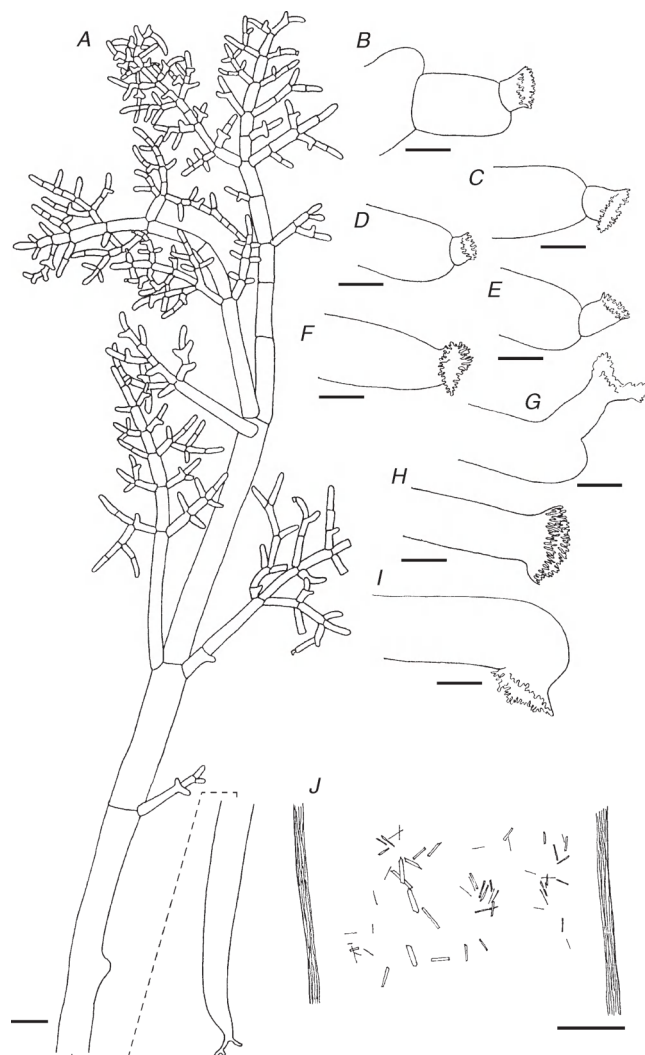


Fig. 1. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *anastomosans* morphotype (lectotype of *Cladophora anastomosans*, BM). (A) Stipitate lamina composed of opposite branches. (B–E) Type-2 tenacular cells. (F–I) Type-1 tenacular cells. (J) Detail of a cell showing the lamellate cell walls and crystalline cell inclusions. Scale bars: (A) = 1 mm; (B–J) = 100 µm.

of the *Boodlea composita*–*Phyllocladion anastomosans* species complex (Table 1). These taxa are all characterised by plants ranging from stipitate, net-like blades to three-dimensional branching filaments forming cushions. Cell division is achieved by centripetal invagination of the cell walls but segregative cell division does occur occasionally, often in response to cell wounding. Branch systems are initially opposite; older cells often produce secondary laterals perpendicular to the first ones. Thallus reinforcement is achieved by tenacular cells (except in *Struveopsis*) and by interweaving of the filaments. Two types of tenacular cells can be distinguished. The first type consists of unspecialised cells with crenulated apices (Fig. 1F–I); the second type consists of small hapteroid cells formed at the distal ends of apical cells (Fig. 1B–D). Diameter of the apical cells is generally within the range of 80–220 µm (except for the

Table 1. Taxa presently considered to fall in the *Boodlea composita*–*Phyllocladon anastomosans* species complex

Basionym	Currently accepted name	Morphotype
<i>Cladophora anastomosans</i> Harvey	<i>Phyllocladon anastomosans</i> (Harvey) Kraft & M.J. Wynne	<i>anastomosans</i>
<i>Struvea multipartita</i> Pilger	<i>Phyllocladon anastomosans</i>	
<i>Boodlea struveoides</i> Howe	<i>Boodlea struveoides</i>	
<i>Conferva composita</i> Harvey	<i>Boodlea composita</i> (Harvey) Brand	<i>composita</i>
<i>Boodlea composita</i> forma <i>contracta</i> Brand	<i>Boodlea composita</i> forma <i>contracta</i>	
<i>Boodlea composita</i> forma <i>elongata</i> Brand	<i>Boodlea composita</i> forma <i>elongata</i>	
<i>Struvea delicatula</i> Kützing	<i>Phyllocladon anastomosans</i>	<i>delicatula</i>
<i>Struvea delicatula</i> var. <i>caracasana</i> Grunow ex Murray & Boodle	<i>Struvea delicatula</i> var. <i>caracasana</i>	
<i>Struvea tenuis</i> Zanardini	<i>Phyllocladon anastomosans</i>	
<i>Cladophoropsis kenyensis</i> Leliaert & Coppejans (nom. prov.)	<i>Cladophoropsis kenyensis</i> (nom. prov.)	<i>kenyensis</i>
<i>Microdictyon montagnei</i> Harvey ex J.E. Gray	<i>Boodlea montagnei</i> (Harvey ex J.E. Gray) Egerod	<i>montagnei</i>
<i>Boodlea siamensis</i> Reinbold	<i>Boodlea composita</i>	<i>siamensis</i>
<i>Cladophora coacta</i> Dickie	<i>Boodlea coacta</i> (Dickie) Murray & De Toni	
<i>Boodlea composita</i> forma <i>irregularis</i> Brand	<i>Boodlea composita</i> forma <i>irregularis</i>	
<i>Boodlea siamensis</i> forma <i>robusta</i> Børgesen	<i>Boodlea composita</i> forma <i>robusta</i> (Børgesen) Børgesen	
<i>Boodlea paradoxa</i> Reinbold	<i>Boodlea montagnei</i>	
<i>Nereodictyon imitans</i> Gerloff	<i>Nereodictyon imitans</i>	
<i>Pseudostruvea siamensis</i> Egerod	<i>Struveopsis siamensis</i> (Egerod) P. C. Silva	<i>struveopsis</i>
<i>Pseudostruvea covalamensis</i> Iyengar	<i>Struveopsis covalamensis</i> (Iyengar) P. C. Silva	

kenyensis morphological entity that has much thicker filaments). The cells contain elongate prismatic calcium oxalate crystals (Leliaert and Coppejans 2004: figs 1–9).

A detailed study, based on field-collected material of a large population of *Phyllocladon anastomosans*, was carried out in Chwaka Bay, Zanzibar (Tanzania), and serves as a good example to show the morphological transformations during thallus development. Initially the thallus consists of a cylindrical stipe initiating a small reticulate blade at its apical pole by a repetitive process of cell division, 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. 5A, B). Later, apical cells generally divide into two (rarely three) 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* morphotype (see below), all laterals are formed strictly in a single plane (Fig. 5C, D). In older blades, most of the newly formed subapical cells, after cell division, produce a single lateral (instead of an opposite pair of laterals), resulting in unilateral or pseudodichotomous ultimate branch systems (Figs 5G, 6C). Older cells generally produce a second lateral, opposite or perpendicular to the first one, resulting in three-dimensional branch systems (Fig. 5G–I). These stipitate blades, referable to the *anastomosans* morphotype, remain flattened as a result of the main axes, branching oppositely in a single plane (Fig. 5E). At a later stage adjacent blades may attach to one another by numerous tenacular cells (Fig. 5F) resulting in irregular cushion-like thalli with masked stipes. 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. 6A–F), but is completely lost in the centre where filaments are thinner, more elongate and three-dimensionally branched (Fig. 6G–L).

Also in attached cushion-like thalli the internal blade-like structure may become indistinct and will eventually be completely lost, referable to the *siamensis* morphotype. 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* morphotype (Fig. 6M–O). In older plants, portions of the thallus can easily dislodge, re-attach to the substrate by tenacular cells and continue growing as irregular cushions. In the field, this stage can easily be recognised 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 areas only cushion-like thalli are found. Stipitate blade-like thalli most likely develop only from settling spores or zygotes as shown by Chihara (1955) (for ‘*Boodlea coacta*’). A similar mode of vegetative reproduction has also been observed in the *composita* morphotype.

Examination of a large number of specimens worldwide (see supplementary material, available as accessory publications on the web) has led to the recognition of seven distinct morphological entities based on differences in thallus morphology, branching systems, apical cell division, thallus reinforcement and cell dimensions (Table 2). This morphological variation 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 geographical areas without the presence of intermediate or transitional forms. It is possible that several cryptic species exist, each with considerable morphological plasticity, resulting in overlapping morphologies. Awaiting the true nature of the seven morphological entities in the species complex (different species or growth forms of the same species),

Table 2. Survey of characters in the seven morphotypes within the *Boodlea composita*–*Phyllocladon anastomosans* species complex

Morphotype	Thallus morphology	Branching systems	Apical cell division	Tenacular cells	Apical cell diameter (ac) and diameter main filaments (mf) (µm)
<i>anastomosans</i> Figs 1–6	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 two (sometimes three) cells	Type-1 and -3, abundant	ac: (60–)80–180(–240) mf: (150–)200–750(–875)
<i>composita</i> Figs 7–10	Cushion-like, composed of loosely entangled filaments. Often sand-trapping. Stipe absent.	Ultimate branch systems composed of regularly, opposite branching filaments, generally with a third (and fourth) lateral produced perpendicular to the branching plane. Branching in main axes opposite, not strictly in a single plane.	Division into two, or simultaneously 3–8 cells	Type-1 and -3, uncommon	ac: (40–)50–90(–125) mf: (140–)180–250(–400)
<i>delicatula</i> Figs 11, 12	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 two (three) cells	Type-2 abundant; type-1 rare	ac: (70–)90–180(–280) mf: (120–)350–540(–620)
<i>kenyensis</i> Figs 13–15	Cushion-like thalli composed of clustered stipitate blades.	Ultimate branch systems composed of regularly, opposite branching filaments; branching in main axes opposite, not strictly in a single plane; older cells often producing a third (to fifth) lateral branch.	Division into two (sometimes three) cells	Type-1 and -3, abundant	ac: 220–400(–560) mf: (370–)450–880(–1050)
<i>montagnei</i> Figs 16, 17	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 two (rarely three) cells	Type-2 abundant; type-1 rare	ac: (50–)70–140(–180) mf: (180–)200–650(–700)
<i>siamensis</i> Figs 18–24	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 second (and third) lateral produced perpendicular or opposite to the first lateral. Branching in main axes opposite or irregular.	Division into two (sometimes three) cells	Type-1 and -3, abundant	ac: (40–)60–140(–250) mf: (120–)160–380(–875)
<i>struveopsis</i> Figs 25, 26	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. Branching in main axes opposite.	Division into two, or simultaneously 3–8 cells	Generally absent	ac: (85–)100–220(–260) mf: (140–)260–570(–930)

we here refer them as ‘morphotypes’. We prefer this term, which has no rank, over infraspecific rank names, governed by the Code of Botanical Nomenclature (subspecies, variety, forma), because it makes no assumptions as to what level of relatedness the group in question is subject to, thus nullifying the problems of potential nomenclatural changes. We also prefer the term ‘morphotype’ over ‘ecad’, because in the latter the assumption

is made that different morphological forms are ecologically induced within a single ‘species’ (Coppejans and Prud’homme van Reine 1992; Silva *et al.* 1996).

Descriptions and illustrations of the seven morphotypes are provided below, along with nomenclatural and taxonomic notes of the corresponding taxa, and indication of their geographical and ecological range.

1. *anastomosans* morphotype (Figs 1–6)

Corresponding taxa:

Cladophora? *anastomosans* Harvey, Phycol. austral. 2: pl. CI (1859) [Lectotype: Fremantle, Western Australia, leg. Harvey, Australian algae exsiccatae no. 582a, BM!; isolectotypes in BM!, S! and MEL!].

Pterodictyon anastomosans (Harvey) J.E. Gray, J. Bot. 4: 70 (1866).

Struvea anastomosans (Harvey) Piccone & Grunow ex Piccone, Crociera Corsaro, alg.: 20 (1884) [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)]; 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 and Chamberlain (1958: 135, 137, figs 1, 10); Pham-Hoàng (1969: 452, fig. 4.58); Chang *et al.* (1975: 41, 59, fig. 13); Schnetter and Bula-Meyer (1982: 29–30, pl. 7G–H); Tseng (1984: 276, pl. 137, fig. 2); Lawson and John (1987: 100, pl. 10, figs 1, 2); Sartoni (1992: 317–319, fig. 12B, C); Wynne (1995: 292, 332, fig. 86).

Phyllocladion anastomosans (Harvey) Kraft & M.J. Wynne, Phyc. Res.: 139, pls 16–25 (1996); Littler and Littler (2000: 328, fig. on p. 329).

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

Boodlea struveoides Howe, In Britton, Fl. Bermuda: 496 (1918) [Holotype: Harrington Sound, Bermuda, leg. Howe 131, NY!].

