

A revision of *Cladophoropsis* Børgesen (Siphonocladales, Chlorophyta)

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A reassessment of the genus *Cladophoropsis* results in the recognition of six morphospecies: *C. macromeres*, *C. magna*, *C. membranacea*, *C. philippinensis*, *C. sundanensis* and *C. vaucheriiformis*. The emended genus *Cladophoropsis* is characterized by mat- or cushion-forming plants attached to the substratum by tenacular cells or by rhizoids that sprout from the proximal pole of the basal cells or are formed in any part of the thallus, cell division by centripetal wall ingrowths or occasionally segregative, cells producing a single lateral but older cells occasionally producing secondary laterals, cross walls at the base of the laterals either absent or their formation markedly delayed and reinforcement of the thallus by entangling of the filaments or by anastomosis of adjacent filaments by tenacular cells. The different species are distinguished from each other based on thallus structure, mode of cell division, organization of branch systems, mode of thallus attachment and reinforcement, shape and dimensions of the cells and shape of the crystalline cell inclusions. Twenty *Cladophoropsis* species are excluded from the genus, including the widely distributed Indo-Pacific species *C. herpestica* and *C. javanica*, which have been found to be unrelated to other *Cladophoropsis* species but instead allied with species of the *Cladophora* section *Longi-articulatae*. Phylogenetic studies based on molecular data have furthermore demonstrated that *Cladophoropsis* is closely related to *Boodlea*, *Phyllocladion*, *Struveopsis*, *Struvea* and *Chamaedoris* and that the genus probably does not form a natural group within this genus complex. Morphologically this can be illustrated by a number of *Cladophoropsis* species (e.g. *C. magna* and *C. membranacea*) crossing generic boundaries by sharing common features with *Chamaedoris*, *Boodlea*, *Phyllocladion* and *Struvea*. For the benefit of taxonomic stability, *Cladophoropsis* is presently maintained, awaiting additional molecular evidence.

KEY WORDS: *Cladophora*, Cladophorophyceae, Cladophorales, *Cladophoropsis*, Siphonocladales, *Siphonocladus*, *Spongocladia*, Taxonomy

INTRODUCTION

The green alga *Cladophoropsis* is widely distributed in warm-temperate and tropical waters of the Atlantic, Indian and Pacific oceans. The genus was created by Børgesen (1905), who assigned seven species to it that were previously placed in the genus *Siphonocladus* Schmitz. However, he made only one new combination, *C. membranacea* (Hofman Bang ex C. Agardh) Børgesen. The other members [*S. brachyartus* Svedelius, *S. fasciculatus* Kjellman, *S. modonensis* (Kützing) Bornet, *S. psyttaliensis* Schmitz, *S. voluticula* Hariot and *S. zollingeri* (Kützing) Bornet] were left as *Siphonocladus* and were transferred only later (along with three additional species: *S. conrescens* Reinbold, *S. exiguus* Möbius and *S. rhodensis* Reinbold) to *Cladophoropsis* by Reinbold (1905) and Wille (1910) (Fig. 1). The original circumscription of the genus – cushion-like thalli composed of unilateral to irregular branch systems with laterals lacking basal cross walls – is still generally accepted today. Two other genera, *Spongocladia* and *Spongodendron*, are considered to be congeneric with *Cladophoropsis* (Murray & Boodle 1888; Papenfuss 1950), although the merger of *Spongocladia* and *Cladophoropsis* has not been accepted by some authors (Millar & Kraft 1994; Silva *et al.* 1996; Kraft 2000).

Despite the extremely simple thallus architecture, 36 different species have been described or transferred to *Cladophoropsis* (*Index Nominum Algarum*). New species have been

defined mainly based on differences in cell dimensions. The number of species that should be recognized, however, remains debatable. Womersley (1984) credited the genus with about 20 species, while Olsen-Stojkovich (1986) remained undecided with 4 to 29 species.

Børgesen (1905) was indecisive about the systematic position of his new genus. Originally, *Cladophoropsis* was placed in the Cladophoraceae based on the simple thallus architecture. Later he considered segregative cell division (cleavage of the protoplast into walled, rounded portions that later expand into new cells) to be characteristic for the genus and therefore included it successively in the Valoniaceae (Børgesen 1913), the Boodleaceae (Børgesen 1925) and finally the Siphonocladaceae (Børgesen 1948). La Claire (1982) found that segregative cell division in *Cladophoropsis* often takes place in response to cell wounding. Van den Hoek (1982) regarded *Cladophoropsis* to be morphologically related to *Cladophora* section *Repentes*, based on a similar branching pattern and presence of rhizoids and tenacular cells. Phylogenetic studies based on ITS, SSU and LSU rDNA gene sequences have demonstrated that *Cladophoropsis* is polyphyletic (Kooistra *et al.* 1993, Bakker *et al.* 1994; Hanyuda *et al.* 2002; Leliaert *et al.* 2003). One group of *Cladophoropsis* species [*Cladophoropsis sensu stricto*, including the type species *C. membranacea*, *C. philippinensis* Taylor, *C. sundanensis* Reinbold and *C. vaucheriiformis* (Areschoug) Papenfuss] is situated in the siphonocladalean lineage and closely related to the genera *Boodlea*, *Phyllocladion*, *Struveopsis*, *Struvea* and *Chamaedoris*, while *Cladophoropsis herpestica* (Montagne)

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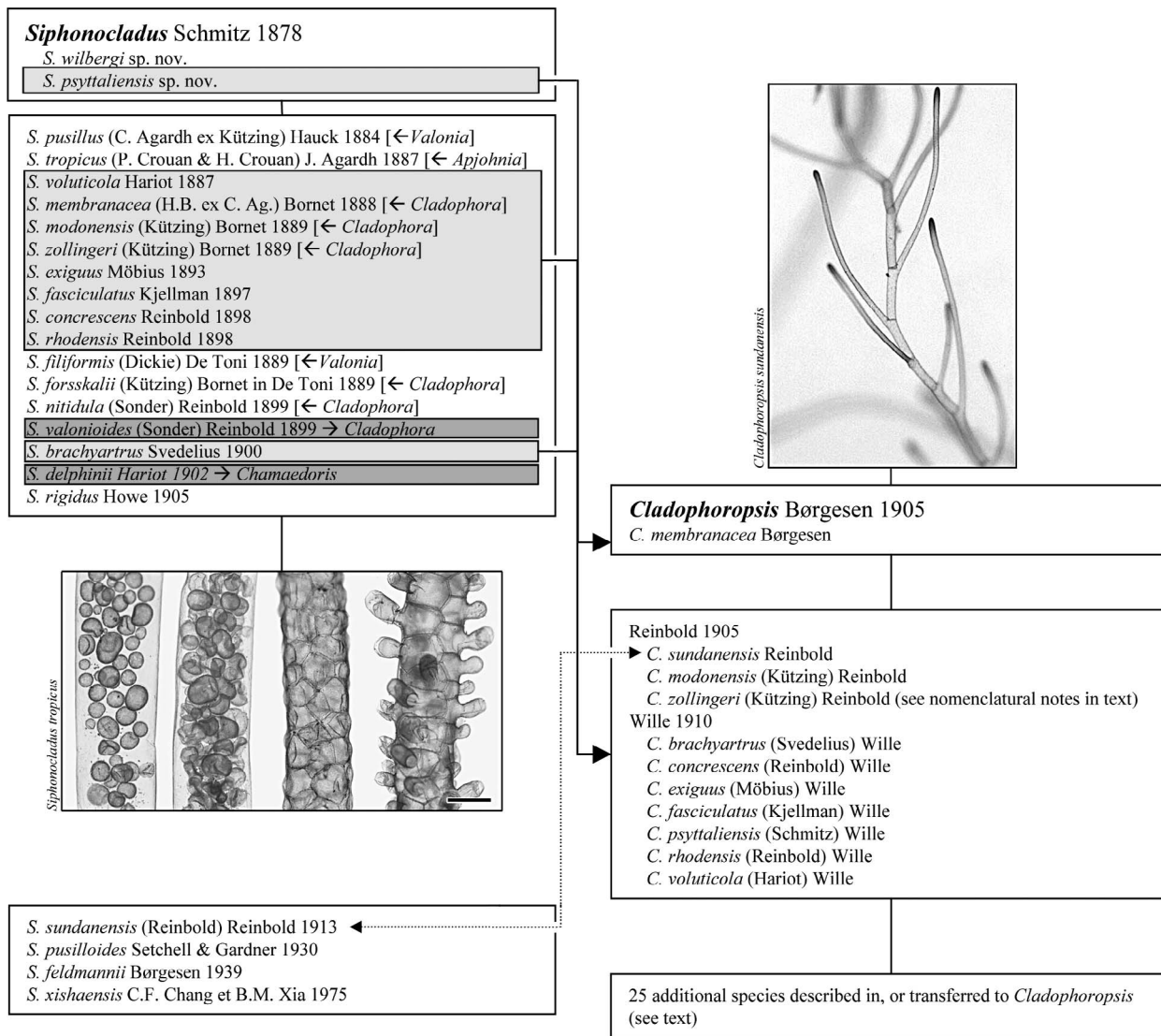


Fig. 1. Diagram showing the nomenclatural relationship between *Cladophoropsis* and *Siphonocladus*. Inserted photographs illustrating different stages of segregative cell division in *Siphonocladus* and the typical branching pattern of *Cladophoropsis*.

Howe and *C. javanica* (Kützing) P. Silva are allied to species of the *Cladophora* section *Longi-articulatae*.

The nomenclatural and taxonomic relationship between *Cladophoropsis* and *Siphonocladus* is somewhat puzzling. *Siphonocladus* was created by Schmitz (1879) to accommodate two new species, *S. wilbergi* Schmitz and *S. psyttaliensis*, with filamentous branched thalli and laterals lacking basal cross walls. In the following years, 17 additional species were described or transferred (mainly from *Cladophora* or *Valonia*) to *Siphonocladus* (Fig. 1). Later Børgesen (1905) redefined *Siphonocladus* and suggested the transfer of the majority of its species to his new genus *Cladophoropsis*. Børgesen distinguished *Siphonocladus* from *Cladophoropsis* by its large clavate cells with basal annular constrictions producing laterals by segregative cell division in all directions (Table 1). Based on this criterion, 10 *Siphonocladus* species were transferred to *Cladophoropsis* (Børgesen 1905; Reinbold 1905; Wille 1910); one other species, *S. delphinii* Hariot, was placed in *Chamaedoris* by Feldmann & Børgesen (in Børgesen 1940),

and *S. valonioides* (Sonder) Reinbold was returned to *Cladophora* by Kützing (1849: 391). Only three additional *Siphonocladus* species have been described since 1905. To this day the separate recognition of *Cladophoropsis* and *Siphonocladus* has been generally accepted, but the taxonomic boundaries and the relationship between the genera have become unclear. Of the 10 *Siphonocladus* species recognized today, only five apparently meet the generic criteria of Børgesen (1905): the type species *S. wilbergi* [a synonym of *S. pusillus* (C. Agardh ex Kützing) Hauck according to Hauck (1885)], *S. feldmannii* Børgesen, *S. filiformis* (Dickie) De Toni, *S. pusilloides* Setchell & N.L. Gardner and *S. tropicus* (Crouan) J. Agardh. The systematic positions of *S. rigidus* M.A. Howe and the morphologically allied *S. xishaensis* C.F. Chang & B.M. Xia remain doubtful. *Siphonocladus rigidus* was originally assigned to *Siphonocladus* based on segregative cell division, although Howe (1905) was not completely confident about this systematic position considering the numerous differences between *S. rigidus* and *S. tropicus* such as the lack

Table 1. Comparison of *Cladophoropsis sensu stricto*, *Cladophora herpestica* and *Siphonocladus*.

	<i>Cladophoropsis s.s.</i>	<i>Cladophora herpestica</i>	<i>Siphonocladus</i>
Phylogenetic relationship	closely related with <i>Boodlea</i> , <i>Phylodictyon</i> , <i>Struveopsis</i> , <i>Struvea</i> and <i>Chameadoris</i>	allied with <i>Cladophora</i> section <i>Longi-articulatae</i>	related with <i>Boergesenia</i> and <i>Ernodesmis</i>
Mode of cell division	centripetal invagination of the cell walls (occasionally segregative)	exclusively centripetal invagination of the cell walls	exclusively segregative cell division
Rhizoidal types (see Fig. 2)	mainly type-1 and -3, occasionally type-2	mainly type-2	exclusively type-1
Tenacular cells (see Fig. 2)	present in most species (type-1 or -3)	absent	absent
Crystalline cell inclusions	prismatic CaOx crystals present; protein crystals absent	CaOx crystals absent; tetrahedral protein crystals present	octahedral CaOx crystals, rare; protein crystals absent

of basal annular constrictions. Two of the remaining species, *S. forsskalii* (Kützing) Bornet *ex* De Toni and *S. nitidula* (Sonder) Reinbold, are characterized by a typical *Cladophora*-type architecture and need to be returned to that genus.

Many authors have emphasized the need of a monographic treatment of the genus *Cladophoropsis* and pointed out that many of the described species may prove to be untenable (Egerod 1971, 1975; Womersley 1984; Sartoni 1992). This study aims to reassess the genus based on detailed morphological investigations and recent molecular evidence, examine the morphological variation within *Cladophoropsis*, determine the number of recognized morphospecies and provide accurate descriptions and illustrations.

MATERIAL AND METHODS

Extensive field collections were made by Eric Coppejans and coworkers in various regions of the (sub)tropical Indo-West Pacific from 1980 onwards; these herbarium numbers are deposited in GENT and prefixed by 'Copp & PvR' (seaweeds from Papua New Guinea, collected by Eric Coppejans and Willem Prud'homme van Reine), 'FL' (collections of Frederik Leliaert), 'HEC' (herbarium of Eric Coppejans), 'HOD' (herbarium of Olivier Dargent), 'KZN' (collections from Kwa-Zulu-Natal, South Africa), 'MAS' (collections from Masirah, Oman of Tom Schils), 'ODC' (collections of Olivier De Clerck), 'PH' (Philippine collections of Leliaert, Liao and Dargent), 'SEY' (Seychelles collection of Coppejans, Kooistra and Audiffred), 'Snellius-II' (collections from the Snellius-II expedition) or 'SOC' (Socotra collection of Leliaert). Other collections, including type specimens, were studied from various herbaria (herbarium abbreviations follow Holmgren *et al.* 1990). Liquid-preserved material and rehydrated herbarium specimens were examined with a light microscope, after portions were prepared on glass microscopic slides and stained with 1% methylene blue. Drawings were made with a camera lucida on a Leitz-Dioplan bright-field light microscope (Leitz, Wetzlar, Germany). Photographs were taken with an Olympus-DP50 digital camera (Olympus, Tokyo, Japan) mounted on the microscope. Cells were also inspected for crystalline inclusions, as the presence and morphologies of these structures have been found to be highly species specific in the Cladophorophyceae. The presence of calcium oxalate crystals were examined using differential interference (Nomarski) contrast for characteristic crystalline birefringence, while protein crystalloids were stained with aniline blue (Leliaert & Coppejans 2004).

The species are presented alphabetically. For each species, the reference to the original description is provided along with other relevant references, followed by nomenclatural and taxonomic synonyms. Information on typification is given; type specimens that have been examined in this study are indicated with an exclamation mark (!) after the herbarium abbreviation. The genus and species accounts are based on the specimens examined in this study (see Appendix 1). Distribution data and habitat description of the species are based on personal observations, data from specimen labels and verifiable literature data.

RESULTS AND OBSERVATIONS

Circumscription of *Cladophoropsis*

This paper deals with species of *Cladophoropsis sensu stricto* (later referred to as '*Cladophoropsis*'), which is morphologically circumscribed as mat- or cushion-forming plants, attached to the substratum by rhizoids issuing from the proximal pole of the basal cells, by tenacular cells, or by rhizoids formed in any part of the thallus; cell division by centripetal wall ingrowths or occasionally segregative; cells producing a single lateral; older cells occasionally producing secondary laterals; cross walls at the base of the laterals either absent or their formation markedly delayed; reinforcement of the thallus by entangling of the filaments and anastomosis of adjacent filaments by tenacular cells; cells containing prismatic calcium oxalate crystals.

Criteria used for the distinction of morphospecies in *Cladophoropsis*

The 11 criteria used for the distinction of the species in *Cladophoropsis* are summarized in Table 2. (1) *Thallus morphology*: Most *Cladophoropsis* species form mat- or cushion-like thalli, composed of tightly interwoven or loosely entangled filaments. One species, *C. vaucheriformis*, lives associated with a sponge (*Halichondria* sp.) and forms large, tough clumps of variable morphology. (2) *Mode of cell division*: Most *Cladophoropsis* species divide by centripetal invagination of the cell wall (CI), but some species also occasionally divide by segregative cell division (SCD). (3) *Organization of branch systems*: In most species, the cells produce single laterals that are unilaterally organized; older branch systems may become more irregular. In several species, the cells occasionally produce a second, opposite lateral. In some species, the

Table 2. Survey of characters of the six *Cladophoropsis* morphospecies.

	<i>C. macromeres</i>	<i>C. magna</i>	<i>C. membranacea</i>	<i>C. philippinensis</i>	<i>C. sundanensis</i>	<i>C. vaucheritiformis</i>
1. Thallus morphology	mat-forming thalli composed of loosely entangling filaments	mat-forming thalli composed of loosely entangling filaments	cushion- or mat-forming thalli composed of tightly interwoven filaments	cushion-like thalli composed of loosely entangled filaments	cushion-like thalli composed of tightly interwoven filaments	large clumps of variable morphology, associated with sponge tissue
2. Mode of cell division	CI	CI	CI (occasionally SCD)	CI	CI (occasionally SCD)	CI + SCD
3. Organization of branch systems	laterals single, unilaterally organized, not displacing the main axes	laterals single or opposite, unilaterally to irregularly organized, not displacing the main axes frequently	laterals single, unilaterally or irregularly organized, occasionally displacing the main axes frequently	laterals single or opposite, irregularly organized, occasionally displacing the main axes frequently	laterals single or opposite, irregularly organized, not displacing the main axes frequently	branching irregular or filaments siphonous
4. Simultaneous cell division	no	frequently	frequently	frequently	frequently	predominantly
5. Cross walls at the base of the laterals	absent	absent	present in some older branches	present in some older branches	often present in basal and ultimate branches	sometimes present
6. Curvature of cells and branch systems	limited	marked	slight	limited	slight	limited to marked
7a. Mode of thallus attachment (see Fig. 2)	unattached	unknown	type-3 tenacular cells, type-1 rhizoids	generally unattached	type-3 rhizoids, type-3 tenacular cells, type-1 rhizoids	type-3 rhizoids, type-1 rhizoids
7b. Mode of thallus reinforcement (see Fig. 2)	loosely entangling of filaments; anastomosis occasionally by type-3 tenacular cells	loosely entangling of filaments	tightly interweaving of filaments; anastomosis occasionally by type-3 tenacular cells	interweaving of filaments; anastomosis occasionally by type-3 tenacular cells	tightly interweaving of filament; anastomosis occasionally by type-3 rhizoids and type-3 tenacular cells	interweaving of filaments and association with sponge tissue
8a. Apical cell diameter (μm)	(140–) 280–360 (–400)	170–700 μm	(70–) 110–290 (–340)	300–670 (–860)	(40–) 60–120 (–140)	(40–) 55–160 (–210)
8b. Main filament diameter (μm)	280–510	(400–) 500–800	(90–) 220–260 (–280)	430–750 (–1300)	(80–) 180–250	(50–) 130–310 (–455)
9. Cell wall thickness of basal branches	up to 10 μm	up to 20 (–36) μm	up to 10 μm	up to 20 μm	up to 8 μm	up to 40 μm
10. Association with sponge tissue	no	no	no	no	no	yes
11. Shape of the prismatic calcium oxalate crystals	elongate rectangular or trapeziform to needle-shaped	diamond shaped	broad to elongated hexagonal, trapeziform or rectangular, often with curved faces	elongate hexagonal or trapeziform	broad to elongate rectangular, often with curved faces	short to elongate rectangular or trapeziform
Specific characteristics	conspicuous stipe cell with annular constrictions	conspicuous stipe cell with annular constrictions	broad to elongated hexagonal, trapeziform or rectangular, often with curved faces	filaments often two or three cells in width owing to oblique cell divisions	filaments siphonous in many parts of the thallus	filaments siphonous in many parts of the thallus

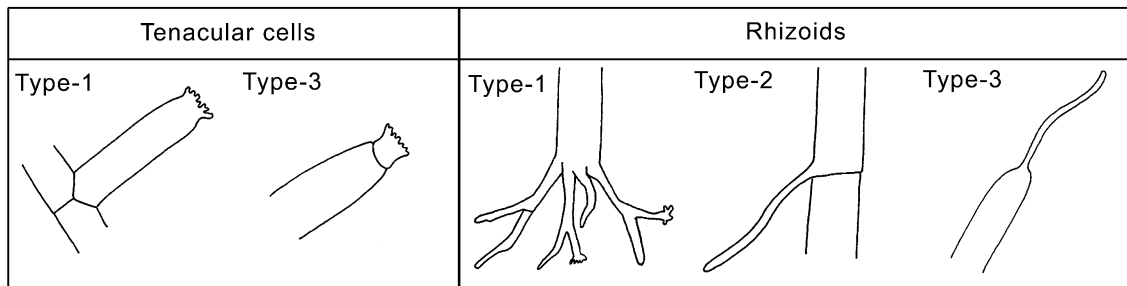


Fig. 2. Types of attachment/reinforcement structures in *Cladophoropsis*. Tenacular cells type-1: crenulate adhesion pads formed distally (or laterally) on apical or lateral cells; Tenacular cells type-3: small tenacular cells produced distally or laterally on apical, lateral or intercalary cells; Rhizoids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

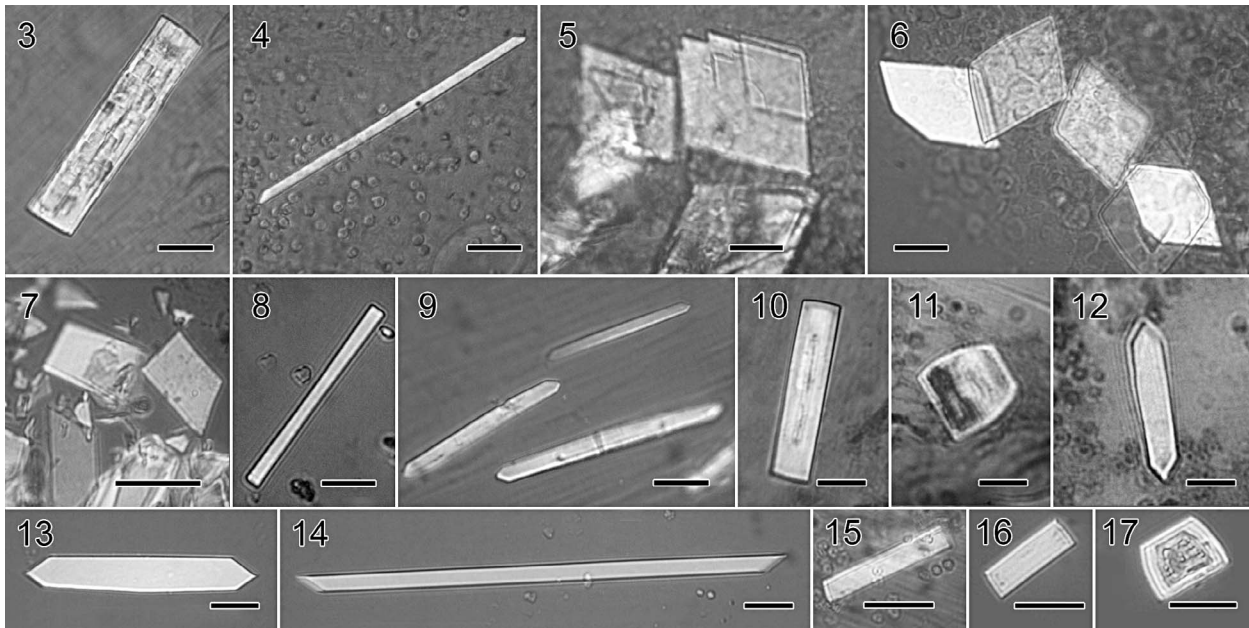
laterals markedly displace the main axis, while in others the laterals clearly remain laterally inserted. (4) *Simultaneous cell division*: In a number of species, apical cells may divide simultaneously into 3–6 cells by centripetal invagination of the cell walls (e.g. *C. membranacea* and *C. philippinensis*) or by segregative cell division (e.g. *C. vaucheriiformis*). Cell division is then followed by more or less equally developing laterals. (5) *Cross walls at the base of the laterals*: Although the absence of cross walls at the base of the laterals is one of the main characteristics of *Cladophoropsis*, some species (e.g. *C. sundanensis*) frequently develop cross walls at the base of older laterals or even in the ultimate branch-systems. (6) *Curvature of cells and branch systems*: In some species, all the cells of the thallus are conspicuously curved (often sinuous), which facilitates entanglement of the filaments (e.g. *C. magna*). Other species (e.g. *C. philippinensis*) have straight or only slightly curved filaments. (7) *Attachment and reinforcement of the thallus*: Structures reinforcing the thallus also often strengthen the attachment of the thallus to the substratum. Most species attach to the substratum by tenacular or rhizoidal cells that develop in any part of the thallus. Some species (e.g. *C. macromeres* and *C. philippinensis*) have only been found unattached or loosely entangled with other macroalgae, while *C. magna* is only known from drift collections (but probably attaches to the substratum by branching, multicellular rhizoids arising from the proximal pole of the stipe or basal cells). Thalli may be reinforced by entangling or interweaving of the filaments, by specialized structures (tenacular or rhizoidal cells) or a combination of the two. Entangling of filaments in the section *Cladophoropsis* is often aided by the curved or sinuous cells or branch systems. Five types of attachment/reinforcement structures can be distinguished in the genus (Fig. 2). Olsen-Stojkovich (1986) defined four types of tenacular cells, two of which occur in *Cladophoropsis* (Fig. 2). *Tenacular cells (type-1)*: Crenulate adhesion pads formed distally or laterally on apical cells or lateral branches, generally attaching to the substratum but occasionally also anastomosing with adjacent filaments. *Tenacular cells (type-3)*: Small tenacular cells produced distally or laterally on apical, lateral or intercalary cells, anastomosing with adjacent filaments; sometimes also attaching to the substratum. Three types of rhizoids can be distinguished. *Rhizoids (type-1)*: Branching, multicellular rhizoids arising from the proximal pole of the stipes or basal cells, reinforcing the attachment to the substratum. Septa are generally absent in young rhizoids and only

formed later in the older ones. *Rhizoids (type-2)*: Rhizoids with or without basal cross walls, issuing from the proximal pole of the cells in any part of the thallus, reinforcing the thallus by entanglement with filaments or attaching to the substratum by hapteroid structures at the tips of these rhizoids. *Rhizoids (type-3)*: Unbranched, septate or aseptate rhizoids, issuing from the tips of apical cells, entangling or anastomosing with adjacent filaments or attaching to the substratum by terminal hapteroid structures. (8) *Cell diameter* (of the apical cells and main axes) is an important taxonomic character, though highly variable. The distinction between delicate species (e.g. *C. sundanensis*) and robust species (e.g. *C. philippinensis*) is obvious, but the existence of a series of taxa with intermediate sizes (e.g. *C. sundanensis*, *C. membranacea*, *C. macromeres*) makes the use of this character by itself often problematic. (9) *Thickness of cell walls* is also a useful but often highly variable character as well. In most species the thickness of the cell walls increases with age, resulting in the basal cells of the thallus being generally thick-walled, but in some delicate species such as *C. membranacea* and *C. sundanensis*, even the basal cells remain thin-walled. (11) *Crystalline cell inclusions* have recently been described in various genera of the Cladophorophyceae, including *Cladophoropsis* (Leliaert & Coppejans 2004). Prismatic calcium oxalate crystals have been observed in all six species.