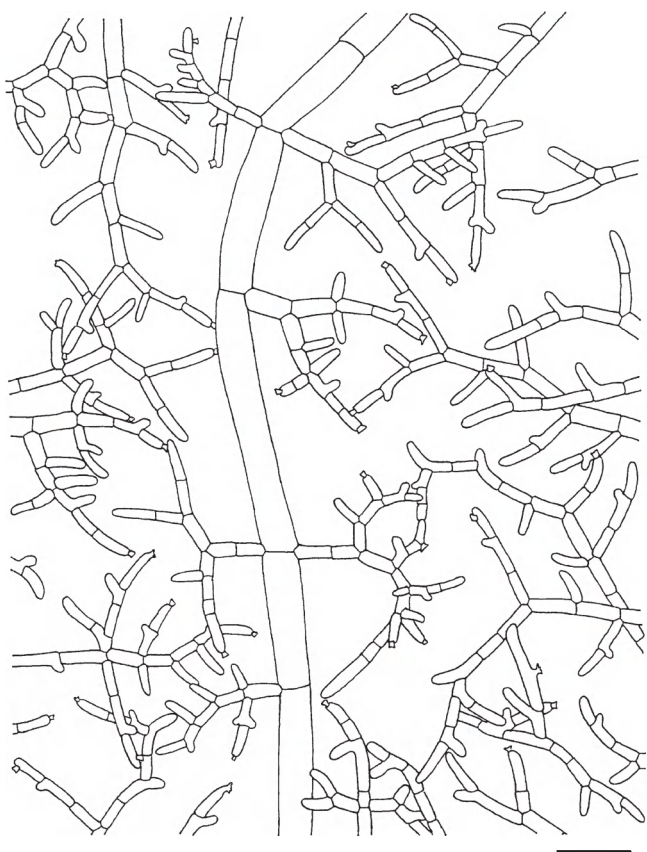


Fig. 2. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *anastomosans* morphotype (isolectotype of *Cladophora anastomosans*, BM). Branch-systems of an older, cushion-like thallus. Scale bar = 1 mm.

Plants forming either stipitate, reticulate blades, composed of densely branched filaments, up to 13 cm high (Figs 1A, 3B, 5A–F), or astipitate blade-like structures (Fig. 6M–O) or cushion-like plants with an internal blade like-structure (Figs 3, 4, 6A–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 1A, 3A, 5C–E). Cushion-like thalli attached by type-1 tenacular cells produced in any part of the thallus (Figs 1G–I, 4C, 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 and growth by a repetitive process of apical and intercalary cell division (C1), formation of lateral branches 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 second, third (or even fourth) lateral, opposite or perpendicular to the first lateral, resulting in three-dimensional

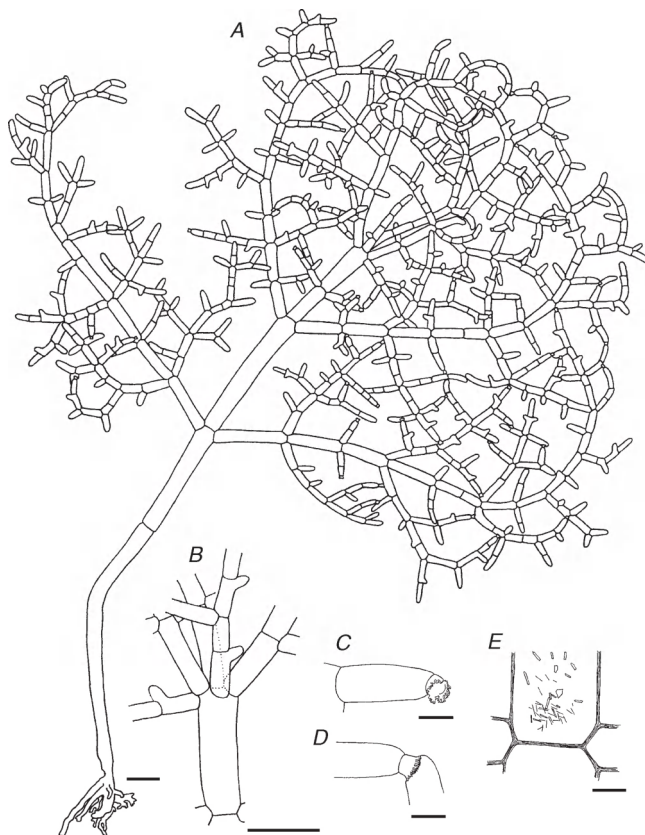


Fig. 3. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *anastomosans* morphotype (holotype of *Boodlea struveoides*, NY). (A) Stipitate blade composed of opposite branches. (B) Cell of the central axis producing laterals in all directions. (C, D) Type-2 tenacular cells. (E) Portion 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.

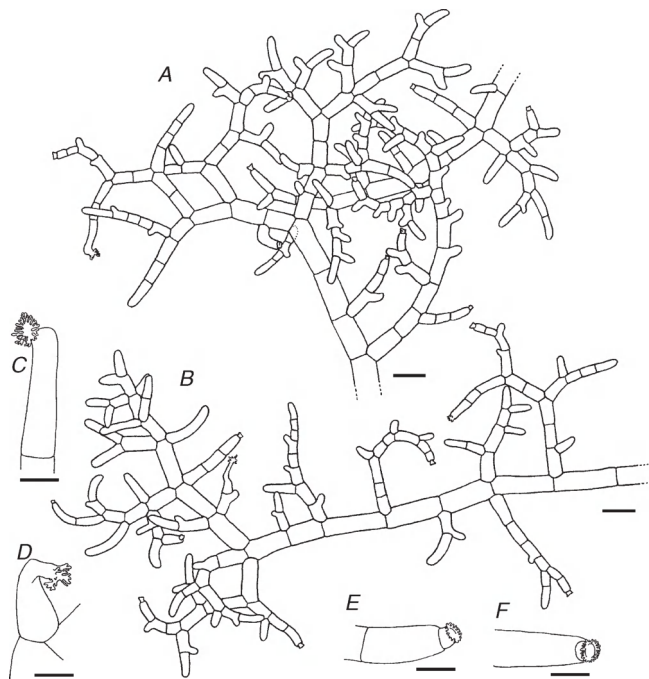


Fig. 4. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *anastomosans* morphotype (Howe 130, NY as *Boodlea struveoides*). (A, B) Pseudodichotomous and opposite terminal branches of a cushion-like thallus; some laterals producing secondary, perpendicular laterals. (C, D) Type-1 tenacular cells. (E, F) Type-2 tenacular cells. Scale bars: (A, B) = 500 μm ; (C–F) = 100 μm .

branch systems; branching of the perpendicular laterals mostly restricted to the first or second order. Ultimate branch systems mostly curved (Fig. 6C). Branching in the main axes generally opposite with all branches essentially in a single plane, resulting in flattened blades (Figs 2, 4A, B, 6A–F, M–O). Intercalary cell divisions in the main axes occurring at regular intervals (Fig. 6N–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 seventh order. The diameter of the stipe cells or cells of the main axes 1.6–8.0 \times that of the apical cells. Angle of ramification 45–90 $^\circ$.

Mature blades with branches in a single plane, irregular in outline, either single or clustered and coalescent by type-2 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-2 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, on average 18–47% of the apical cells form a type-2 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 c. 2 μm in the ultimate branches, up to 10 μm in the main axes (Fig. 1J).

Prismatic calcium oxalate crystals present in all cells of the thallus (except for the type-2 tenacular cells), elongate hexagonal to needle-shaped, up to 5 μm in diameter and 30 μm long (Figs 1J, 3E).

Notes

Four herbarium specimens of *Cladophora anastomosans*, all numbered Harvey Australian algae 582a, and consisting of cushion-like thalli, 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. 1). Although the type material clearly illustrates that mature *P. anastomosans* thalli form irregular cushion-like plants, the general concept of the species until today has been that of thalli forming stipitate, reticulate blades with branching essentially in a single plane (see Kraft and Wynne [1996: 131, figs 16–25] and the numerous descriptions and illustrations in the above listed references).

Struvea multipartita was described from the tropical west African coast, as cushion-like plants, composed of branched stipes bearing reticulate blades (Pilger 1920). It was treated as a taxonomic synonym of *S. anastomosans* by Steentoft (1967) and Lawson and John (1982). Examination of the holotype confirms that this taxon falls within the limits of the *anastomosans* morphotype.

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. 3). 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* morphotype.

Struvea anastomosans var. *canariensis*, described from the Canary Islands by Piccone & Grunnow in Piccone (1884) is referable to *Phyllocladon pulcherrimum* J.E. Gray as pointed out by Murray and Boodle (1888: 266–267) and Børgesen (1925: 72), and is therefore not part of the *Boodlea composita*–*Phyllocladon anastomosans* species complex (Leliaert 2004).

The *anastomosans* morphotype has a pantropical distribution 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.

2. *composita* morphotype (Figs 7–10)

Corresponding taxa:

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

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

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



Fig. 5. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *anastomosans* morphotype (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 μ m; (*C–F*) = 1 mm.

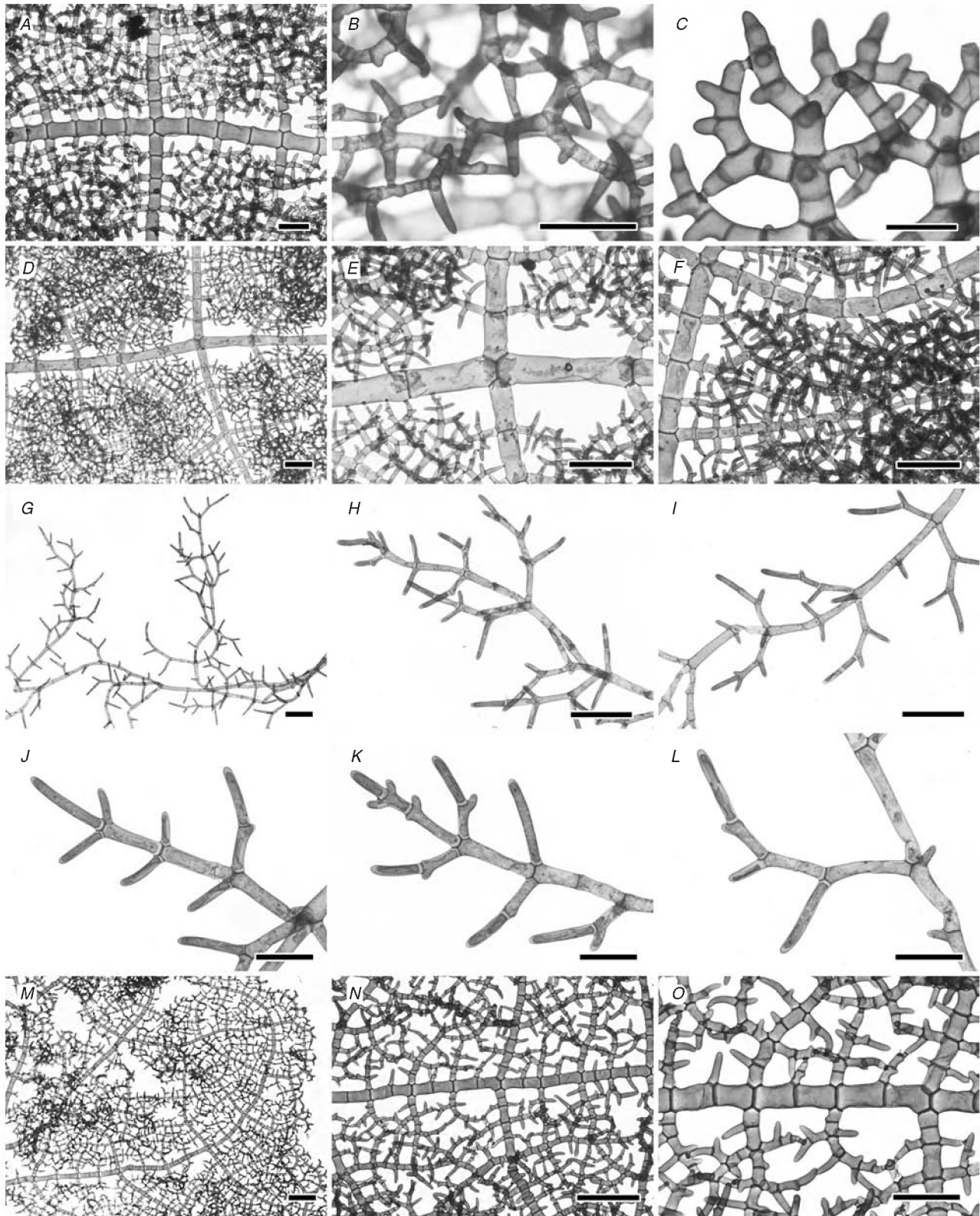


Fig. 6. *Boodlea composita-Phyllocladon anastomosans* species complex: *anastomosans* morphotype (Chwaka Bay, Zanzibar). (A–F) Branch-systems in the peripheral parts of a loose-lying cushion-like thallus (FL 958). (G–L) Branch-systems in the central part of the same loose-lying cushion: elongate, three-dimensionally 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, L, O) = 500 μ m; (C) = 250 μ m; (D–I, M–N) = 1 mm.