Based on these morphological criteria, six morphospecies are recognized in this study: *C. macromeres*, *C. magna*, *C. membranacea*, *C. philippinensis*, *C. sundanensis* and *C. vaucheriiformis* (Table 2).

Key to the species of *Cladophoropsis*

- 1.a. Plant associated with a sponge, forming tough clumps of variable morphology (prostrate mats or upright forms with branched subcylindrical processes or thick blade-like outgrowths); branching of the filaments irregular or filaments siphonous in many parts of the thallus *C. vaucheriiformis*
- 1.b. Plants forming cushions or mats, composed of loosely entangling or tightly interwoven filaments, not associated with sponge tissue; branching of the filaments generally unilateral or irregular, sometimes opposite, filaments never siphonous 2
- 2.a. Mat-forming plants composed of loosely entangling filaments; basal (stipe) cell conspicuous, clavate, sin-



Figs 3–17. Prismatic calcium oxalate crystalline cell inclusions.

Figs 3, 4. *Cladophoropsis macromeres* (holotype, MICH). Scale = 10 μm .

Figs 5, 6. *Cladophoropsis magna* (isotype, MEL 3012). Scale = 10 μm .

Figs 7–12. *Cladophoropsis membranacea* [6–7: CmCI TF PdH2 (GENT), 8: lectotype (LD), 9–11: holotype of *Boodlea trukensis* (BISH)]. Scale = 10 μm .

Figs 13, 14. *Cladophoropsis philippinensis* (holotype, MICH). Scale = 10 μm .

Figs 15–17. *Cladophoropsis sundanensis* (lectotype, L). Scale = 10 μm .

- uous, with annular constrictions; cells enclosing diamond shaped crystals *C. magna*
- 2.b. Cushion- or mat-forming thalli lacking conspicuous basal cells with annular constrictions; cells enclosing rectangular, hexagonal, trapeziform or needle-shaped crystals 3
- 3.a. Thalli unattached or loosely entangled with other macroalgae; apical cell diameter generally larger than 280 μm 4
- 3.b. Thalli attached to the substratum by tenacular or rhizoidal cells sprouting from cells in any part of the thallus; apical cell diameter generally smaller than 280 μm 5
- 4.a. Laterals single, unilaterally organized; apical cell diameter (140–) 280–360 (–400) μm ; diameter of the main filaments 280–510 μm *C. macromeres*
- 4.b. Laterals single or opposite, irregularly organized; apical cell diameter 300–670 (–860) μm ; diameter of the main filaments 430–750 (–1300) *C. philippinensis*
- 5.a. Apical cell diameter (70–) 110–290 (–340) μm *C. membranacea*
- 5.b. Apical cell diameter (40–) 60–120 (–140) μm *C. sundanensis*

Taxonomic account

Cladophoropsis Børgeesen

Cladophoropsis Børgeesen (1905: 288), *nom. cons.* vs. *Spongocladia* J.E. Areschoug, 1854 (Papenfuss 1950: 211).

LECTOTYPE: According to Papenfuss (1950: 211): *Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgeesen. Basionym:

Conferva membranacea Hofman Bang ex C. Agardh (1824: 120–121).

Spongocladia J. E. Areschoug (1854: 202), *nom. rej.* vs. *Cladophoropsis* Børgeesen (Papenfuss 1950: 211). TYPE: *Spongocladia vaucheriformis* J.E. Areschoug.

Spongodendron Zanardini (1878: 37). TYPE: *Non designatus*.

***Cladophoropsis macromeres* Taylor**

Figs 3, 4, 18–22

Cladophoropsis macromeres Taylor (1928: 64, pl. 4, figs. 15, 16); Taylor (1960: 118, pl. 2, fig. 2); Littler & Littler (2000: 330, figs on p. 331).

HOLOTYPE: Fort Jefferson (Garden Key), Dry Tortugas, Florida, U.S.A., leg. Taylor 903, MICH!; paratype: same locality, leg. Taylor 1143, NY!

DESCRIPTION: Thallus bright green, forming loose lying mats, up to 15 cm across and 2–10 (–15) cm thick, composed of loosely entangled, coarse filaments. Cell division by centripetal invagination of the cell walls. Growth mainly by apical cell division, followed by cell elongation and limited cell enlargement. The diameter of the thickest part of the main axes about 1–1.3 times that of apical cells. Newly formed cells producing one lateral at the apical pole. Laterals generally lacking basal cross walls (length/width [l/w] ratio of laterals in open connection with the mother cell up to 45). Ultimate branch systems unilateral to irregular (Figs 18–20). Branching limited to the first order. Angle of ramification 20°–55°. Structural reinforcement of the thallus limited, by loosely entangling of the filaments and occasionally by anastomosis of cells by tenacular cells (intermediate forms between type-3 tenacular cells and type-2 rhizoids; Figs 21, 22), produced laterally or basally on the intercalary cells, 40–50 μm in diameter, 170–260 μm long; on average less than 1% of the cells forming a tenacular cell. Apical cells cylindrical, straight, or slightly curved or sinuous, (140–) 280–360 (–400) μm in diameter, up to 22 mm long, l/w ratio up to 60. Laterals 220–300 μm in diameter, up to 5 mm long, l/w ratio up to 17. Main



Figs 18–22. *Cladophoropsis macromeres*.

Figs 18–20. Unilateral to irregular terminal branch systems. (Figs 18, 19: paratype, Taylor 1143, NY; Fig. 20: holotype, MICH). Scale = 1 mm.

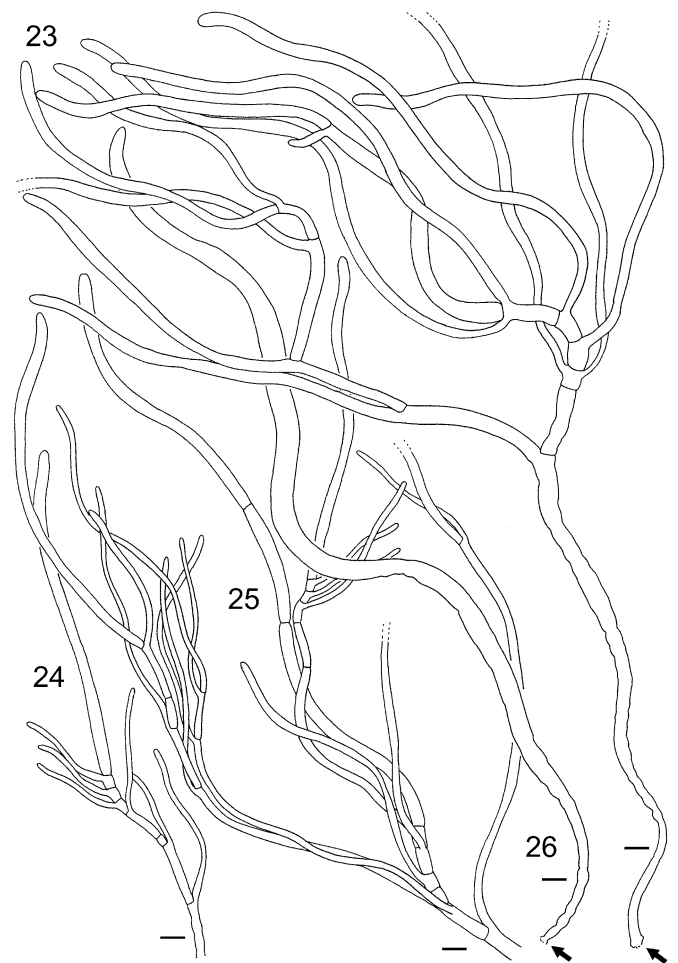
Fig. 21. Anastomosis by a type-3 tenacular cell (holotype, MICH). Scale = 500 μm .

Fig. 22. Detail of a type-3 tenacular cell (holotype, MICH). Scale 50 μm .

axes cylindrical, straight or slightly curved, 280–510 μm in diameter, 100–5500 μm long, l/w ratio 2.3–18. Cell walls 2–4 μm thick in the ultimate branches; up to 10 μm thick in main axes. Chloroplasts polygonal or rounded, forming an open to dense parietal reticulum, 7–10 μm in diameter. Most chloroplasts with a single large pyrenoid, 3.8–6.4 μm in diameter. Prismatic calcium oxalate crystals present in most cells of the thallus, elongate rectangular or trapeziform to needle-shaped, numbers ranging from 1 to several per cell; crystals 1–14 μm broad, up to 150 μm long, l/w ratio 1.5–55.

HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis macromeres* grows in sheltered intertidal pools down to the shallow subtidal (to 5 m depth), free floating, loosely attached to the substratum, or entangled with other attached seaweeds. It is common in the Caribbean Sea and Gulf of Mexico (Littler & Littler, 2000) and has also been recorded from the Canary Islands (Gil-Rodríguez *et al.* 1985: 102, fig. 2) (Fig. 78).

NOTES ON MORPHOLOGY AND TAXONOMY: *Cladophoropsis mac-*



Figs 23–26. *Cladophoropsis magna* (isotype, MEL 666096).

Fig. 23. Thallus consisting of a large basal stipe cell with annular constrictions, giving rise to terminal branch systems; basal attachment structures missing (arrow). Scale = 1 mm.

Figs 24, 25. Terminal branch systems. Scale = 1 mm.

Fig. 26. Young thallus consisting of a single, large cell with basal annular constrictions; basal attachment structures missing (arrow). Scale = 1 mm.

romeres is most easily confused with *C. philippinensis*, *C. magna* and *C. membranacea*. It differs from *C. philippinensis* by the thinner filaments and by the more regular branching pattern with a maximum of one lateral per parent cell. *Cladophoropsis magna* can be distinguished from *C. macromeres* by the presence of conspicuous stipe cells, the occurrence of opposite laterals, the thicker main filaments and the diamond-shaped calcium oxalate crystals. *Cladophoropsis macromeres* differs from *C. membranacea* by the filaments being about twice as thick in the former (Table 2).

Cladophoropsis magna Womersley

Figs 5, 6, 23–26

Cladophoropsis magna Womersley (1955: 390, fig. 7, '*C. magnus*'); Womersley (1984: 185, figs 58C, 59D).

HOLOTYPE: Smoky Bay, west coast of Eyre Peninsula, South Australia, Australia, leg. H.B.S. Womersley A13615, ADU; isotypes distributed under numbers A13615 and A13616 in MEL! and NY!

DESCRIPTION: Thallus light to medium green, forming large, free

floating masses, up to 50 cm across and 7 cm thick, composed of loosely entangled, coarse filaments. Attachment probably by rhizoids produced at the proximal pole of the large stipe cells (type-1 rhizoids) (several stipe cells were found in the material, all with torn basal parts; Figs 23, 26, arrows); tenacular cells absent. Cell division by centripetal invagination of the cell walls. Growth by apical and intercalary cell division, followed by cell elongation and limited cell enlargement. Diameter of the thickest part of the main axes about 1.5–3.2 times that of apical cells. Young thallus consisting of a single large cell with basal annular constrictions, up to 43 mm long (Fig. 26). The apical part of this cell dividing into 4–6 cells, the basal part remaining undivided and forming the stipe cell. Newly formed cells producing one lateral at their distal pole; older cells in the basal part of the thallus occasionally producing a second, often opposite, lateral. Laterals not displacing the main axes, lacking basal cross walls and remaining considerably thinner than the mother cell. Laterals often developing from short axial cells that are clustered in groups of 3–7 (Figs 24, 25). These clusters of short branched cells alternate with long undivided cells. Thallus branching to 3 or 4 orders. Angle of ramification 25°–90°. Apical cells subcylindrical, markedly sinuous, diameter highly variable within a single plant; apical cells of the first- and second-order branches 170–350 µm in diameter at the base, increasing towards their apices to 500–700 µm; apical cells of the higher-order branches 200–250 µm in diameter; length 13.8–17.5 mm; l/w ratio 15–35. Cells of the ultimate branch systems, 150–300 µm in diameter, 1.8–15 mm long, l/w ratio 4–30. Cells of the main filaments, first- and second-order laterals subcylindrical, often with a few annular constrictions, (400–) 500–800 µm in diameter, 0.7–16 mm long, l/w ratio 1.5–30. Stipe cells generally unbranched, clavate, sinuous, with numerous annular constrictions over the entire length, diameter near the base 300–500 µm, increasing distally to 750–1000 (–1200) µm, l/w ratio 25–46. Cell walls 2–8 µm thick in the ultimate branches, up to 20 (–36) µm thick in basal cells and stipe. Chloroplasts polygonal or rounded, 6–16 µm in diameter, forming an open to dense parietal reticulum. Most chloroplasts with a single large pyrenoid, 3.8–7.6 µm in diameter. Diamond-shaped calcium oxalate crystals present in all cells of the thallus, including the stipe cell; numbers ranging from a few to c. 100 per cell; crystals single or clustered (Figs 5, 6), 10–30 µm in diameter, 20–55 µm long, l/w ratio 1.2–1.7.

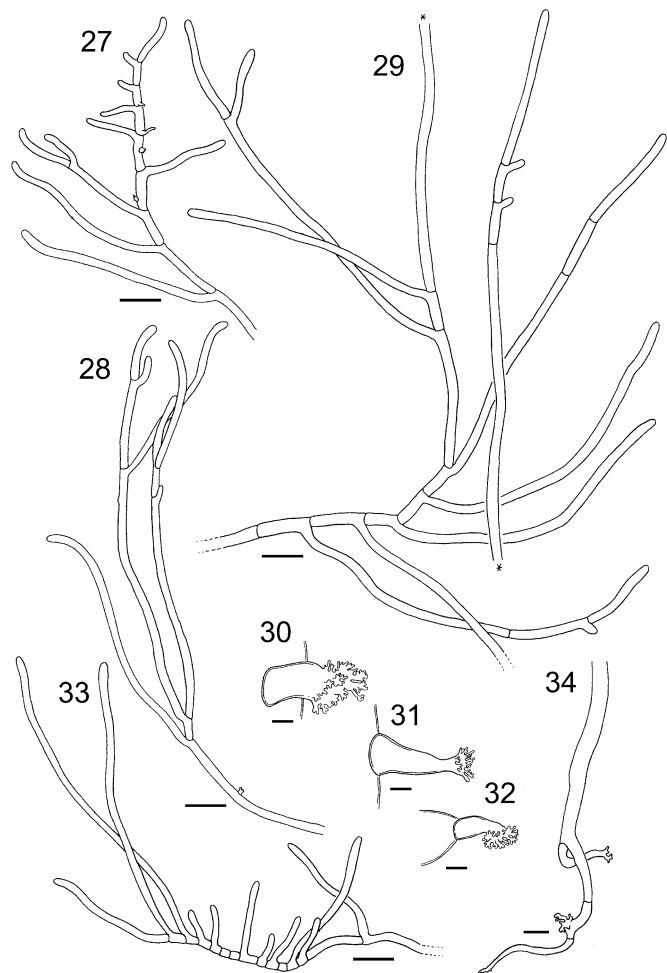
HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis magna* has only been collected from drift but probably grows attached subtidally according to Womersley (1984). The species is known only from Smoky and Denial Bay, on the west coast of Eyre Peninsula, South Australia (Fig. 78).

NOTES ON MORPHOLOGY AND TAXONOMY: *Cladophoropsis magna* can easily be distinguished from other coarse *Cladophoropsis* species by the conspicuous stipe cells with annular constrictions and the presence of diamond-shaped crystalline cell inclusions (Table 2). Surprisingly, the conspicuous stipe cells were not described by Womersley (1955, 1984). Annulated stipe cells and diamond-shaped calcium oxalate crystals also occur in the genera *Chamaedoris peniculum* (J. Ellis & Sölander) Kuntze, *Phyllocladon orientale* (A. Gepp & E. Gepp) Kraft & M.J. Wynne, *P. pulcherrimum* J.E. Gray, *Struvea gardineri* A. Gepp & E. Gepp and *S. plumosa* Sonder (Leliaert 2004; Leliaert & Coppejans 2004).

***Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgesen**

Figs 7–12, 27–34

Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen (1905: 275–290, figs 8–13); Børgesen (1913: 42–48, figs 26–33; 1925: 24, fig. 1); Taylor (1928: 65, pl. 4, fig. 14); Taylor (1960: 117–118, pl. 2, fig. 1, pl. 3, fig. 2); Littler *et al.* (1995: 2, fig. on p. 2); Littler & Littler (2000: 332, figs on p. 333).



Figs 27–34. *Cladophoropsis membranacea*.

Figs 27–29. Unilateral to irregularly organized terminal branch systems; type-3 tenacular cells and short type-2 rhizoids produced by some cells (lectotype, LD). Scale = 500 µm.

Figs 30–32. Type-3 tenacular cells (lectotype, LD). Scale = 500 µm.

Fig. 33. Unilateral terminal branch system (L 996 222 055). Scale = 500 µm.

Fig. 34. Branched type-1 rhizoids arising from the lower poles of the basal cells (L 993 113 339). Scale = 200 µm.

BASIONYM: *Conferva membranacea* Hofman Bang ex C. Agardh (1824: 120–121).

LECTOTYPE: St. Croix, Virgin Islands, collector unknown, LD! 7287. St. Croix is indicated as type locality in the original prologue. Several specimens of this species from that locality are present in LD; one of these, labeled ‘Conf. membranacea Hoffm, Ins St. Crucis’ from the Agardh herbarium, is here indicated as lectotype.

NOMENCLATURAL SYNONYMS: *Cladophora membranacea* (Hofman Bang ex C. Agardh) Kützing (1843: 271); *Aegagropila membranacea* (Hofman Bang ex C. Agardh) Kützing (1854: 145); *Siphonocladus membranacea* (Hofman Bang ex C. Agardh) Bornet, in Askenasy (1888: 6).

TAXONOMIC SYNONYMS

Boodlea kaenana Brand (1904: 190, pl. VI, figs 36–39).

LECTOTYPE: Kaenana point, Hawaii, leg. J.E. Tilden 146, Herb. Stockmayer ex Herb. Brand, B! 09449; isolectotype: B! 09450. Two specimens of *Boodlea kaenana* collected by Mrs. J.E. Tilden from Kaena point, Hawaii are present in B. The most intact specimen is

here designated as lectotype. Both specimens are intermixed with *Cladophora coelothrix*.

Cladophoropsis gerloffii Nizamuddin (1988: 229–234, figs 1–3).

HOLOTYPE: Andulus Beach near Tripoli, Libya, leg. M. Nizamuddin N-1905, B–Alg. 35585.

Boodlea trukensis Trono (1972: 49, pl. 4).

HOLOTYPE: Reef between Falø and Moen Island, Truk Group, Caroline Islands, leg. E.G. Meñez, Doty no. D23458.2, 29 Jul. 1960, BISH! 510376.

DESCRIPTION: Thallus light to medium green, forming compact spongy cushions, up to 12 cm across or moss-like mats, up to 50 cm across, 2–5 (–10) cm high, often sediment-trapping, composed of much ramified, tightly interwoven or loosely entangled filaments. Attachment to the substratum by branching, multicellular rhizoids arising from the proximal pole of the basal cells (type-1 rhizoids, Fig. 34); also by type-3 tenacular cells which are produced distally or laterally on apical or intercalary cells in any part of the thallus, occasionally by rhizoids issuing from the proximal pole of the cells (type-2 rhizoids). Cell division by centripetal invagination of the cell walls or by segregative cell division. Growth mainly by apical cell division and subsequent cell elongation, also by intercalary cell division in the basal parts of the thallus. The diameter of the thickest part of the main axes about 1–1.5 times that of the apical cells. Cell division followed by formation of a single lateral at the distal pole of the newly formed cell (Figs 27–29). Cells sometimes dividing simultaneously into 3–6 cells followed by the formation of more or less equally developing laterals. Older cells frequently producing a second, generally opposite, lateral (Indo-Pacific representatives). Laterals not displacing the main axis. Formation of cross walls at the proximal pole of newly formed laterals markedly delayed, or cross walls absent; laterals in open connection with the mother cell up to 750–5000 μm long, l/w ratio 8–55. Older branches laterally inserted with a steeply inclined cross wall cutting it off from the parent cell. Terminal branch systems unilaterally or irregularly organized; basal branch systems with a more irregular organization. Thallus branching to 2 or 3 (sometimes 4) orders. Angle of ramification 30°–90°. Structural reinforcement of the thallus mainly achieved by interweaving of the filaments; adjacent cells occasionally anastomosing by means of type-1 or -3 tenacular cells (Figs 30–32). On average, 2%–8% of the cells producing a tenacular cell. Zoidangia formed by transformation of apical or intercalary cells in the terminal branch systems, which form a few ob-conical outgrowths, each with an apical pore. Apical cells cylindrical, straight or curved, dimensions highly variable, even within a single thallus, (70–) 110–290 (–340) μm in diameter, 0.7–12.5 (–17.5) mm long, l/w ratio 1.7–70. Cells of the terminal branch systems cylindrical, (90–) 140–290 μm in diameter, 180–5000 μm long. Basal filaments cylindrical, (90–) 220–260 (–280) μm in diameter, 250–1700 (–3000) μm long, l/w ratio 1.3–12. Tenacular cells 80–120 μm in diameter, 180–290 μm long. Cell walls c. 2 μm thick in the terminal branches, up to 5–10 μm thick in the basal filaments. Chloroplasts polygonal, elongated to star-shaped, forming an open parietal reticulum, 2.5–7 μm in diameter with strands spanning up to 20 μm . Each chloroplast containing a single pyrenoid, 1.4–2.6 μm in diameter. Prismatic calcium oxalate crystals extremely variable in morphology, broad to elongated hexagonal, trapeziform or rectangular, often with curved faces (Figs 7–12), present in most cells of the thallus; numbers per cell ranging from 1 to 30 in the apical cells to more than 200 in the cells of the main axes. Calcium oxalate crystals broad to elongated hexagonal, trapeziform or rectangular, often with curved faces, 1.5–10 μm broad, up to 60–90 μm long, l/w ratio 1–15 (–40).

HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis membranacea* grows epilithically as cushions or mat-forming thalli, or loose-lying as *Aegagropila*-like clumps, in exposed or sheltered intertidal to shallow subtidal habitats (occasionally to 10 m depth). The species is widely distributed in the tropical to subtropical seas and especially common in the Atlantic Ocean. In the western Atlantic it is reported from as far

north as Bermuda and as far south as southern Brazil (Wynne 1998). In the eastern Atlantic *C. membranacea* is reported from the Canary Islands, the Cape Verde Islands, and the tropical West African coast, as well as in the Mediterranean Sea (Børgesen 1925; Gallardo *et al.* 1993; van der Strate *et al.* 2002) (Fig. 78). *Cladophoropsis membranacea* has occasionally been reported from the Indo-West Pacific (Kooistra 1993). The Hawaiian record of this species (Egerod 1952: 356, fig. 3) turns out to be a misapplied name for *Cladophora catenata* (Linnaeus) Kützting after examination of the reference specimens collected by Papenfuss (nos. 10502, 10503, 10504, 10505, 10505, 10775, 10776 in UC).

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

Cladophoropsis membranacea can be confused with *C. sundanensis* and *C. macromeres* because of its intermediate cell dimensions. The filaments of *C. macromeres* are about twice as thick, whereas those in *C. sundanensis* are about half the diameter of those in *C. membranacea* (Table 2).

Nizamuddin (1988) distinguished his new species *C. gerloffii* from *C. membranacea* on the basis of differences in branching pattern, position of rhizoidal and tenacular cells and the slightly larger cell diameter. These characters are now known to be extremely variable in *C. membranacea*, and we therefore consider *C. gerloffii* conspecific with *C. membranacea*.

The close morphological affinity of *C. membranacea* with *Boodlea composita* (Harvey) F. Brand has been confirmed by molecular evidence based on ITS and LSU rDNA sequences (Kooistra *et al.* 1993; Wysor 2002; Leliaert *et al.* 2006). These studies have demonstrated that *C. membranacea* is more closely related to *Boodlea composita* and *Phyllocladon anastomosans* (Harvey) Kraft & M.J. Wynne than to the morphologically similar *C. sundanensis*. Recently, van der Strate *et al.* (2002) demonstrated, based on ITS sequence divergence, differential microsatellite amplification and thermal ecotypes, that *C. membranacea* consists of at least three cryptic species in the Atlantic Ocean.

The Indo-Pacific representatives (often referred to as *Boodlea kaenana* or *B. trukensis*) resemble the Atlantic plants in thallus morphology and architecture, mode of thallus reinforcement and crystal morphology but differ by the cells frequently producing opposite pairs of laterals (in the Atlantic plants generally one lateral is formed per parent cell). Indo-Pacific plants may therefore be confused with irregular plants of *Boodlea composita*, from which they can be distinguished by the longer apical cells, the lower abundance of tenacular cells and crystal morphology. Both rectangular and elongate hexagonal crystals occur in *C. membranacea* (both morphologies often occurring within the same thallus or cell), whereas in *B. composita* the cells contain only elongate hexagonal to needle-shaped crystals. The evolutionary relationship between the Indo-Pacific and the Atlantic *C. membranacea* plants remains to be studied.