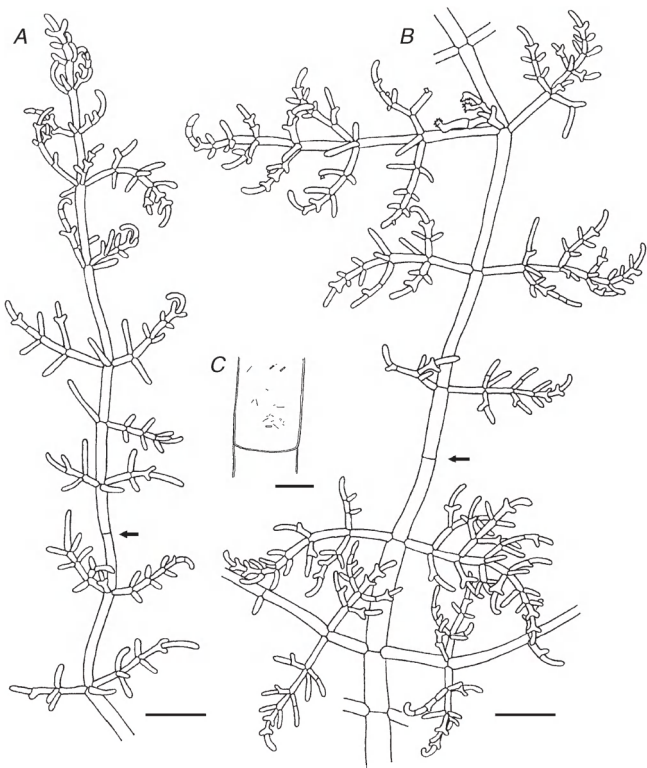


Fig. 7. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *composita* morphotype (lectotype of *Conferva composita*, BM). (A) Terminal, opposite branches and older cells producing perpendicular laterals. (B) Main axis with opposite branches, producing terminal branch-systems; arrows indicating intercalary cell divisions. (C) Base of a cell with prismatic calcium oxalate crystals. Scale bars: (A, B) = 1 mm; (C) = 250 μm.

Boodlea composita (Harvey) Brand, Beih. Bot. Centralbl. 18: 187–190 (1904); Børgesen (1940: 21–25, fig. 6); Jaasund (1976: 11, fig. 23); Sartoni (1992: 306–307, fig. 7C).

Boodlea composita forma *contracta* Brand, Beih. Bot. Centralbl. 18: 190, pl. VI: fig. 28 (1904) [Lectotype: Waianae, Oahu, Hawaii, leg. Tilden, American Algae s.n., M!, ‘as *Cladophora* (*Aegagropila*) *composita* var. *contracta* F. Brand’; syntypes: same locality, leg. Tilden, American Algae no. 539, MIN, NY! and PC!].

Boodlea composita forma *elongata* Brand, Beih. Bot. Centralbl. 18: 190, pl. VI: fig. 30 (1904) [Type: Hawaii, leg. Tilden; the location of the type material could not be retrieved].

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 7A, 9A, 10A). Cushions often sand-trapping, loosely attached to the substratum by type-1 tenacular or rhizoidal cells (Figs 8E–J, 9F, 10H–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. 10A–D). Older cells generally producing a third (sometimes a fourth) lateral, perpendicular to the first pair, resulting in three-dimensional branch systems (Figs 7A, B, 8A, 9A–E). Intercalary cell divisions may appear below the seventh primary cross wall, but are most common in the main axes (Fig. 7A, B, arrows). Branching in the

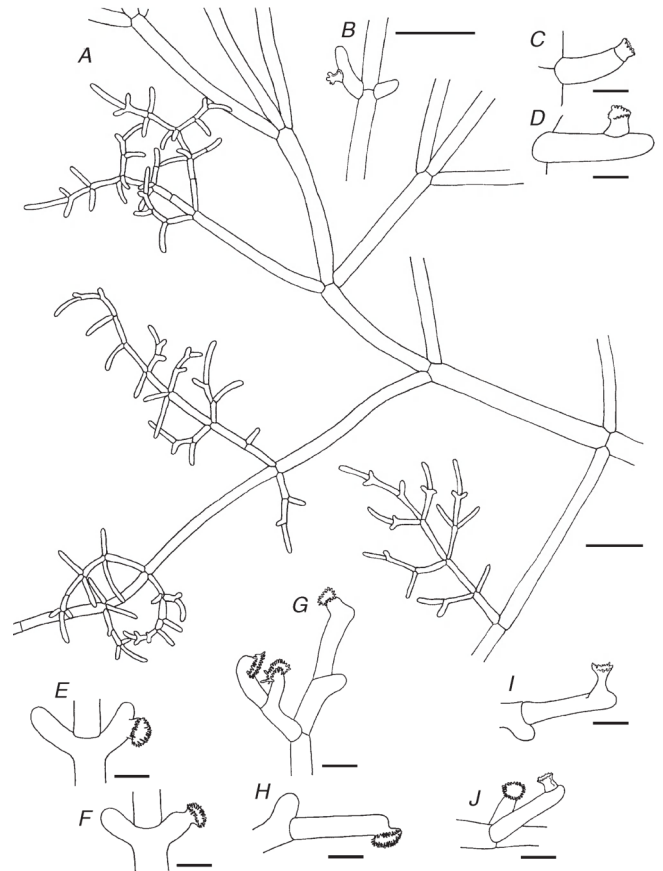


Fig. 8. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *composita* morphotype (lectotype of *Conferva composita*, BM). (A) Main axis with opposite branches, producing terminal branch-systems. (B–D) Type-2 tenacular cells. (E–J) Type-1 tenacular cells. Scale bars: (A) = 1 mm; (B–J) = 100 μm.

main axes generally opposite (Figs 7B, 8A). 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 fifth order. The diameter of the main axes 1.4–5(–8)× 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-2 tenacular cells (Fig. 8B–D). The latter borne singly, terminally or subterminally on apical cells. In mature thalli, on average 0–6% of the apical cells produce 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 *c.* 2 μm in the ultimate branches, up to 5 μm in the main axes.

Prismatic calcium oxalate crystals present in all cells of the thallus, except for the tenacular cells, very abundant in cells of

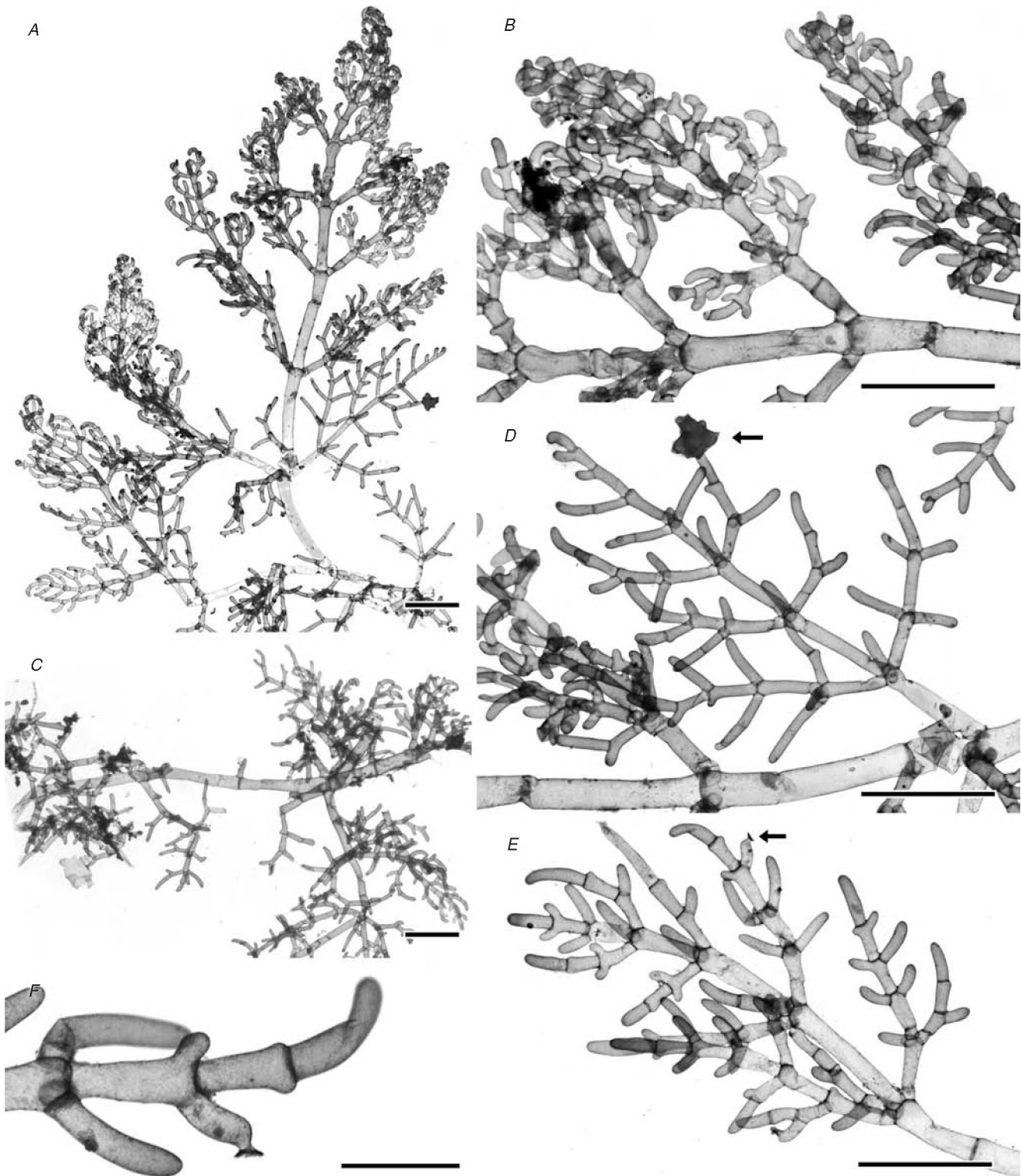


Fig. 9. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *composita* morphotype (FL 694, Chwaka Bay, Zanzibar). (A) Terminal branch-systems forming a ‘*Struvea*’-like plumule, sticking out of the cushion-like thallus. (B) Detail of densely branched and incurved, short celled filaments. (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 coral rubble by type-1 tenacular cells (arrows). (F) Terminal branches with a type-1 tenacular cell. Scale bars: (A–E) = 1 mm; (F) = 250 μ m.

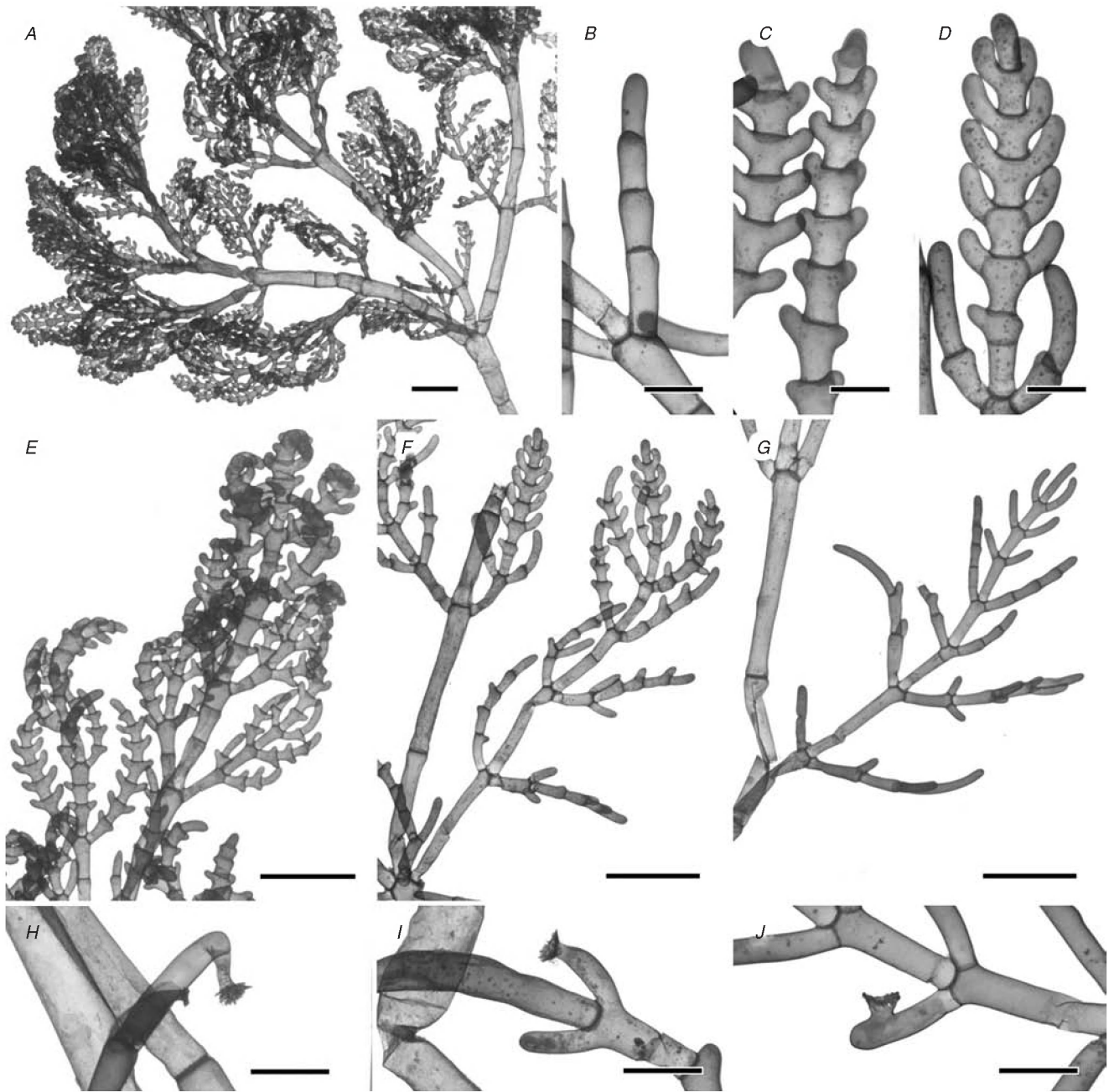


Fig. 10. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *composita* morphotype (FL 662, Chwaka Bay, Zanzibar). (A) Regular opposite terminal branches and main axes. (B–D) Apical cells dividing simultaneously into 3–8 cells, followed by the formation of opposite pairs of laterals. (E) 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 μ m.

the main axes, elongate hexagonal to needle-shaped, up to 6 μ m in diameter and 45 μ m long (Fig. 7C).