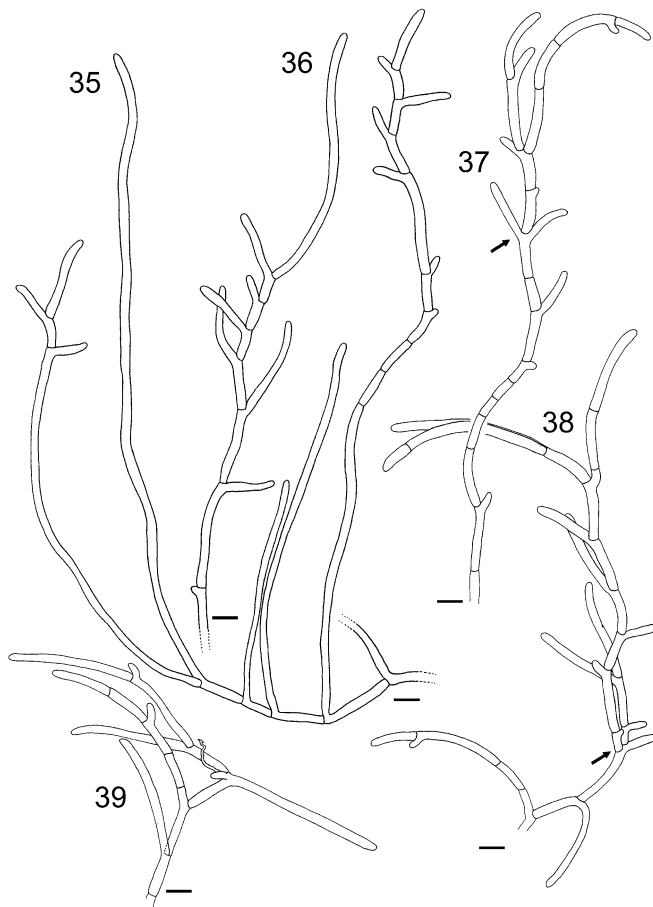


Fig. 35–39. *Cladophoropsis philippinensis*.
Figs 35, 36. Irregularly organized branch systems (holotype, MICH). Scale = 2 mm.
Figs 37–39. Terminal branch systems. Arrow indicating formation of opposite laterals (PH 567). Scale = 2 mm.

Cladophoropsis philippinensis Taylor

Figs 13, 14, 35–39

Cladophoropsis philippinensis Taylor (1961: 58, figs 1–6).

HOLOTYPE: Little Santa Cruz Island, near Zamboanga City, Mindanao, Philippines, leg. H.H. Bartlett 195, MICH!

DESCRIPTION: Thallus light to dark green, forming large masses or tufts, free floating or loosely attached to the substratum, 5–20 cm across, 1–3 cm thick, composed of stiff, loosely entangled, often curved branch systems. Cell division by centripetal invagination of the cell walls. Growth by division of apical and intercalary cells, followed by cell elongation and limited cell enlargement. Diameter of the thickest part of the main axes about 1–1.3 times that of apical cells. Generally, each newly formed subapical or intercalary cell producing one lateral at its distal pole. Apical cells frequently dividing simultaneously into 3–6 cells, followed by cell elongation and formation of more or less equally developing branches (Figs 35, 36). Occasionally opposite pairs of laterals simultaneously initiated from one cell (Fig. 37, arrow). Older cells sometimes producing a second and even a third lateral branch (Fig. 38, arrow). Cross walls at the base of the laterals only formed occasionally in older (basal) parts of the thallus; l/w ratio of laterals in open connection with the mother cell up to 60. Laterals occasionally displacing the main axes, especially in the basal parts of the thallus. Laterals unilateral or irregularly organized in the terminal branch

systems, more irregular lower down. Thallus generally branching up to 2 (sometimes 3) orders. Angle of ramification 40°–90°. Thalli generally unattached; sometimes entangled with other macroalgae or seagrasses, or loosely attached by a small number of type-3 tenacular cells which are produced distally or laterally on terminal or intercalary cells. On average less than 1% of the cells producing a tenacular cell. Apical cells subcylindrical, straight or curved, 300–670 (–860) μm in diameter, 1.3–5.5 mm long, l/w ratio 3–40. Cells of the terminal branch systems subcylindrical, straight or slightly curved, 300–550 (–600) μm in diameter, 1–7 mm long, l/w ratio 3–30. Basal cells subcylindrical, straight, 430–750 (–1300) μm in diameter, l/w ratio 5–10. Cell walls 2–5 μm thick in the cells of the terminal branch systems, up to 20 μm thick in the basal cells. Chloroplasts polygonal, elongated to star-shaped, 3–8 μm in diameter with strands spanning up to 14 μm long, forming an open parietal reticulum. Each chloroplast containing a single pyrenoid, 1.4–2.5 μm in diameter. Large, elongate hexagonal or trapeziform prismatic calcium oxalate crystals present in most cells of the thallus (Figs 13, 14), up to 55 crystals per cell, 2–25 μm broad, up to 170 μm long, l/w ratio 5–40. Star-shaped clusters of fine needle-shaped crystals (possibly composed of silica) present in most cells, 20–35 μm in diameter; up to 8 clusters per cell.

HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis philippinensis* grows in sheltered localities, on sandy substratum, often associated with seagrass beds in the infralittoral fringe to shallow subtidal (to 5 m depth). Until now *C. philippinensis* was only known from the Zamboanga and the Basilan Island area in the Philippines. The Kenyan and Tanzanian specimens are the first records outside the Philippines, indicating that this species possibly has a disjunct Indo-Pacific distribution (Fig. 78).

NOTES ON MORPHOLOGY AND TAXONOMY: *Cladophoropsis philippinensis* somewhat resembles two other coarse *Cladophoropsis* species, *C. macromeres* and *C. magna*. It differs from *C. macromeres* by its much broader filaments and from *C. magna* in its crystal morphology and lack of stipe cells (Table 2).

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

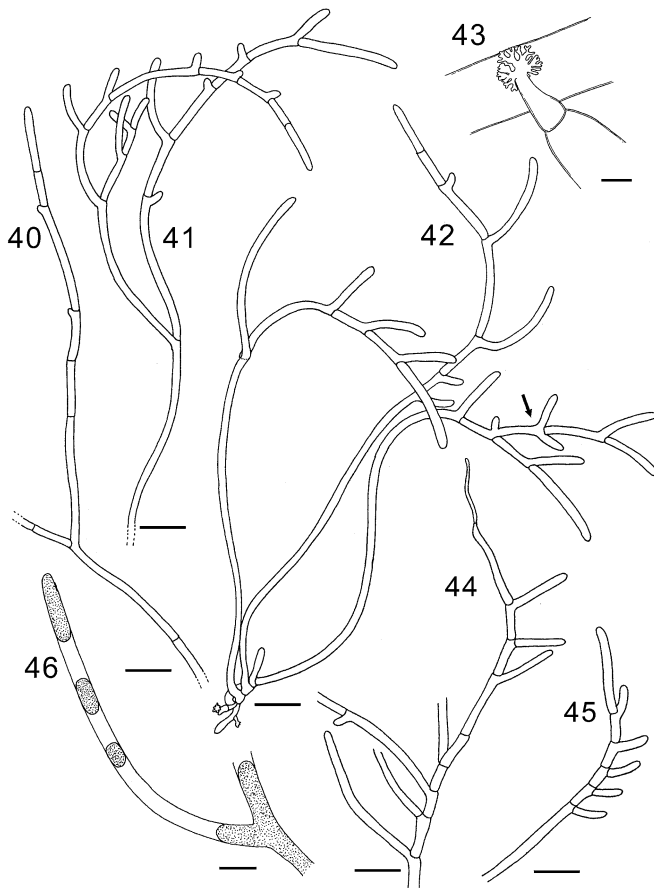
Cladophoropsis sundanensis Reinbold

Figs 15–17, 40–46

Cladophoropsis sundanensis Reinbold (1905: 147); Weber-van Bosse (1913: 77–79, fig. 18); Børgesen (1935: 10–11, fig. 1); Yamada (1944: 11); Cribb (1960: 10); Dawson (1961: 404, pl. 1, figs 9, 10); Egerod (1974: 141, figs 32–36; 1975: 46, figs 8–10); Jaasund (1976: 11, fig. 24); Sartoni (1976: 118, fig. 4; 1986: 365, fig. 6B; 1992: 313); Tseng (1984: 274, pl. 136, fig. 1); De Clerck & Coppejans (1996: 215, fig. 22); Leliaert *et al.* (2001: 452, figs 6–8).

LECTOTYPE: Kangean, Indonesia, leg. Weber-van Bosse, Siboga Expedition s.n., L! 937.279.372. Several locations were indicated in the original prologue: ‘Timor, Labuan, etc.’; only a single specimen from the Siboga Expedition, identified by Reinbold and labeled in his hand was found in L and is here indicated as lectotype.

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



Figs 40–46. *Cladophoropsis sundanensis*.

Figs 40–42. Thallus composed of unilaterally to irregularly organized terminal branch systems; arrow indicating a cell producing a pair of opposite laterals (lectotype, L). Scale = 500 μm .

Fig. 43. Type-3 tenacular cell (lectotype, L). Scale = 50 μm .

Fig. 44. Terminal branch systems with type-3 rhizoids (FL 953). Scale = 500 μm .

Fig. 45. Terminal branch systems with formation of cross walls at the base of newly formed laterals (FL 953). Scale = 500 μm .

Fig. 46. Lateral, undergoing segregative cell division (FL 953). Scale = 200 μm .

TAXONOMIC SYNONYMS

Siphonocladus fasciculatus Kjellman (1897: 36, pl. 7: figs 10–17).

HOLOTYPE: Yokohama, Japan, leg. FR. Kjellman, Vega-expedition, 18 Sep. 1879, UPS! A-000356–251828.

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

Cladophoropsis carolinensis Trono (1972: 48, pl. 3); Kraft (2000: 573, fig. 25A–D); Skelton & South (2002: pl. VII, figs 52–54).

HOLOTYPE: Reef flat near Utwa Village, Kusaie Island, Caroline Islands, leg. E.G. Meñez, Doty no. D23616, 7 Jul. 1960, BISH! 586970.

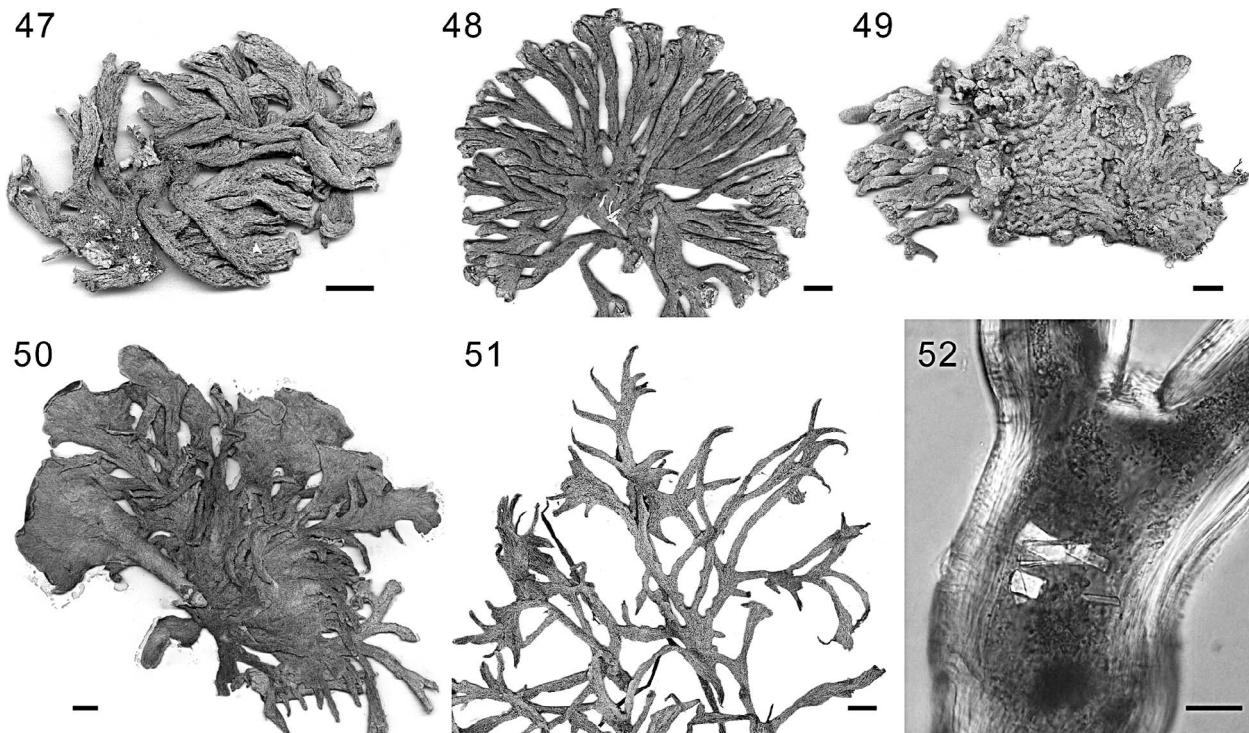
DESCRIPTION: Thallus light to medium green, forming compact spongy cushions or moss-like mats, firmly attached to the substratum, often sand or sediment-trapping, generally 2–7 cm across, occasionally reaching a diameter of up to 15 cm, 1–1.5 cm thick, composed of strongly entangled branch systems. Attachment to the substratum by branched, multicellular rhizoids arising from the proximal pole of the basal cells and other cells in the basal region (type-1 rhizoids; Fig. 42), and by type-3 hapteroidal rhizoids (Fig.