Notes

Three specimens of *Conferva composita*, collected in Mauritius by Mrs C. Telfair, are present in BM; the largest one is here designated as lectotype (Figs 7, 8). 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, 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 ratios of the cells. Both formas fall within the limits of the *composita* morphotype.

The *composita* morphotype has a pantropical distribution and grows in the high to low intertidal, mostly in sheltered

habitats, epilithic (often on sand-covered substrates) or epiphytic on seaweeds and seagrasses.

3. *delicatula* morphotype (Figs 11, 12)

Corresponding taxa:

Struvea delicatula Kützing, Tab. phycol. 16: 1, pl. 2: figs e–g (1866) [Holotype: New Caledonia (Wagap), leg. Vieillard, s.n., L! 937 183 109]; Murray and Boodle (1888: 281, figs 6, 8); Okamura (1908: 201–203, pl. 40, figs 9–12); Børgesen (1933: 3); Yamada (1934: 46, fig. 10); Segawa (1938: 135–136, fig. 3).

Struvea delicatula var. *caracasana* Grunow ex Murray & Boodle, In Murray and Boodle, Ann Bot. 2: 281, pl. XVI: fig. 7 (1888) [Type: Caracas, Cabo Blanco, Venezuela, leg. 'Gollma' (probably Julius Gollmer); the location of the type material could not be found].

Struvea anastomosans var. *caracasana* (Grunow ex Murray and Boodle) Collins, Tufts Coll. Stud. Sci. 2: 376 (1909).

Struvea tenuis Zanardini, Nuovo Giorn. Bot. Ital. 10: 39 (1878) [Holotype: Sorong, Iryan Jaya, Indonesia ('Sorog, Novam Guineam'), leg. Beccari, FI, MB or MCVE?]; Murray and Boodle (1888: 281, fig. 5); Okamura (1908: 201, pl. 40, figs 7–8); Yamada (1934: 45–46, fig. 9).

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

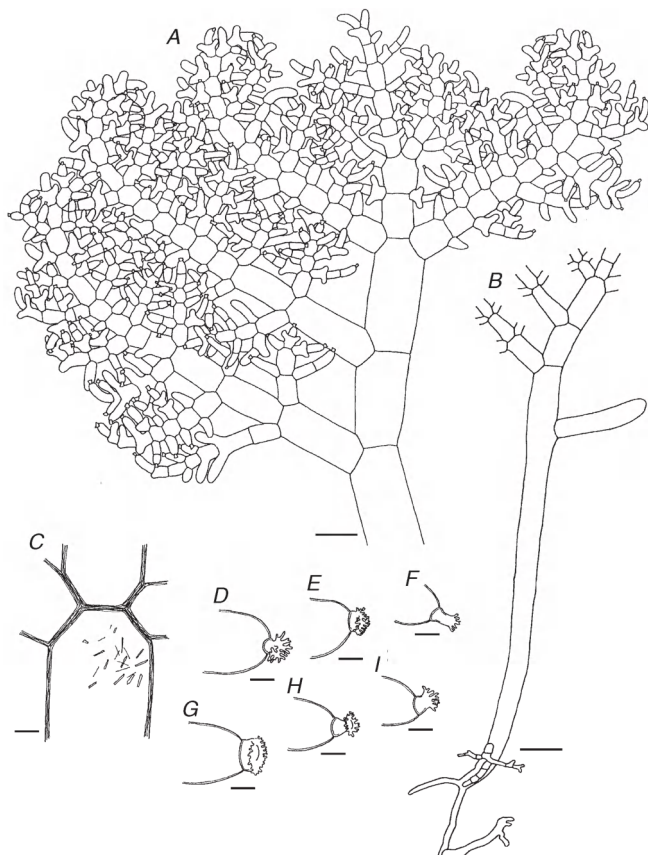


Fig. 11. *Boodleia composita*–*Phyllocladion anastomosans* species complex: *delicatula* morphotype (holotype of *Struvea delicatula*, L). (A) Lamina composed of regular opposite branches lying in a single plane. (B) Stipe cell, attached by basal rhizoids. (C) Detail of cell walls, cross walls at the base of the laterals, and prismatic calcium oxalate crystals. (D–I) Type-2 tenacular cells. Scale bars: (A) = 500 μ m; (B) = 1 mm; (C–I) = 50 μ m.

rhizoids arising from the lower pole of the stipe (Fig. 11B). 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 and growth by a repetitive process of cell division, formation of lateral branches and cell elongation

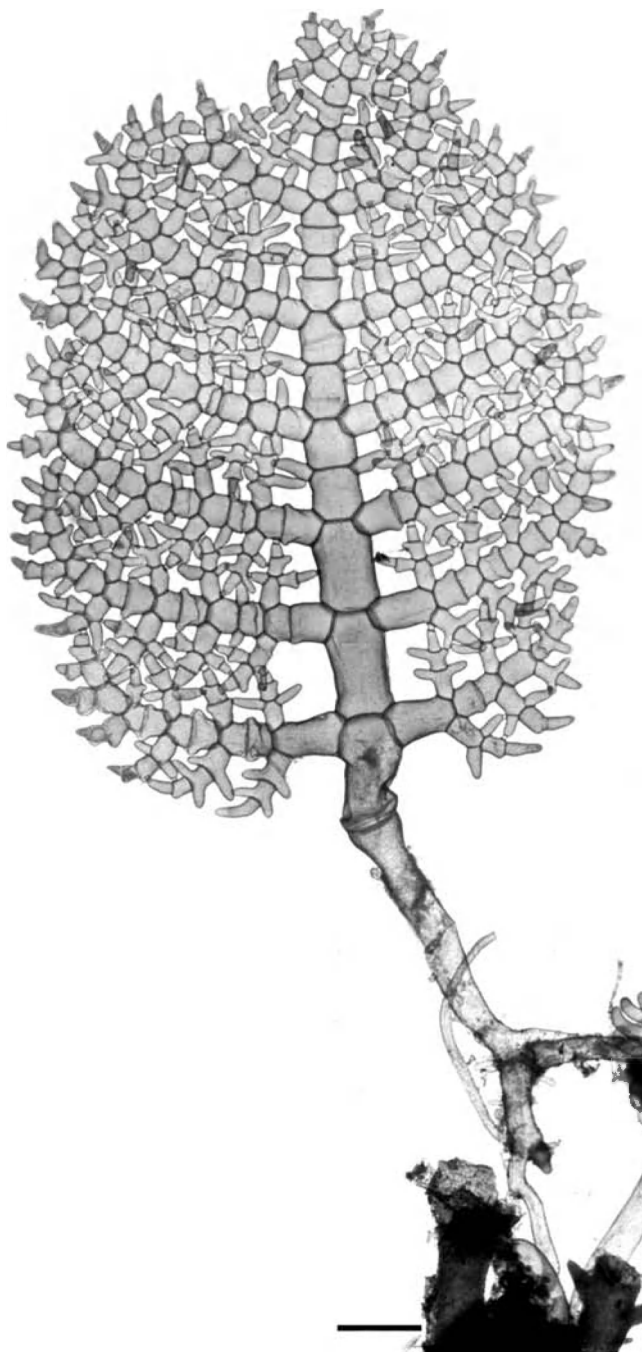


Fig. 12. *Boodleia composita*–*Phyllocladion anastomosans* species complex: *delicatula* morphotype (PH 451, Philippines). Stipitate lamina composed of regularly opposite branches lying in a single plane. Scale bar = 500 μ m.

and enlargement. Cell division by centripetal invagination of the cell walls. Growth by apical and intercalary cell divisions; apical cells dividing into two or simultaneous three 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 11A, 12). 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 fourth order; first order branches curved towards the blade apex. The diameter of the stipe 2–7× that of the apical cells. Angle of ramification 45–90°.

Mature blades elliptical in outline; reinforcement by anastomosis of adjacent cells by type-2 tenacular cells, borne singly on the tips of apical cells or laterals in open connection with the mother cell (Figs 11D–I, 12B). In mature blades, on average 34–65% of the apical cells produce a type-2 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 c. 2 µm in the ultimate branches, up to 7 µm in the main axes (Fig. 11C).

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. 11C).

Notes

Struvea delicatula was originally described and illustrated as a plant with a branched stipe bearing tripinnate blades (Kützinger 1866: 1, pl. 2: figs e–g). The conspecificity of *S. delicatula* and *S. anastomosans* was proposed by Murray and Boodle (1888: 281) who, however, erroneously adopted the younger name (Silva *et al.* 1996). Børgesen (1913) at first followed Murray and 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 and Boodle (1888: 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). On the basis of the original illustrations we consider this taxon similar to the *delicatula* morphotype.

Murray and Boodle (1888: 281, fig. 5) described and illustrated the type of Zanardini's (1878) *S. tenuis* as a small stipitate blade composed of strictly opposite branching filaments up to the second order. Egerod (1952) followed Murray and Boodle (1888) 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. tenuis* might represent a juvenile thallus of *S. anastomosans*, but it was Cribb (1960) who formally considered both species conspecific, on the basis of Børgesen's (1913) observations.

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

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

4. *kenyensis* morphotype (Figs 13–15)

Corresponding taxon:

Cladophoropsis kenyensis Leliaert & Coppejans, In Leliaert, Taxon. Phyllog. Stud. Cladophorophyceae: 113–115, figs 3A, B, 6, 7 (2004) (nom. prov.) [Holotype: Mwamba Beach, Mombasa, mid- to low intertidal rock pools, epilithic, leg. Coppejans, 5.ix.1991, HEC 8669a (GENT)].

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 -2 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 14A, 15A).

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 two 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 third and fourth

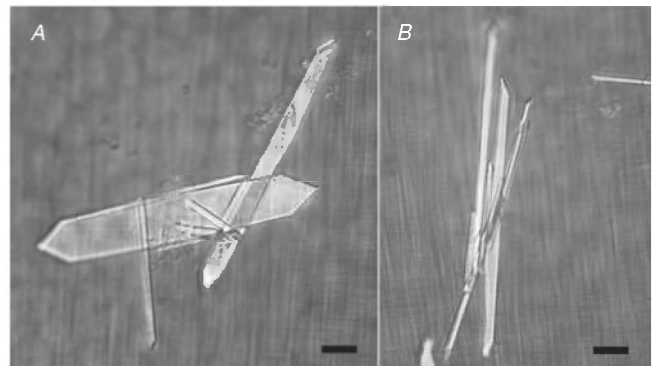


Fig. 13. (A, B) *Boodlea composita*–*Phyllocladion anastomosans* species complex: *kenyensis* morphotype (HEC 8669a, GENT). Prismatic calcium oxalate crystalline cell inclusions. Scale bars = 10 µm.