44) or type-3 tenacular cells (Fig. 43) produced at the cell apices in any part of the thallus. Cell division generally by centripetal invagination of the cell walls and occasionally by segregative cell division (Fig. 46). Growth by apical and intercalary cell division, followed by cell elongation and limited cell enlargement. Diameter of the thickest part of the main axes about 1.3–3.5 times that of apical cells. Apical cells generally dividing more or less simultaneously into 3–7 cells followed by the development of laterals (Figs 40–42, 44, 45). Generally, each newly formed cell producing a single branch at its distal pole; occasionally an opposite pair of laterals is initiated simultaneously (Fig. 42, arrow); older (basal) cells also sometimes producing a second lateral. Laterals not displacing the main axes. Cross wall formation at the base of the laterals is usually delayed (Figs 41, 42), but in some terminal branch systems steeply inclined cross walls may be formed almost immediately after formation of laterals (Figs 44, 45); l/w ratio of laterals in open connection with the mother cell up to 40. Branches mostly unilaterally arranged in the terminal branch systems, more irregular proximally. Thallus generally branching to 3 (occasionally 4) orders. Angle of ramification 30°–90°. Structural reinforcement of the thallus achieved by interweaving of the filaments and by anastomosis of the cells by hapteroid rhizoids and tenacular cells (Fig. 43). On average, 1%–4% of the apical cells producing a tenacular cell. Apical cells (sub)cylindrical to slightly tapering, with rounded tip, straight, slightly curved or sinuous, (40–) 60–120 (–140) μm in diameter, length up to 6 mm, l/w ratio ranging from 1.5 to 80. Cells of the terminal branch systems straight or slightly curved, 80–140 μm in diameter, l/w ratio 4–50. Basal filaments usually straight, (80–) 180–250 μm in diameter, l/w ratio 3–40. Cell walls 1–2 μm thick in the cells of the terminal branch systems, (2–) 5–8 μm thick in the main axes and basal cells. Chloroplasts polygonal, elongated or star-shaped, (3–) 4–6 μm in diameter with strands spanning up to 15 μm , forming an open parietal reticulum. Each chloroplast containing a single (occasionally 2) pyrenoid(s), 1.4–2.5 μm in diameter. Prismatic calcium oxalate crystals broad to elongate rectangular, often with curved faces (Figs 15–17), present in most cells of the thallus, up to 7 crystals per cell, 2–15 μm in diameter, 15–25 μm long, l/w ratio 1–6 (–12).

HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis sundanensis* grows epilithically on horizontal to vertical surfaces, often on sand-covered substrata, or epiphytically on various algae, seagrasses and mangrove pneumatophores (e.g. *Sonneratia*), or epizoically on sponges, from the high intertidal to shallow subtidal (down to 3 m depth), on exposed and semiexposed shores, sometimes extending into mangrove creeks (Cribb 1960; Egerod 1974, 1975). The species often grows intermixed with other filamentous Chlorophyta, such as *Boodleopsis pusilla*, *Cladophora* spp. and *Chaetomorpha* spp. The abundance of rhizoids varies greatly between plants. Those growing in the upper tide level produce less rhizoids throughout the thallus than those found at lower tide levels or exposed to surf. *Cladophoropsis sundanensis* is a common and widely distributed species in the Indo-Pacific, Mediterranean Sea and Persian Gulf and has also been reported from the Atlantic Ocean (see Wynne 1998) (Fig. 78).

NOTES ON MORPHOLOGY AND TAXONOMY: The original diagnosis of *Cladophoropsis sundanensis* was rather cryptic, and the species became better known through the description and illustration of Weber-van Bosse (1913) (who listed the species both under *Cladophoropsis* and *Siphonocladus*). *Cladophoropsis sundanensis* can be most easily confused with *C. membranacea*, from which it mainly differs by its smaller cell diameter (Table 2).

Siphonocladus fasciculatus has been treated as a taxonomic synonym of *Cladophoropsis zollingeri* by Yoshida *et al.* (1990: 272). The holotype of *S. fasciculatus*, however, is very different from the latter and characterized by slender filaments



Figs 47–52. *Cladophoropsis vaucheriiformis*.

Fig. 47. Upright thallus with subcylindrical, finger-like, irregularly branched processes (lectotype, S). Scale = 1 cm.

Fig. 48. Upright thallus with cylindrical, finger-like, dichotomously branched, fastigate processes (syntype, S A2570). Scale = 1 cm.

Fig. 49. Prostrate mats with short, papillose protuberances (HEC 9423). Scale = 1 cm.

Fig. 50. Upright thallus with blade-like outgrowths (HEC 11394). Scale = 1 cm.

Fig. 51. Upright thallus with cylindrical, irregularly branched processes with pointed tips (HEC 11135). Scale = 1 cm.

Fig. 52. Prismatic calcium oxalate crystalline cell inclusions in the siphonous filaments; note the extreme thick and lamellate cell walls (FL 954). Scale = 10 μm .

(apical cells 65–130 μm in diameter), thin cell walls (up to 4 μm in basal cells), branching being unilateral or opposite, the presence of tenacular cells, and of elongate prismatic calcium oxalate crystals. Based on this set of characters we consider *C. fasciculatus* to be synonymous with *C. sundanensis*.

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

Cladophoropsis vaucheriiformis (Areschoug) Papenfuss

Figs 47–77

Cladophoropsis vaucheriiformis (Areschoug) Papenfuss (1958: 104, 'vaucheriaeformis'); Cribb (1960: 11–12, pl. 4, figs 1–4); Pham-Hoàng (1969: 446, fig. 4.50); Sartoni (1992: 313–314, figs 9C, 10).

BASIONYM: *Spongocladia vaucheriiformis* Areschoug (1854: 201, 202, pl. 2, 'vaucheriaeformis') [see art. 60.8, ex. 13 of the ICBN

(Greuter *et al.* 2000) for the correct spelling of the species epithet]; Murray & Boodle (1888: 175, figs 8–11); Weber-van Bosse (1890: 79–94, pls. 16, 17); Heydrich (1894: 276–281, pl. 14); Okamura (1928: 189–190, 200–201, pl. 250, figs 5–12); Lucas (1935: 196); Børgesen (1946: 17; 1948: 23, figs A, B); Papenfuss (1950: 208, fig. 1a); Gerloff (1960: 612–614, fig. 1); Jaasund (1976: 13, fig. 25); Tseng (1984: 274, fig. 4 on p. 136), Kraft (2000: 576, fig. 26), Huisman (2000: 241 with fig.).

LECTOTYPE: Mauritius, leg. Areschoug or Pike, S! A2572; syntypes: Mauritius, S! A2569, A2570 & A2571. Several specimens from Mauritius are present in S; one of these, labeled 'Spongocladia vaucheriaeformis Aresch. Ad litora insula Mauritius, dedit Areschoug' from the Areschoug herbarium, is here indicated as lectotype.

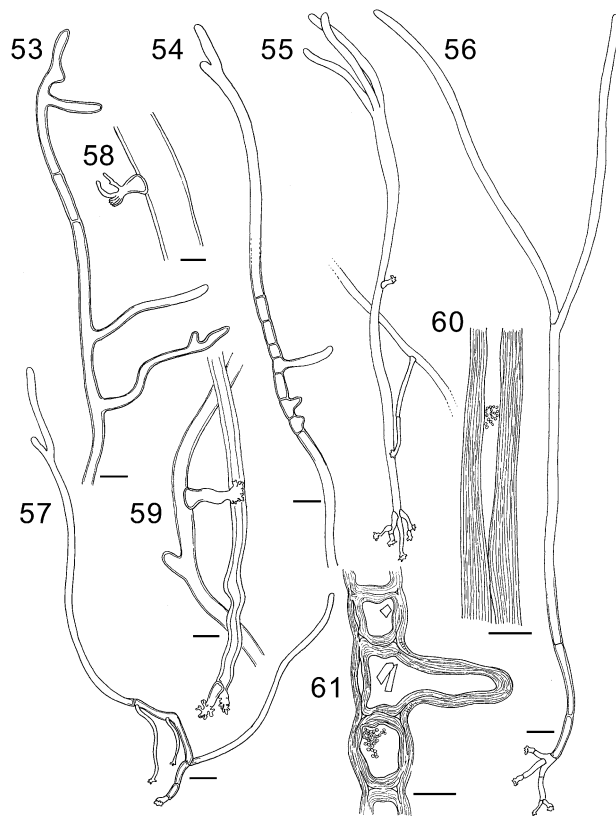
TAXONOMIC SYNONYMS

Spongodendron crassum Zanardini (1878: 38).

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

Spongodendron dichotomum Zanardini (1878: 38).

LECTOTYPE: Sorong, W Irian Jaya, Indonesia, leg. O. Beccari, May 1872, BM! No type locality was indicated in the original prologue ('ubi praecedens'). The single specimen (marked as type in BM) and labelled in Beccari's hand 'Nova-Guinea, Sorong (non Ins. Aru) v.1872' is here indicated as lectotype. The Beccari collections are normally housed in FI, but the type of *S. dichotomum* was sent to



Figs 53–61. *Cladophoropsis vaucheriiformis* (lectotype, S).
Figs 53–57. Terminal branch systems and basal type-1 rhizoids. Scale = 250 μm .
Figs 58, 59. Type-3 tenacular cells. Scale = 100 μm .
Fig. 60. Detail of the very thick, lamellate cell walls. Scale = 50 μm .
Fig. 61. Detail of cells divided by segregative cell division with thick, double and lamellate cell walls; cells with chloroplasts and calcium oxalate crystals. Scale = 50 μm .

Murray & Boodle (BM) by Beccari (Murray & Boodle 1888: 169) and apparently never sent back (Sartoni & Nepi, pers. comm.).

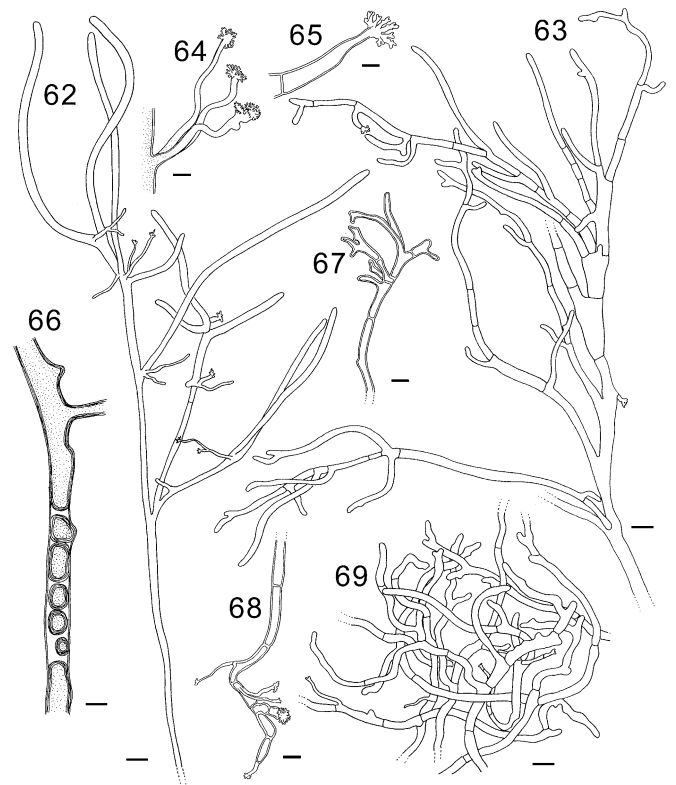
NOMENCLATRURAL SYNONYMS: *Spongocladia dichotoma* (Zanardini) Murray & Boodle (1888: 175); *Cladophoropsis dichotoma* (Zanardini) Papenfuss (1958: 104).

Spongocladia neocaledonica Grunow ex G. Murray & Boodle (1888: 175).

HOLOTYPE: Poro, New Caledonia, leg. Grunow 3558, 9 Oct. 1884, W!; isotype in BM!

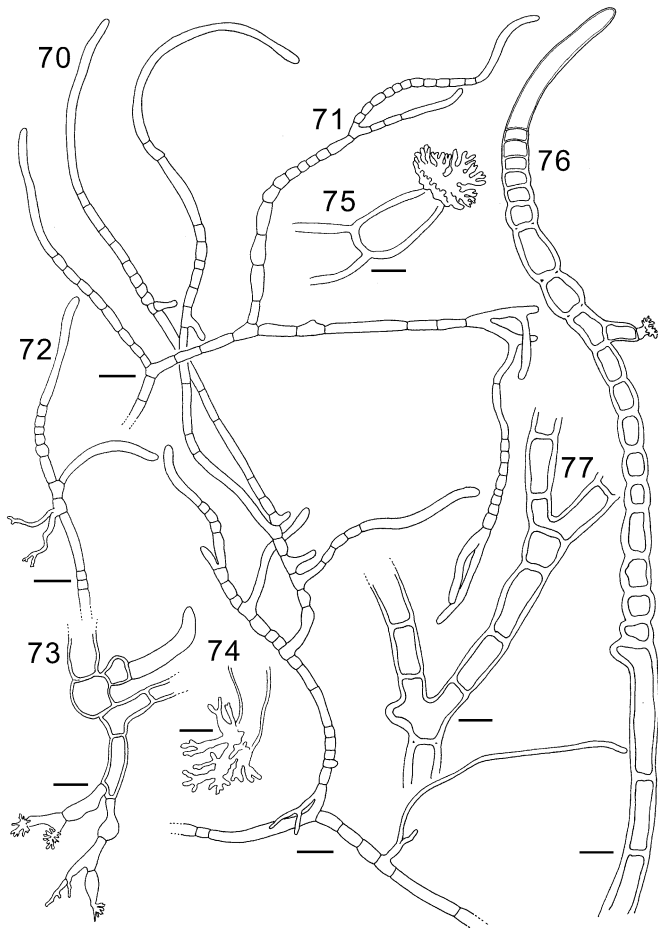
NOMENCLATRURAL SYNONYM: *Cladophoropsis neocaledonica* (Grunow ex G. Murray & Boodle) Papenfuss (1958: 104).

DESCRIPTION: Thallus dull green, forming large tough clumps of variable morphology, up to 50 cm across and up to 15 (–20) cm high, consisting of numerous individual plants, each composed of much ramified and entangling filaments (Fig. 69), living associated with a *Halichondria* species (Porifera) (R. van Soest, pers. comm.). Thallus morphology ranging from prostrate mats, with or without short, papillous protuberances (Fig. 49), to upright forms with subcylindrical, finger-like, dichotomously branched, fastigiata processes, 2–10 (–20) mm in diameter and up to 9 cm long (Figs 47, 48), irregularly branching processes, 2–5 mm in diameter, with pointed tips, up to 20 cm high (Fig. 51), or thick blade-like outgrowths, up to 5 cm broad and 15 cm long (Fig. 50). Adjacent cylindrical processes frequently anastomosing by type-3 tenacular cells or rhizoidal cells. Cell division by centripetal invagination of the cell walls or by segregative cell division (Fig. 66). Growth mainly by elongation



Figs 62–69. *Cladophoropsis vaucheriiformis*.
Fig. 62. Aseptate branch system with numerous rhizoids developing at the base of the laterals (FL 954b). Scale = 250 μm .
Fig. 63. Terminal branch systems with cross walls and unilateral branches (HEC 10570). Scale = 250 μm .
Figs 64, 65. Rhizoids (type-2) (HEC 11135). Scale = 100 μm .
Fig. 66. Filament dividing by segregative cell division (FL 989). Scale = 100 μm .
Fig. 67. Thick-walled terminal cells (FL 683). Scale = 250 μm .
Fig. 68. Basal type-1 rhizoids (HEC 11394). Scale = 100 μm .
Fig. 69. Entangled filaments (FL 607). Scale = 250 μm .

and branching of the filaments without cell division, resulting in siphonous branch systems (Figs 55, 62), also by apical and intercalary cell division, and subsequent cell elongation (Fig. 76). Diameter of the thickest part of the main axes 0.4–1.2 times that of apical cells. Branching of the filaments irregular and extremely variable, even within a single thallus. Newly formed subapical or intercalary cells possibly producing one lateral at their apical or subapical pole (Figs 56, 63). Apical or intercalary cells sometimes dividing by segregative cell division into 3–11 short cells, followed by the formation of more or less equally developing unilateral branches (Figs 54, 70–73). Cross walls at the base of the laterals absent; laterals not displacing the main axes. Branching generally to 2 or 3 orders. Angle of ramification extremely variable, from 25° to 90°. Attachment to the substratum by hapteroidal rhizoids (Figs 56, 57, 68, 74) or tenacular cells. Rhizoids septate or aseptate, most often produced at the proximal pole of the cells, with or without a basal cross wall separating it from the mother cell. Structural reinforcement of the thallus achieved by interweaving and anastomosis of the filaments by numerous tenacular cells or rhizoids (Figs 58, 59, 64, 65, 75) as well as through investment of the fine tissues of the associated sponge. Cell dimensions extremely variable, even within a single cell. Filaments of the ultimate branch systems subcylindrical to irregularly shaped, straight to strongly curved, (40–) 55–160 (–210) μm in diameter, 225 μm –12.5 mm long. Cells of the main axes (50–) 130–310 (–455) μm in diameter. Basal cells long and slender, 40–95 μm in diameter, up to 14 mm long. Cell walls very variable in thickness, in apical cells ranging from 2 to 30 μm , in the main axes up to 40 μm and often closing the entire



Figs 70–77. *Cladophoropsis vaucheriiformis* (FL 954).

Figs 70–72. Terminal branch systems composed of short cells. Scale = 250 μm .

Fig. 73. Basal type-1 rhizoids. Scale = 100 μm .

Fig. 74. Detail of hapteroidal tip of a basal rhizoid. Scale = 25 μm .

Fig. 75. Type-3 tenacular cell. Scale = 25 μm .

Fig. 76. Apical cell division and subsequent cell elongation in terminal filament. Scale = 100 μm .

Fig. 77. Pseudodichotomous branching. Scale = 100 μm .

cell (Fig. 60). Thick cell walls coarsely striated longitudinally (Figs 60, 61) and less markedly in the transverse direction. Chloroplasts elongated or star shaped, 2.5–6.5 μm in diameter with shoots spanning up to 20 μm , forming an open parietal reticulum. Most chloroplasts with a single pyrenoid, 1.9–2.5 μm in diameter. Short to elongate rectangular or trapeziform prismatic calcium oxalate crystals present in a few cells (Figs 52, 61), 3–18 μm in diameter, up to 15–50 μm long, l/w ratio 1–8; number of crystals per cell 1–5 (–10).

HABITAT AND GEOGRAPHICAL DISTRIBUTION: *Cladophoropsis vaucheriiformis* generally grows epilithically, occasionally on calcified seaweeds (e.g. *Halimeda opuntia*) in the mid-intertidal to shallow subtidal (down to 1 m depth). The species is widely distributed in the tropical to subtropical Indo-West Pacific (Papenfuss 1950; Gerloff 1960; Sartoni 1992; Silva *et al.* 1987, 1996) (Fig. 78).

NOTES ON MORPHOLOGY AND TAXONOMY: *Cladophoropsis vaucheriiformis* is a somewhat unusual member of the genus. Firstly, because of its association with sponge tissue and the resulting tough, spongy thallus morphology. Secondly, be-

cause of the atypical branching pattern, probably as a consequence of the association. The branch systems in many parts of the thallus lack cross walls altogether, resulting in an apparently siphonous architecture. Because of its deviant morphology and anatomy, the systematic position of the species has long been undecided. The species was originally assigned to a separate genus, *Spongocladia* by Areschoug (1854). Later, Murray & Boodle (1888) merged *Spongodendron* Zanardini (including the sponge-associated species *S. crassum* and *S. dichotoma*) with *Spongocladia*, which in its turn, was merged with *Cladophoropsis* by Papenfuss (1958: 104) (without giving any justification), who proposed to conserve the latter. Several authors accepted the merger (Cribb 1960; Sartoni 1992), while others did not. Millar & Kraft (1994: 430), for example, argued that segregative cell division can be used as a character to discriminate the two genera. We choose to place *C. vaucheriiformis* in *Cladophoropsis* based on the following morphological grounds: (1) the presence of tenacular cells; (2) the presence of prismatic calcium oxalate crystals in the cells; and (3) the typical ‘*Cladophoropsis*’-type branching which can be observed in at least some parts of the thallus. Based on SSU nrDNA gene sequence analysis, Hanyuda *et al.* (2002) demonstrated a close relationship between *C. vaucheriiformis* and *Chamaedoris peniculum*, with *Cladophoropsis membranacea* forming a sister taxon.

Cladophoropsis neocaledonica was distinguished from *C. vaucheriiformis* by Murray & Boodle (1888) and Womersley & Bailey (1970) by the unbranched macroscopic thallus and by the larger filament diameter. Cribb (1960), who observed intermediate morphologies in his Queensland material and found similar cell diameters in both species, argued that thallus morphology and differences in cell diameter can hardly be regarded as distinguishing characters and therefore reduced *C. neocaledonica* to a synonym of *C. vaucheriiformis*.

The conspecificity of *S. crassum* and *C. vaucheriiformis* was proposed by Murray & Boodle (1888), who compared the types of both species. Zanardini (1878) distinguished *S. dichotomum* from *C. vaucheriiformis* solely by its more slender thallus. Taking into account the great morphological plasticity of *C. vaucheriiformis* (Figs 47–51), we propose to also reduce this species to a synonym of *C. vaucheriiformis*.

Cladophoropsis taxa of uncertain systematic affinity

Four species of *Cladophoropsis* (*C. brachyartrus*, *C. gracillima*, *C. psyttaliensis* and *C. voluticula*) are of doubtful taxonomic affinity and are therefore not considered in the present study.

Cladophoropsis brachyartrus (Svedelius) Wille (1910: 116). Basionym: *Siphonocladus brachyartrus* Svedelius (1900: 304–311, pl. 16: figs 2, 3; pl. 18; text fig. 3). Holotype: Puerto Angosto, Isla Desolacion, Chile, leg. P. Dusén.

The Dusén collection is usually housed in S or UPS but in both herbaria specimens of *S. brachyartrus* were untraceable. Svedelius (1900) depicts his new species with a typical *Cladophoropsis* or *Cladophora* type architecture (delay of cross wall formation at the base of the laterals and rhizoids issuing from the proximal pole of the basal cells). The detailed illustrations also shows typical cladophoralean chloroplasts, forming a parietal network. In many but not all of the chloroplasts, there is a single pyrenoid. Remarkably, the illustrated pyrenoids are not bilenticular, like in most members of the Cladophorophyceae, but clearly polypyramidal, a characteristic feature of the *Aegagropila*-clade (Hanyuda *et al.* 2002). Moreover, the fact that *C. brachyartrus* has an Antarctic to subantarctic distribution (Hylmö

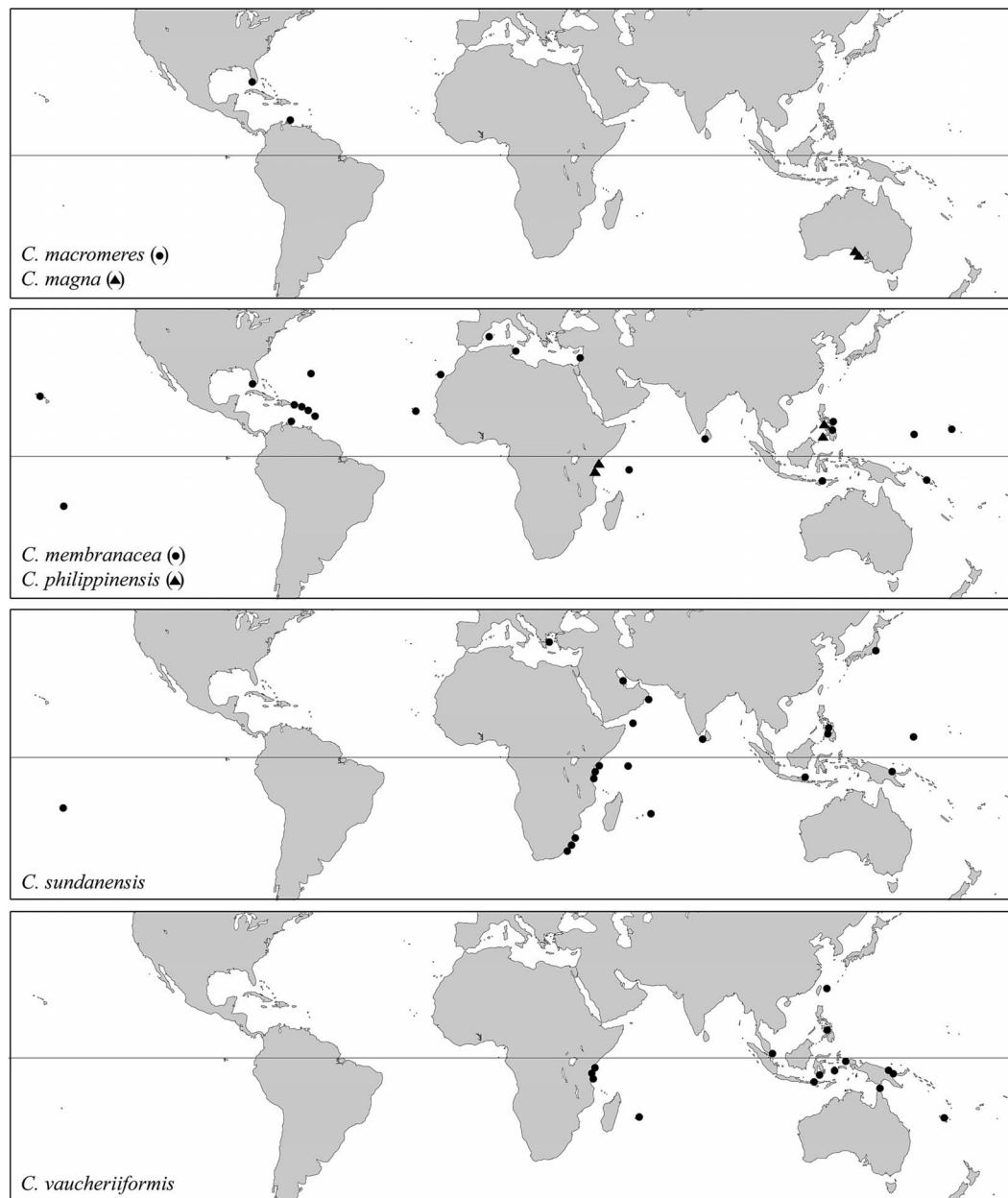


Fig. 78. Geographical distribution of the six *Cladophoropsis* morphospecies based on the investigated specimens.

1938; Papenfuss 1964) makes its relationship with the tropical to subtropical genus *Cladophoropsis* unlikely.

Cladophoropsis gracillima Dawson (1950: 149, figs 12, 13). Holotype: Punta Palmilla, Baja California Sur, Mexico, leg. Dawson 3233, 7 Nov. 1946, AHFH 36937; isotypes in BM! and NY!

The systematic position of this species is uncertain because of the absence of calcium oxalate crystals and the chloroplasts containing up to four pyrenoids. *Cladophoropsis gracillima* is described and illustrated by Leliaert (2004).

Cladophoropsis psyttaliensis (Schmitz) Wille, in Engler & Prantl (1910: 116). Basionym: *Siphonocladus psyttaliensis* Schmitz (1879: 20). Holotype: Psyttalia Island, Gulf of Athens, Greece; paratypes: Gulf of Saronikos, Greece and Gulf of Naples, Italy; leg. probably F. Schmitz.