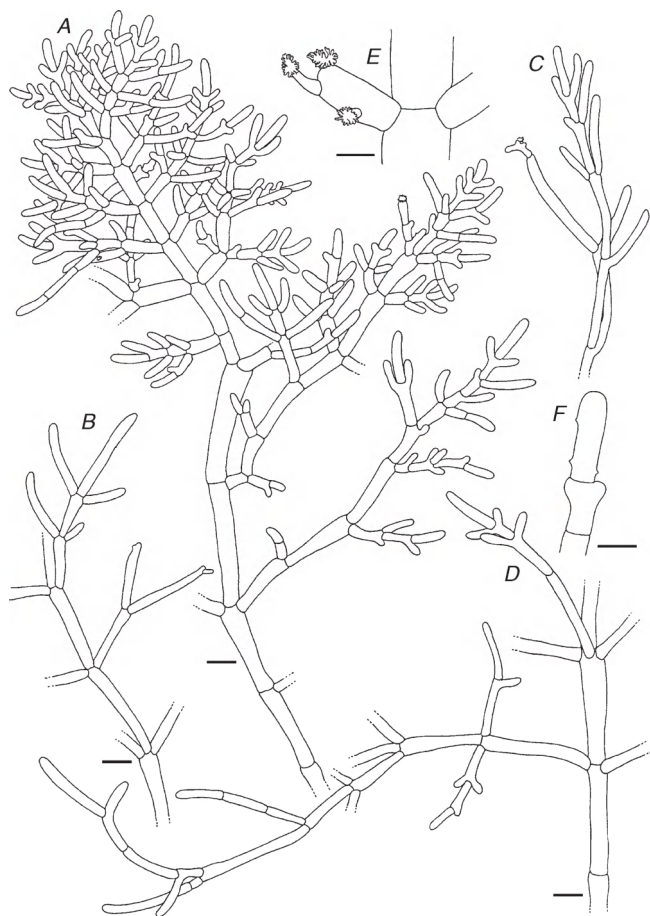


Fig. 14. *Boodlea composita-Phyllocladon anastomosans* species complex: *kenyensis* morphotype (HEC 8669a, GENT). (A–C) Terminal, mainly opposite branches. (D) Basal branches. (E) Type-2 tenacular cells. (F) Sporangium with lateral conical projections. Scale bars: (A–D) = 1 mm; (E) = 200 µm; (F) = 500 µm.

lateral, perpendicular to the first opposite pair, resulting in three-dimensional branch systems; occasionally a fifth lateral is produced resulting in verticillate branches (Fig. 15C). 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 fourth order. The diameter of the basal (stipe) cells 0.8–3× that of the apical cells. Angle of ramification 30–75°.

Structural reinforcement of the lamina limited; adjacent filaments sporadically attach by type-1 or -2 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 14E, 15D–H). In mature blades, on average 1–4% of the apical cells produce a type-2 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



Fig. 15. *Boodlea composita-Phyllocladon anastomosans* species complex: *kenyensis* morphotype (HEC 8669a, GENT). (A) Terminal, mainly opposite branches. (B) Basal branches and stipe cell with rhizoids. (C) Cells in the central part of the thallus producing up to five laterals (arrow). (D–F) Type-2 tenacular cells. (G) Type-1 tenacular cells. (H) Type-2 tenacular cells produced at the basal pole of a cell. Scale bars: (A–C) = 1 mm; (D–H) = 200 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. 15B), 370–740 µm in diameter, l/w ratio 5–7. Type-2 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. 14F).

Chloroplasts small, polygonal or round, 3–4 µm in diameter, each with a single pyrenoid, c. 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. 13).

Notes

The *kenyensis* morphotype is characterised by stipitate blades clustering together to form cushion-like thalli and thus has a similar gross morphology to the *anastomosans* and *struveopsis* morphotypes. It differs, however, from the other morphotypes by the much coarser filaments (Table 2).

Plants of the *kenyensis* morphotype have been found epilithic in mid-to-low intertidal rock pools. This morphotype is only known from the area around Mombasa, Kenya.

5. *montagnei* morphotype (Figs 16, 17)

Corresponding taxon:

Microdictyon montagnei Harvey ex J.E. Gray, J. Bot. 4: 69 (1866) [Holotype: Lifuka, Ha'apai group, Tonga, leg. Harvey, Friendly Island Algae no. 89, Herbarium Dickie, BM!, isotype in PC!]; Setchell (1929: 573–580, figs 97–105).

Boodlea montagnei (Harvey ex J.E. Gray) Egerod, Univ. Calif. Publ. Bot. 25: 332, footnote (1952).

Thallus forming astipitate, reticulate blades, composed of densely branched filaments (Figs 16A, 17A), attached to the substratum by type-1 tenacular cells or rhizoidal cells.

Blade formation and growth by a repetitive process of apical and intercalary cell division (CI), formation of lateral branches, cell elongation and enlargement. Division of apical cells into two (rarely three) cells. Newly formed cells either producing a single lateral (eventually displacing the apical cell resulting in pseudodichotomous branch systems, Fig. 17E) or an opposite pair of laterals (Fig. 17D). Axes branching regularly, opposite with intercalary cell divisions occurring at regular intervals (Figs 16B, 17C). 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 seventh 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× that of the apical cells. Angle of ramification (60–)75–90°.

Reinforcement of the lamina by attachment of adjacent cells by type-2 tenacular cells, borne singly on the tips of apical cells or laterals in open connection with the mother cell (Figs 16D, E, 17D). In mature blades, on average 30–55% of the apical cells produce a type-2 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 c. 2 µm in the ultimate branches, up to 12 µm in the main axes.

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. 16F).

Notes

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-2 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* morphotype. We recognise a separate *montagnei* morphotype based on the fact that in certain localities (e.g. in areas in Indonesia and the Philippines) this morphological form is found by itself without the presence of intermediate forms such as stipitate or cushion-like plants. As already described by Setchell (1929: 573), branching in the *montagnei* morphotype may become three-dimensional in certain parts of the thallus, and consequently the distinction from the *siamensis* and *anastomosans* morphotype becomes vague.

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

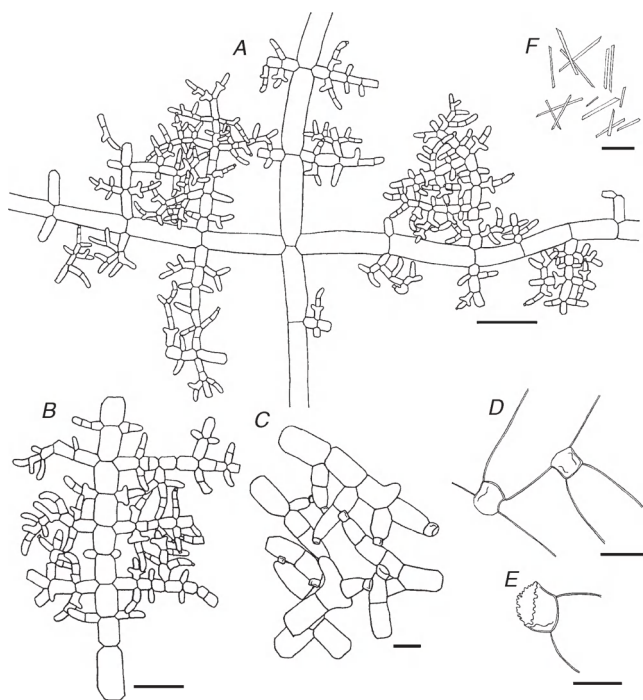


Fig. 16. *Boodlea composita*–*Phyllocladion anastomosans* species complex: *montagnei* morphotype (holotype of *Microdictyon montagnei*, BM). (A, B) Part of a reticulate lamina composed of opposite branching main axes; terminal branch-systems unilateral, pseudodichotomous or opposite. (C–E) Type-2 tenacular cells. (F) Elongate trapeziform to needle shaped prismatic calcium oxalate crystals. Scale bars: (A) = 1 mm; (B) = 500 µm; (C) = 100 µm; (D, E) = 50 µm.

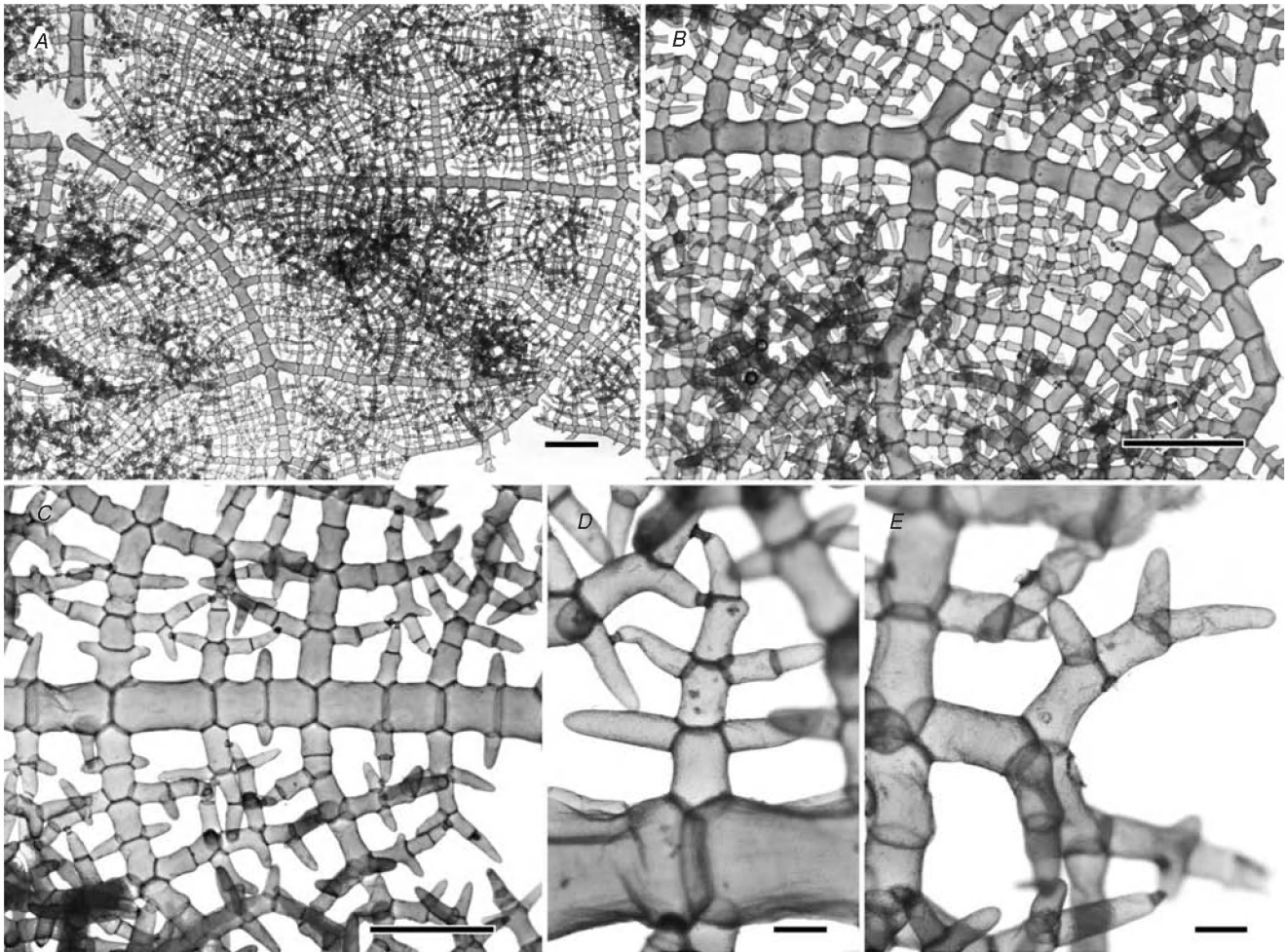


Fig. 17. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *montagnei* morphotype (PH 572, Philippines). (A, B) Reticulate lamina composed of oppositely branched main axes interspersed among a dense meshwork of narrower filaments representing the higher branch orders. (C) Main axes with intercalary cell divisions at regular intervals. (D) Ultimate, opposite branches; anastomosis by type-2 tenacular cells. (E) Ultimate, unilateral to pseudodichotomous branches. Scale bars: (A, B) = 1 mm; (C) = 500 μ m; (D, E) = 100 μ m.

6. *siamensis* morphotype (Figs 18–24)

Corresponding taxa:

Boodlea siamensis Reinbold, Bot. Tidsskr. 24: 191–192 (1901) ‘*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, J. Linn. Soc. Bot. 15: 451 (1876) [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, J. Linn. Soc. Bot. 25: 245, pl. 49 (1889); Okamura (1901: 41, pl. 15); Chihara: (1955: 9–18, figs 1–5).

Boodlea composita forma *irregularis* Brand, Ber. Deutsch. Bot. Ges. 29: 145 (1911) [Lectotype: Tahiti (“*Tautira insulae* Tahiti ad scopulos”), leg. J.E. Tilden 105, x.1909, B!; isolectotypes: M! and MIN].

Boodlea siamensis forma *robusta* Børgesen, J. Indian Bot. Soc. 9: 153–155, fig. 2 (1930) [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, Biol. Meddel. Kongel. Danske Vidensk. Selsk. 11 (6): 9–10 (1934).

Boodlea paradoxa Reinbold, Nuova Notarisa 16: 148–149 (1905) [Lectotype: Buru Island, Moluccas, Indonesia, leg. Weber-van Bosse, Siboga Expedition, Herbarium Reinbold, M!].

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

Thallus forming firm cushions, composed of densely branched, tightly interwoven filaments, forming a three-dimensional reticulum. Young thalli attached to the substratum by rhizoids sprouting from the base of the stipe cell (Fig. 19A); mature plants attached by type-1 tenacular cells and by rhizoids produced at the distal pole of apical cells (Figs 19B, 21F, G).

Young thalli stipitate with opposite or unilateral branch systems (Fig. 19A). 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 two (sometimes three) cells. Newly formed (sub-apical) cells producing a single lateral, eventually displacing the apical cell, resulting in pseudodichotomies (Figs 18A, 20C, 21A, 22A, 24A). Older cells often producing

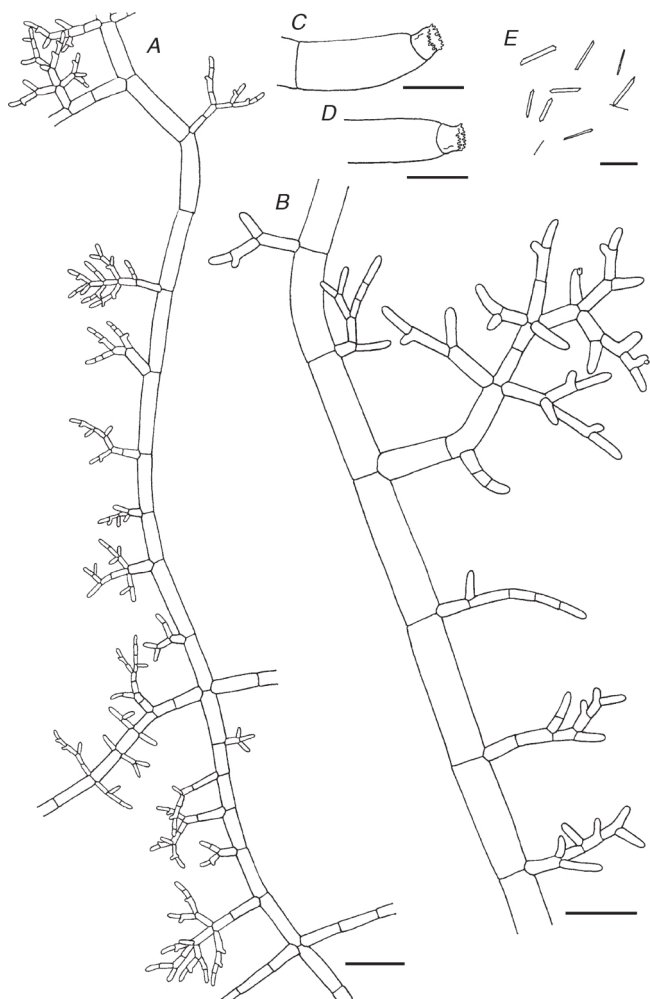


Fig. 18. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *siamensis* morphotype (holotype of *Boodlea siamensis*, M). (A, B) Oppositely or unilaterally branched main axes; opposite or pseudodichotomous terminal branch-systems, some cells producing laterals perpendicular on the original branching plane (arrows). (C, D) Type-2 tenacular cells. (E) Elongate hexagonal or trapeziform calcium oxalate crystals. Scale bars: (A) = 1 mm; (B) = 500 μ m; (C, D) = 100 μ m; (E) = 50 μ m.

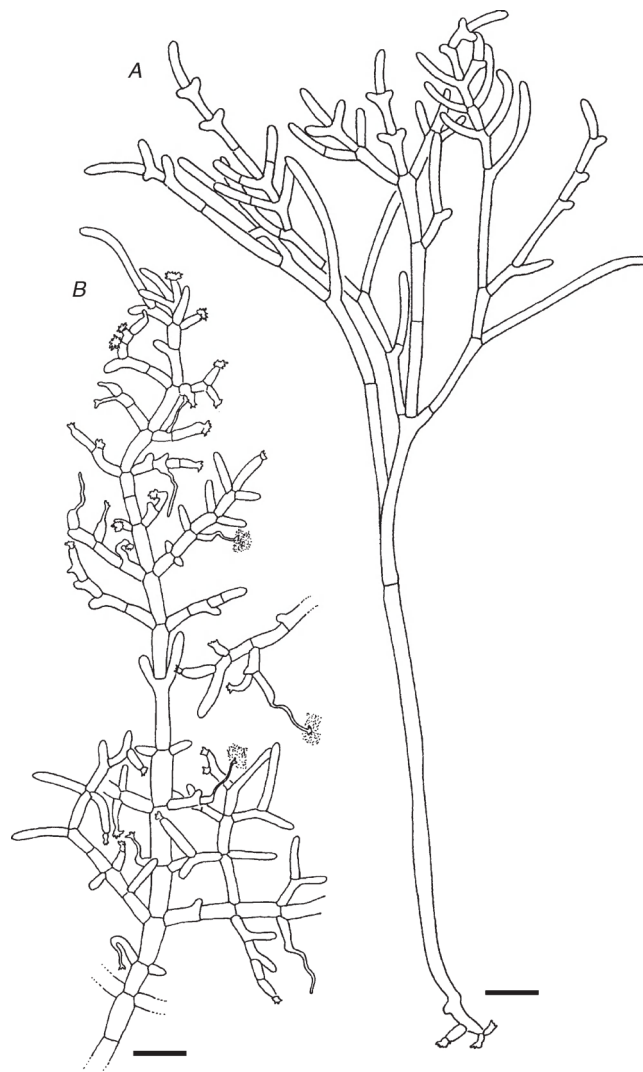


Fig. 19. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *siamensis* morphotype. (A) Young, stipitate thallus with opposite or unilateral terminal branch-systems (L 936.181.459). (B) Thallus growing on sand-covered rock, producing numerous type-1 and -2 tenacular cells and rhizoids formed at the distal pole of apical cells (FL 722). Scale bars = 500 μ m.

a second lateral, perpendicular or opposite to the first one (Figs 21A, 23A). Main branch systems regularly opposite to irregularly organised with frequent intercalary cell divisions (Figs 18A, 20E, 21A, 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 320(–500) μ m 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 fifth (–6th) order. The diameter of the main axes 1.2–8 \times that of the apical cells. Angle of ramification 40–90 $^{\circ}$.

Reinforcement of the lamina by tightly interweaving of the, often curved, branch systems and attachment of adjacent cells by type-2 tenacular cells, borne singly on the tips (occasionally

laterally) of apical cells or laterals in open connection with the mother cell (Figs 18C, D, 21B–E, 22C–I, 23E–G, 24B, C). In mature blades, on average 10–55% of the apical cells produce a type-2 tenacular cell.

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

Thickness of the cell wall *c.* 2 μ m in the ultimate branches, up to 7 μ m in the main axes.

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 μ m in diameter and 40 μ m long (Fig. 18E).

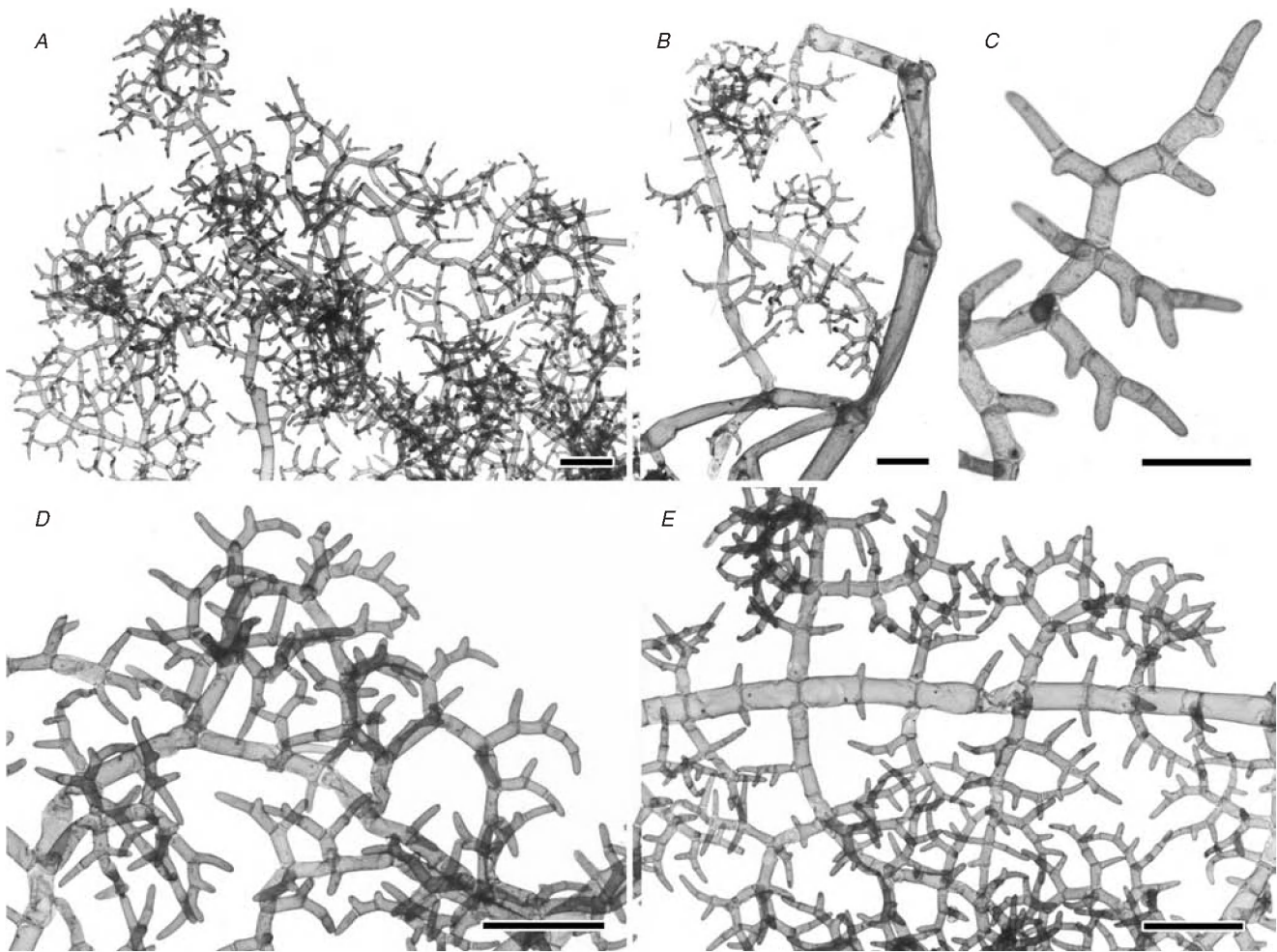


Fig. 20. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *siamensis* morphotype (FL 714, Chwaka Bay, Zanzibar). (A, B) Branching filaments forming a three-dimensional reticulum. (C) Unilateral or pseudodichotomous terminal branches. (D) Incurved terminal branch-systems. (E) Main axes with intercalary cell divisions at regular intervals. Scale bars: (A, B, D, E) = 1 mm; C = 500 μ m.

Notes

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 second (and third) lateral, perpendicular or opposite to the first one. The original description by Reinbold (1901) was rather cryptic and the species became better known by the work of Weber-van Bosse (1913: 68–70, fig. 11). Børgesen (1913: 49, figs 34–36) described and illustrated a Caribbean *B. siamensis* with an intermediate morphology between the *siamensis* and the *composita* morphotype. Later, Børgesen (1930: 153, fig. 2; Børgesen 1934: 9–10; 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* morphotype [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 and Littler (2000:

326, fig. on p. 327; 2003: 200, fig. on p. 201)]. Two forms of *B. siamensis* (*irregularis* and *robusta*) have been described by Brand (1911) and Børgesen (1930) respectively. Examination of the type material of both taxa (Figs 22 and 23, respectively) shows that they both fall within the limits of the *siamensis* morphotype.

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. 22). 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). Dickie (1876: 451) commented on the similarities between *C. coacta* and *C. anastomosans*. The type of *C. coacta* is characterised by opposite terminal branch systems (Fig. 22B) in some parts of the thallus and unilateral or pseudodichotomous terminal branch systems (Fig. 22A) in other parts; the taxon can

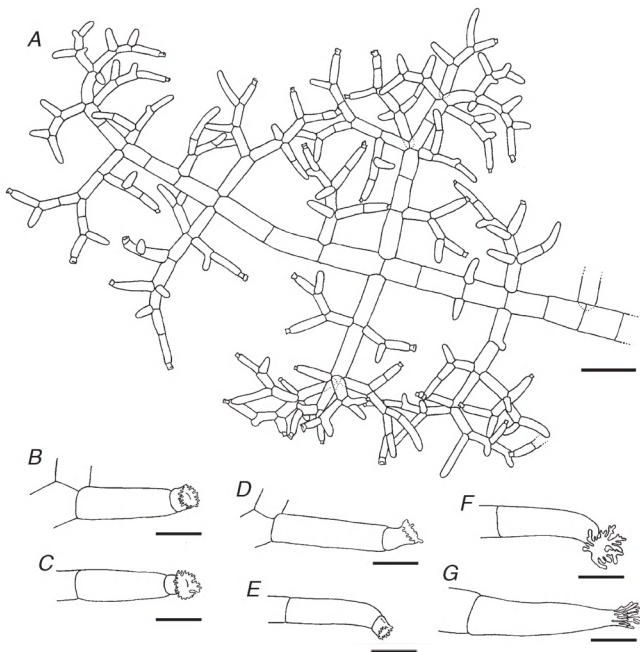


Fig. 21. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *siamensis* morphotype (lectotype of *Boodlea paradoxa*, M). (A) Oppositely branched main axis with numerous intercalary cell divisions; unilateral to pseudo-dichotomous or opposite terminal branch-systems, many cells producing branches perpendicular on the original branching plane (arrows), resulting in a three-dimensional reticulum. (B–E) Type-2 tenacular cells. (F, G) Type-1 tenacular cells. Scale bars: (A) = 500 μ m; (B–G) = 100 μ m.

therefore be regarded as intermediate between the *composita* and the *siamensis* morphotype.

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. The original diagnosis by Reinbold (1905) 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 and 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* morphotype), we consider this taxon equivalent to the *siamensis* morphotype.

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* morphotype. 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 examine the type material.

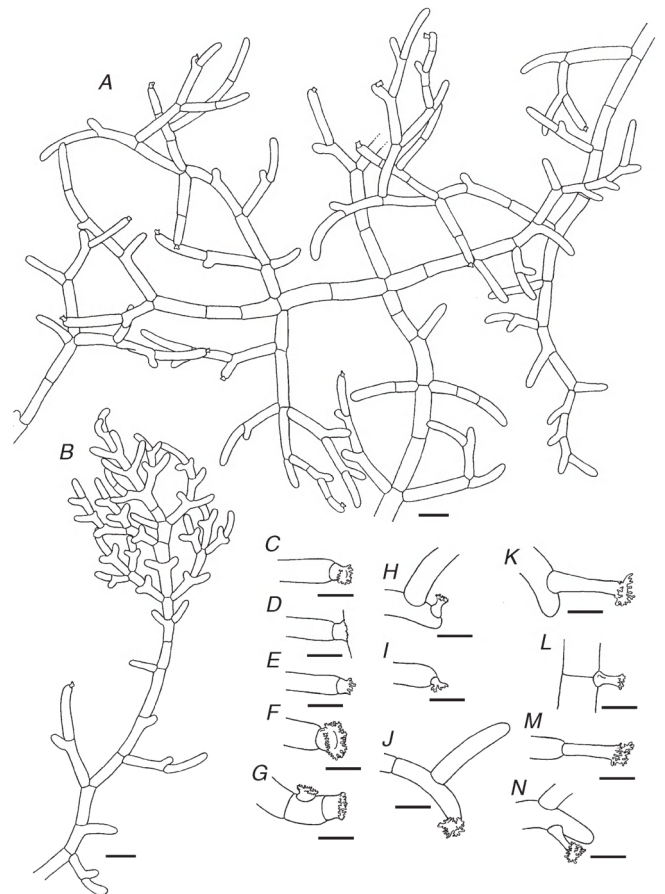


Fig. 22. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *siamensis* morphotype (holotype of *Cladophora coacta*, BM). (A) Oppositely branched main axis, unilateral to pseudodichotomous terminal branch systems. (B) Terminal opposite branch systems forming a '*Struvea*'-like plumule. (C–I) Type-2 tenacular cells. (J, K) Type-1 tenacular cells. (L–N) Intermediate forms between type-1 and -3 tenacular cells. Scale bars: (A, B) = 200 μ m; (C–N) = 100 μ m.

The cushion-like morphotypes, *composita* and *siamensis*, differ in branching pattern and the abundance of tenacular cells (type-1 and -2). The *composita* morphotype is characterised by regular, opposite ultimate branch systems, often resulting in small *Struvea*-like plumules sticking out of cushion-like thalli. Older cells generally produce a third and fourth 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* morphotype 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-2), in combination with tight interweaving of the often curved branch systems. However, many intermediates between the *composita* and *siamensis* morphotypes have been

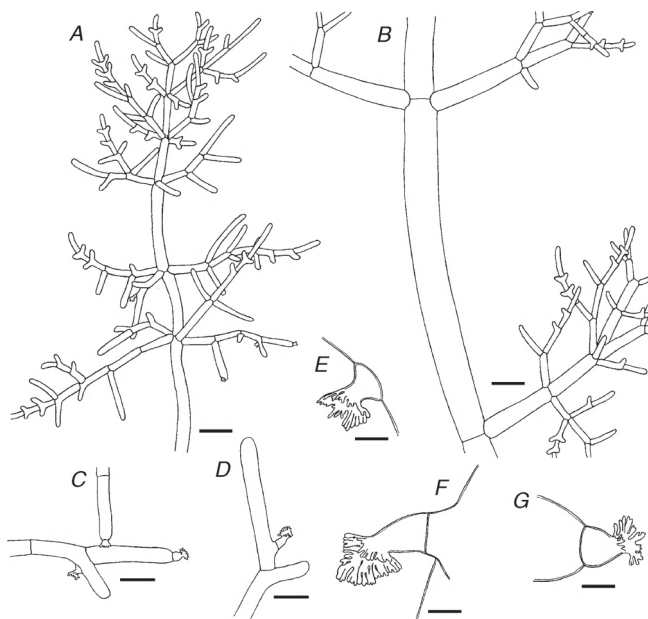


Fig. 23. *Boodlea composita*-*Phyllocladon anastomosans* species complex: *siamensis* morphotype (lectotype of *Boodlea composita* forma *irregularis*, B). (A) Terminal branch-system with unilateral or opposite laterals and branches perpendicular to the original branching plane. (B) Large cells of a main axis; side branches single or opposite. (C-G) Type-2 tenacular cells. Scale bars: (A, B) = 500 μ m; (C, D) = 200 μ m; (E-G) = 50 μ m.

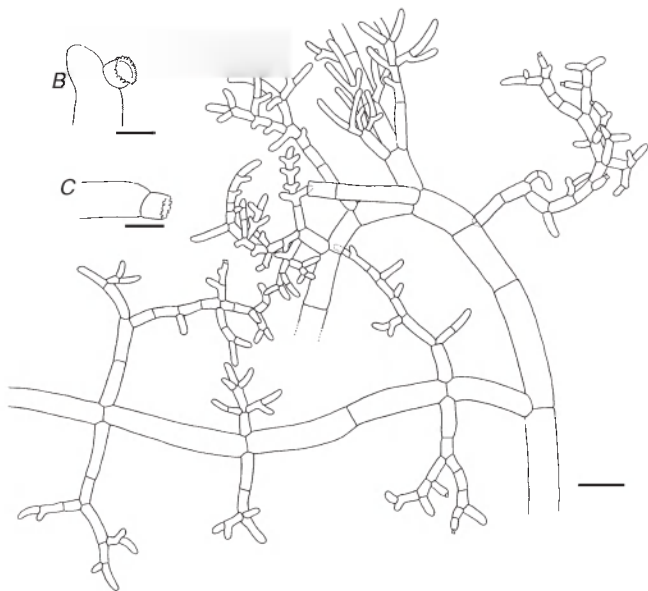


Fig. 24. *Boodlea composita*-*Phyllocladon anastomosans* species complex: *siamensis* morphotype (lectotype of *Boodlea siamensis* forma *robusta*, C). (A) Main axes with opposite or single side branches; ultimate branches opposite, unilateral or pseudodichotomous, many cells producing laterals perpendicular to the original branching plane. (B, C) Type-2 tenacular cells. Scale bars: (A) = 1 mm; (B, C) = 100 μ m.

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, and 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 swimmers are formed. At about the same time one or more short conical projections are observed on the lateral side or summit of each sporangium. The swimmers escape through an aperture formed in the apex of the projections as described by Børgesen (1913) for *B. siamensis*. Every swimmer is long and pear-shaped, ~16–22.5 μ m long, 9–12.5 μ m wide, and has four flagella, one eye-spot and numerous chloroplasts. They show a tendency to 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.

The *siamensis* morphotype has a pantropical distribution and is generally observed from the high intertidal to the subtidal (down to 25 m depth), epilithic on rocky substratum or on dead coral, or epiphytic on macro-algae, seagrasses or mangroves.

7. *struveopsis* morphotype (Figs 25, 26)

Corresponding taxa:

Pseudostruvea siamensis Egerod, Bot. Mar. 18: 48–50, figs 12–14 (1975) [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 outcrop, leg. L. Egerod LE 71–2–26, 9.iv.1971, UC and C!; Sartoni (1992: 314–315, fig. 11).

Struveopsis siamensis (Egerod) P. C. Silva, In Silva *et al.*, Cat. benthic mar. algae Indian Ocean: 800 (1996).

Pseudostruvea covalamensis Iyengar Seaweed Res. Utilis. 4: 59–64, figs 1–27 (1980). [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.*, Cat. benthic mar. algae Indian Ocean: 800 (1996) [Iyengar (ms.) intended to name this species *Struveopsis covalamensis* gen. et sp. nov. but in the meantime *Struveopsis* was described independently by Rhyne and 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*].

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 25A, 26B). Attachment to the substratum by multicellular rhizoids, arising from the lower pole of the stipe cells (Fig. 25B). 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

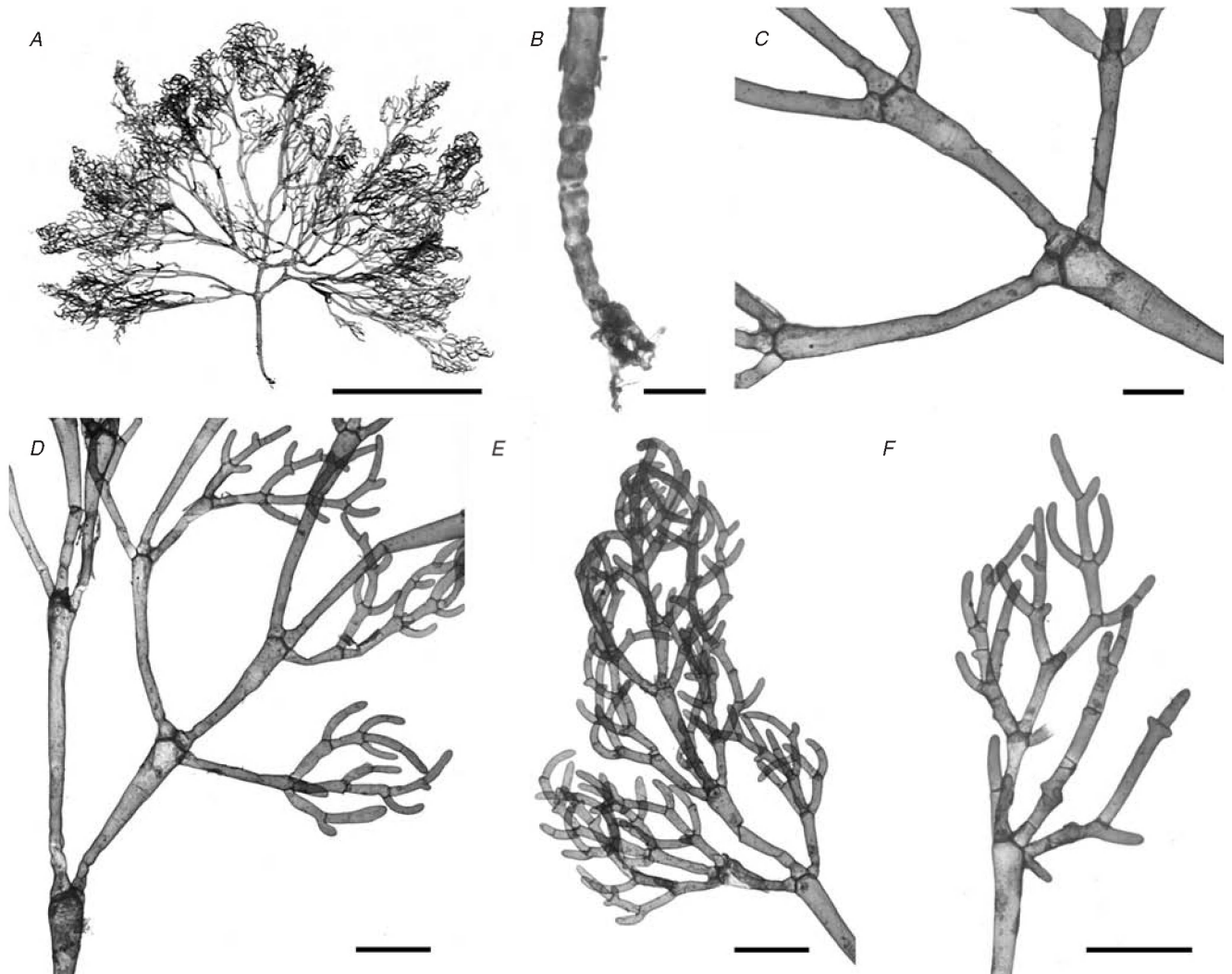


Fig. 25. *Boodlea composita*–*Phyllocladon anastomosans* species complex: *struveopsis* morphotype (FL 677, Kiwengwa, Zanzibar). (A) Stipitate thallus. (B) Base of stipe cell with annular constrictions. (C, D) Opposite or pseudodichotomous main axes: clavate cells with a basal bulge and a few annular constrictions. (E, F) Opposite or pseudodichotomous terminal branch-systems. Scale bars: (A) = 1 cm; (B, C) = 500 μ m; (D–F) = 1 mm.

of the stipe cell possibly segregative (Fig. 26A, 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 3–7 cells, followed by the formation of opposite pairs of laterals (Fig. 26C, D). Intercalary cell division starting from the third to fifth cell under the apical cell. Older cells (mostly in the main axes) possibly producing a second, third and fourth lateral, in any direction (Fig. 26C). Cross wall formation at the proximal pole of laterals somewhat delayed; laterals in open connection with the mother cell up to 380 μ m 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 25C, D, 26E, F). The diameter of the thickest part of the main axes (not including stipe cells) \sim 2.5–5 that of the apical cells. Branching three-dimensional, up to the fifth (or sixth) 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) μ m in diameter, l/w ratio 1.2–8(–12). Cell of the main axes subcylindrical to club-shaped, (140–)260–570(–930) μ m in widest diameter, length/width ratio 2.2–10(–20). Stipe cells subcylindrical to clavate, (190–)340–1150 μ m in diameter, up to 14 mm long.

Thickness of the cell walls of ultimate branches less than 1 μ m, of the main axes and stipe 5–15 μ m.

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

Notes

The holotype of *Pseudostruvea siamensis* consists of small fragments of erect stipitate blades and has been accurately described and illustrated by Egerod (1975).

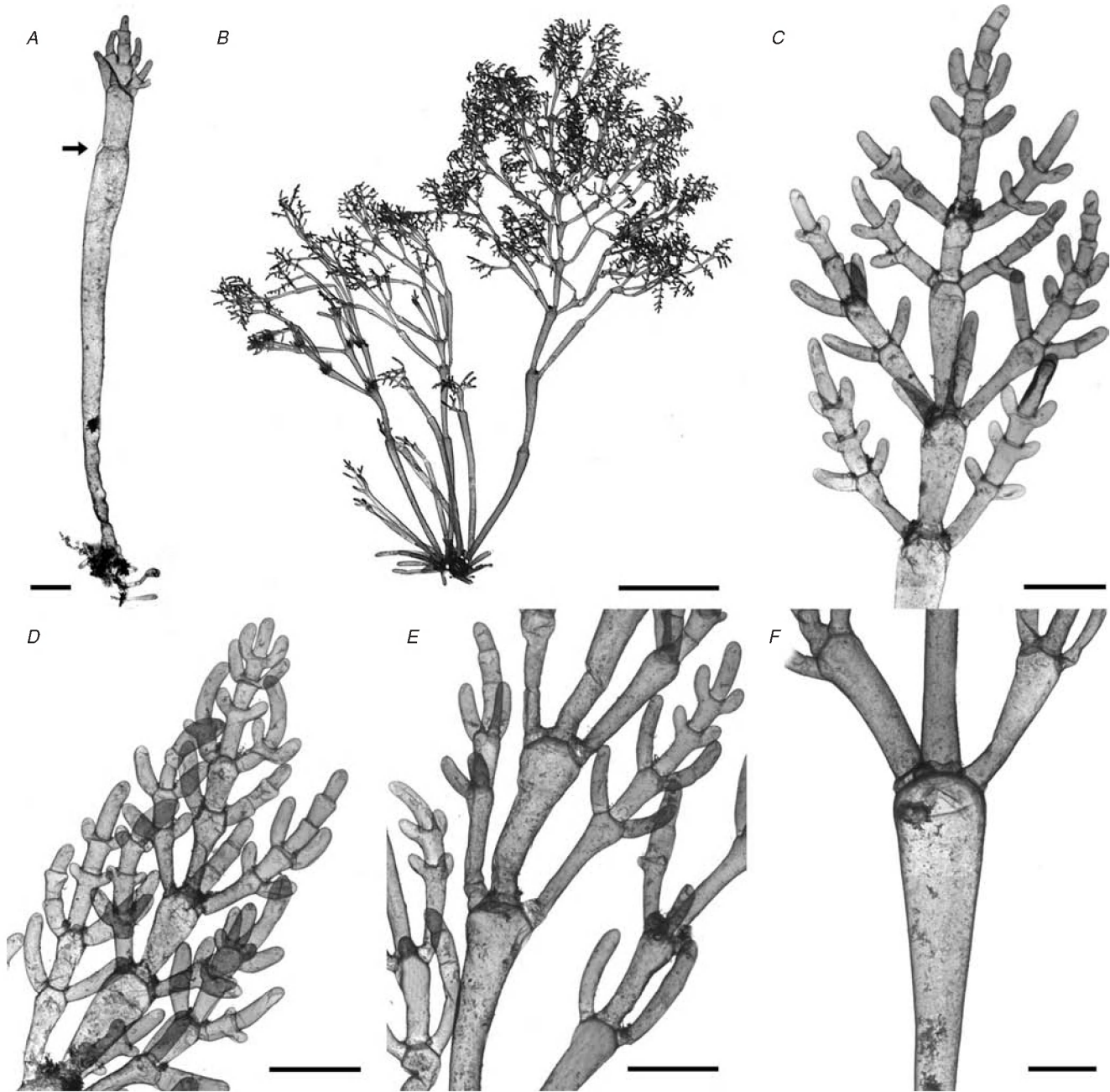


Fig. 26. *Boodlea composita*-*Phyllocladon anastomosans* species complex: *struveopsis* morphotype (FL 916, Mbudya Island, Tanzania). (A) Young thallus consisting of a stipe with basal annular constrictions and terminal, opposite branches: initial division of the stipe cell segregative (arrow). (B) Stipitate 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.

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* morphotype.

The *struveopsis* morphotype 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 -2 tenacular cells may be produced, fading the boundary with the *composita* morphotype.

The *struveopsis* morphotype has only been observed 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.

Discussion

This work shows that species and generic boundaries based on single morphological characters prove to be untenable in *Boodlea*, *Phyllocladon* and allied genera. The sole character that is traditionally used to distinguish the genera *Boodlea* and *Phyllocladon*, the formation of cushion like thalli vs flat blades, appears to be a variable one and is, at least to some extent, attributable to a combination of environmental factors and the developmental stage of the plants. Young plants in the *Boodlea composita*–*Phyllocladon anastomosans* species complex generally form stipitate reticulate blades. Older plants can either retain this thallus architecture or grow into irregular, cushion- or sponge-like plants. The latter thallus morphology could be regarded an adaptation to intertidal habitats given that the sponge-like thallus, mediated by the interweaving of the densely branched filaments and anastomosis of the filaments by tenacular cells, is able to retain water during low tide. However, blade-like forms could be seen as an adaptation to low light intensities in shaded and deep-water habitats (e.g. the *delicatula* morphotype is found down to 40 m depth). The single morphological character that distinguishes *Struveopsis* and *Nereodictyon* from *Phyllocladon* and *Boodlea*, i.e. the absence of tenacular cells, is apparently also subject to environmental conditions. For example, plants of the *composita* morphotype growing in sheltered habitats often fail to form tenacular cells and become indistinguishable from the *Struveopsis* morphotype. Tenacular cells not only have an attachment and thallus-reinforcement function, but also promote the formation of cushions loaded with sand that are unattractive to herbivores, and could therefore be viewed as an adaptation to environments with high grazing pressure.

The vague species boundaries within the *Boodlea composita*–*Phyllocladon anastomosans* species complex are confirmed by preliminary phylogenetic analyses based on 65 rDNA internal transcribed spacer (ITS) sequences of isolates worldwide (Wysor 2002; Leliaert and Wysor, unpubl. data). These analyses show that thallus morphology, distinguishing *P. anastomosans* and *B. composita*, is indeed incongruous with the evolutionary history. A tentative ITS-based phylogenetic hypothesis, including several samples of both *B. composita* and *P. anastomosans*, suggests the resolution of at least three distinct clades, each containing a mixture of thallus forms. This could indicate that the different thallus morphologies have evolved several times independently (possibly by hybridisation events), or alternatively, that the different architectural types are ecologically determined, or represent different developmental stages of the same species.

Several *Boodlea* and *Phyllocladon* species apparently do not fall within the morphological boundaries of the *Boodlea composita*–*Phyllocladon anastomosans* species complex. *Boodlea kaenana* Brand and *B. trukensis* Trono are characterised by very long apical cells and lateral branches lacking basal

cross walls and thus are morphologically more closely allied to the *Cladophoropsis membranacea* cryptic species complex (Leliaert and Coppejans 2006). *Boodlea vanbosseae* Reinbold fits in the *Cladophora* section *Boodleooides* as circumscribed by van den Hoek (1963), whereas *B. mutabile* (Dellow) Adams should be returned to its original genus, *Microdictyon* (Leliaert 2004). *Phyllocladon orientale* and *P. pulcherrimum* differ from the *Boodlea composita*–*Phyllocladon anastomosans* species complex by the typical flabellate branching pattern in the blades, the presence of small tenacular cells formed at the basal poles of the cells and attaching to the cell below, and the diamond-shaped crystalline cell inclusions. Molecular data based on partial LSU rDNA sequences has confirmed that *P. orientale* is not closely related to *P. anastomosans* (Leliaert and Coppejans 2007).

The branch systems in *Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgesen are typically unilateral, and thus seem completely different from those in the *Boodlea composita*–*Phyllocladon anastomosans* species complex. However, culture isolates of '*B. composita*' grown under certain conditions (e.g. low temperatures and stagnant water) develop typical *Cladophoropsis*-like branch systems. However, the Indo-Pacific representatives of *C. membranacea* often develop opposite laterals and may be very similar to irregular growth forms of '*B. composita*'. *Cladophoropsis membranacea* differs from representatives of the *Boodlea composita*–*Phyllocladon anastomosans* species complex by the much longer cells, a more pronounced delay of cross wall formation at the base of the laterals and the shape of the crystalline cell inclusions. The length/width ratio of the apical cells is generally 4–40 in *C. membranacea* v. 1–10(–18) in the *Boodlea composita*–*Phyllocladon anastomosans* species 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 *Boodlea composita*–*Phyllocladon anastomosans* species complex. Calcium oxalate crystals in the *Boodlea composita*–*Phyllocladon anastomosans* species complex are elongate hexagonal or trapeziform (often needle-shaped) (Figs 1J, 3E, 7C, 11C, 13, 16F, 18E), whereas in thalli of *C. membranacea* broad to elongate rectangular, and broad trapeziform crystals are also found (Leliaert and Coppejans 2006). The idea that the *Boodlea composita*–*Phyllocladon anastomosans* species complex and *C. membranacea* are distinct 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 and Nguyen 1994). However, both species groups are extremely closely related as evidenced by rDNA ITS and LSU rDNA sequence data (Kooistra *et al.* 1993; Wysor 2002).

In future studies, we will aim to complement the present morphological work with molecular data (in particular, rDNA ITS sequences) to answer specific questions with greater confidence: How many species should be recognised in the *Boodlea composita*–*Phyllocladon anastomosans* species complex? What is the exact extent of phenotypic plasticity? What is the relationship with the cryptic species complex *Cladophoropsis membranacea*, in particular, the Indo-Pacific representatives?

Acknowledgements

We are grateful to the curators and researchers of the following herbaria for loans and information on collections: B (Regine Jahn), BM (Jennifer Bryant), L (Willem Prud'homme van Reine), M (Dagmar Triebel), MEL (Pembe Ata), NY (Ellen Bloch), PC (Bruno de Reviers), S (Marianne Hamnede), and UC (Richard Moe and Paul Silva). Funding was provided by the Fund for Scientific Research Flanders (Research Project 3G002496). E.L. is indebted to the Bijzonder Onderzoeksfonds (Ghent University) for a grant as postdoctoral researcher.

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Manuscript received 26 September 2006, accepted 21 November 2006

Supplementary material: Specimens examined

This supplementary material is available on the web.

Morphological re-assessment of the *Boodlea composita*–*Phyllocladion anastomosans* species complex (Siphonocladales: Chlorophyta)

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Supplementary material

Specimens examined

1. *anastomosans* morphotype: **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*); **Caribbean 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 & 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 macroalgae 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).

2. composita morphotype: **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).

3. delicatula morphotype: **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); Kamaragi 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).

4. kenyensis morphotype: **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).

5. montagnei morphotype: **Indian Ocean: Zanzibar (Tanzania).** Chwaka Bay, intertidal flat, loose lying, (leg. Leliaert, 18.vii.1997, FL 611, FL 614); Chwaka, intertidal seagrass bed, epizoid 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).

6. siamensis morphotype: **Caribbean 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, Mactan 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).

7. *struveopsis* morphotype: **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*).