The type material is untraceable (possibly destroyed in B), and the original description is too vague to permit a conclusion as to its identity. As far as we know, this species has been mentioned only once since its original description (Gerloff & Geissler, 1974).

Cladophoropsis voluticola (Hariot) Wille, in Engler & Prantl (1910:

116). Basionym: *Siphonocladus voluticola* Hariot (1887: 56, fig. 1) (misspelled 'voluticula', correct in caption to fig. 1). Holotype: on rejected shells of *Voluta magellanica*, Orange Bay, Tierra del Feugo, Chile, leg. M.P. Hariot, s.n., PC!

The cell dimensions of this minute filamentous species (cell diameter 6–8 μm) are so small that its taxonomic position in the Cladophorophyceae is questionable. The holotype material consists of some shells with green crusts, but no filaments could be observed.

Taxa excluded from *Cladophoropsis*

Nine *Cladophoropsis* species are found to be referable to various *Cladophora* species: *Cladophoropsis pallida* (= *Cladophora albida*), *C. concrescens*, *C. fallax*, *C. limicola*, *C. mondonensis*, *C. peruviana* (*Cladophora coelothrix*), *C. rhodensis* (= *Cladophora laetevirens*), *C. infestans* (= *Cladophora socialis*) and *C. luxurians* (= *Cladophora catenata*); four others belong to other genera: *Cladophoropsis lyallii* (*Wittrockiella*),

C. bulbosa (*Chlorodesmis*), *C. palauensis* (*Siphonocladus*) and *C. robusta* (*Valoniopsis*). *Cladophoropsis herpestica* is excluded from the genus and returned to its original genus *Cladophora* based on molecular and morphological evidence. Six species are found to be referable to *Cladophora herpestica*: *C. adhaerens*, *C. corallinicola*, *C. coriacea*, *C. exiguus*, *C. howensis* and *C. javanica*.

Cladophoropsis adhaerens Gilbert (1962: 136, fig. 2). Holotype: between Natatorium & Elks Club, Waikiki, Honolulu, Oahu, Hawaii, leg. W.J. Gilbert 9410, 9 Apr. 1959, MICH!

Gilbert (1962) distinguished his new species from *Cladophoropsis herpestica* (= *Cladophora herpestica*, see below) by its preference for shaded habitats, which he considered to be unique in the genus. Since shaded localities are now known to fall within the ecological range of the *Cladophora herpestica* and because the holotype of *Cladophoropsis adhaerens* is morphologically indistinguishable from this species, both taxa are here considered conspecific.

Cladophoropsis bulbosa Womersley (1955: 391, figs 8, 9). Holotype: Queenscliff, Victoria, Australia, leg. Sonder 3; MEL! Nomenclatural synonym: *Chlorodesmis bulbosa* (Womersley) Ducker (1965: 149, figs 1–4).

This species was moved to *Chlorodesmis* by Ducker (1965) and later reduced to a synonym of *Chlorodesmis baculifera* (Ducker 1966).

Cladophoropsis concrescens (Reinbold) Wille, in Engler & Prantl (1910: 116). Basionym: *Siphonocladus concrescens* Reinbold (1898: (88)). Lectotype: Rhodos Island, Greece, leg. J. Nemetz 46, M! 0066781.

The lectotype of this species is referable to *Cladophora coelothrix*.

Cladophoropsis corallinicola Kajimura (1987: 178, figs 1–6). Holotype: Off Tsudo, Oki Island, Japan, 40 m depth, leg. Kajimura, 31 May 1985, OS 9900, TNS; topotype: 20 m depth on *Lithothamnion* sp., leg. Kajimura, 7 Jan. 1993, BM!

Apart from the aberrant ecology of *C. corallinicola* (growing in deep water, down to a depth of 40 m, on crustose coralline rhodophytes) it is morphologically indistinguishable from *Cladophora herpestica* (see below).

Cladophoropsis coriacea Yendo (1920: 1). Lectotype: Osezaki, Goto Islands, Nagasaki Prefecture, Japan, collector unknown, 6 Aug. 1916, TI in SAP; syntype: Kojima, Tamanoura, Goto Islands, Nagasaki Prefecture, collector unknown, 8 Aug. 1916, TI in SAP.

Okamura (1921: 76), who examined the authentic material of *C. coriacea*, considered this species conspecific with *Cladophora herpestica* (see below).

Cladophoropsis exiguus (Möbius) Wille, in Engler & Prantl (1910: 116). Basionym: *Siphonocladus exiguus* Möbius (1893: 129, pl. 9: figs 9a–d). Type: Coast of Semarang, Java, Indonesia, leg. F. Benecke.

The location of the type material could not be retrieved. The description of *C. exiguus* is based on juvenile thalli. Branching pattern and the presence of descending rhizoids issuing from the proximal pole of most cells indicates that this species most likely belongs to *Cladophora herpestica* (see below).

Cladophoropsis fallax Schiffner (1933: 304, figs 10–19). Holotype: Lacroma Island, near Ragusa (Dubrovnic), South Dalmatia, Croatia, leg. F. Berger, Schiffner Algae Marinae no. 964, NY!; isotype in BM! and MICH!

The type material of *Cladophoropsis fallax* is morphologically indistinguishable from *Cladophora coelothrix* Kützing and therefore reduced to a synonym of the latter.

Cladophoropsis herpestica (Montagne) Howe (1914: 31). Basionym: *Cladophora herpestica* (Montagne) Kützing (1849: 415). Basionym: *Conferva herpestica* Montagne (1842: 15). Lectotype: New Zealand, leg. Hombron s.n., PC! herbier général, folder 48; isotype in NY! Nomenclatural synonyms: *Aegagropila herpestica* (Montagne) Kützing (1854: 14).

Cladophoropsis herpestica (including *C. javanica*, see below) is excluded from the genus based on molecular and morphological evidence. The species lacks CaOx crystals, but the cells contain tetrahedral protein crystals, similar to those found in some species of *Cladophora*

section Longi-articulatae (Jonsson 1962; van den Hoek & Chihara 2000; Leliaert & Coppejans 2004). *Cladophoropsis herpestica* is furthermore characterized by rhizoids issuing from the proximal pole of nearly every cell of the thallus (including the subapical cells). This type of rhizoid formation is also found in some species of the *Cladophora* section Longi-articulatae (e.g. *C. minisakii*: van den Hoek & Chihara: 108, fig. 49). Rhizoids issuing from the base of the cells also occur in some *Cladophoropsis (sensu stricto)* species, but only in the basal parts of the thallus. Therefore, we adopt *Cladophora herpestica* for this entity. Table 1 summarizes the morphological differences between *Cladophoropsis (sensu stricto)* and *Cladophora herpestica*. Apart from *Cladophoropsis javanica*, five other species are found to be referable to *Cladophora herpestica*: *C. adhaerens*, *C. corallinicola*, *C. coriacea*, *C. exiguus* and *C. howensis*.

Cladophoropsis howensis Lucas (1935: 197). Holotype: Lord Howe Island, leg. Lucas, Jun. 1933, NSW 416126.

Cladophoropsis howensis is morphologically indistinguishable from *Cladophora herpestica* and is therefore regarded as a synonym of the latter by Womersley (1955: 377), Cribb (1960) and Kraft (2000).

Cladophoropsis infestans Setchell (1924: 177, fig. 41). Holotype: Tutuila Island, Samoa, leg. Setchell 1134, NY!; isotype in BM!

The holotype is morphologically indistinguishable from *Cladophora socialis* Kützing and therefore reduced to a synonym of the latter.

Cladophoropsis javanica (Kützing) P. Silva, in Silva *et al.* (1996: 792). Basionym: *Aegagropila javanica* Kützing (1847: 773). Holotype: Java, Indonesia, leg. Zollinger 2379, L! 937.276.41; isotypes in NY! and PC! Nomenclatural synonyms: *Cladophora zollingeri* Kützing (1849: 415). *Aegagropila zollingeri* (Kützing) Kützing (1854: 14, pl. 64: fig. II). *Siphonocladus zollingeri* (Kützing) Bornet *ex De Toni* (1889: 359); *Cladophoropsis zollingeri* (Kützing) Reinbold (1905: 147).

Based on morphometric analyses of a large number of specimens of *C. javanica* and *C. herpestica* (including the types), Leliaert (2004) concluded that there was no morphological basis to separate the two species.

Cladophoropsis limicola Setchell (1924: 176, fig. 40). Holotype locality: Tutuila Island, Samoa, leg. Setchell 1167, NY!

Based on the holotype of *Cladophoropsis limicola*, this mud-inhabiting, estuarine species is referable to *Cladophora coelothrix* as previously suggested by Cribb (1960: 10). *Cladophora coelothrix* is often found in sheltered inner bays or estuaries where it can grow on muddy substratum (van den Hoek 1963: 42; 1982: 48).

Cladophoropsis luxurians Gilbert (1962: 136, fig. 3). Holotype: Shore of Molokai opposite Mokuhooniki Island, Hawaii, leg. W.J. Gilbert, 10077, 6 Jun. 1959; MICH! Nomenclatural synonym: *Cladophora luxurians* (Gilbert) Abbott & Huisman (2003: 275–285).

The type specimen and three other specimens from Hawaii (Oahu, leg. Wilkes, South Pacific Exploring Expedition 1838–1842, NY; Waikiki Beach, Oahu, leg. Tsuda & Chock, 21 Oct. 1965, RT 989, L 01757; Oalm Island, Punaluu, leg. Coppejans, 7 Jun. 1988, HEC 8112, GENT), identified as *C. luxurians* by Gilbert, Tsuda and Coppejans, respectively, are referable to *Cladophora catenata* (Linnaeus) Kützing.

Cladophoropsis lyallii (Harvey) V.J. Chapman (1956: 471). Basionym: *Cladophora lyallii* Harvey (1855: 262, pls CXXI, C). Holotype: Lyall, South Island, New Zealand, collector unknown, BM.

This species was moved to *Wittrockiella* by van den Hoek *et al.* (1984: 45).

Cladophoropsis modonensis (Kützing) Reinbold (1905: 147). Basionym: *Cladophora modonensis* Kützing (1849: 416). Type: Modon, Morea Peninsula, Peloponnesos, Greece, leg. Bory St. Vincent. Specimen dedit amic. Lenormand No. 61. Nomenclatural synonyms: *Cladophora (aegagropila) modonensis* Kützing (1854: 14, table 68A); *Siphonocladus modonensis* (Kützing) Bornet, in De Toni (1889: 359).

According to Reinbold (1905), the cell dimensions of *C. modonensis* fall within the limits of *C. sundanensis*, but the species differs in forming tufts and being flaccid. The location of the type material could not be ascertained, but we examined one specimen identified as *C. modonensis* from the type locality (leg. J.M. Despréaux, BR). This specimen and the drawings based on the authentic material by Kützing (1854: 14, table 68A) demonstrate that *C. modonensis* is characterized by septate laterals and rhizoids developing from the proximal pole of

numerous cells in all parts of the thallus. *Cladophora modonensis* is probably referable to *Cladophora coelothrix* Kützing. Other Mediterranean specimens identified as *C. modonensis* are often referable to *C. membranacea*.

Cladophoropsis palauensis Trono (1972: 47, pl. 2). Holotype: Reef flat, Iwayama Bay, Palau Island, West Caroline, Caroline Islands, leg. E.G. Meñez, Doty no. D15108, BISH! 586962.

The type material of *C. palauensis* falls within the morphological circumscription of *Siphonocladus rigidus* and is here treated as a taxonomic synonym of the latter.

Cladophoropsis pallida Baardseth (1941: 13, figs 3G, 4A). Holotype: Between North Point and Blenden Hall, Inaccessible Island, South Atlantic, leg. Baardseth 354, station 137, 19 Feb. 1938, O!; paratype: Julia Point, Tristan da Cunha, leg. Baardseth 122, station 23, 24 Dec. 1937, O!

The specimen denoted 'Type specimen' by Baardseth (from station 137, Inaccessible) is the one that is illustrated in his fig. 4A. Another sheet gives the specimens from station 23; no collections seem to have been made from the stations 37 and 76 (Per Sunding, pers. comm.). Both specimens most likely belong to *Cladophora albida* (Hudson) Kützing as described by van den Hoek (1963, 1982).

Cladophoropsis peruviana Howe (1914: 30, pl. 2, figs 1–9). Holotype: La Palisada, Peru, leg. Coker, 370, p.p., NY!

This mud-inhabiting species is referable to *Cladophora coelothrix* as previously suggested by Cribb (1960: 10).

Cladophoropsis rhodensis (Reinbold) Wille, in Engler & Prantl (1910: 116). Basionym: *Siphonocladus rhodensis* Reinbold (1898: 88). Holotype: Harbour of Rhodos, Greece, leg. J. Nemetz, 50, M! 0066782; isotypes in BR! and NY!

The holotype represents reduced thalli of *Cladophora laetevirens* (Dillwyn) Kützing.

Cladophoropsis robusta Setchell & Gardner (1924: 714–715, pl. 13; fig. 16). Holotype: Isla Tortuga, Baja California Sur, Mexico, leg. I.M. Johnston 135, CAS in UC 1330. Nomenclatural synonyms: *Pseudostruvea robusta* (Setchell & Gardner) Egerod (1975: 47); *Struveopsis robusta* (Setchell & Gardner) Rhyne & H. Robinson (1968: 470).

The holotype of *C. robusta* does not correspond with its original description and illustration. This specimen is characterized by laterals that are exclusively initiated from lenticular cells, whereas the original illustration of *C. robusta* shows a typical *Struveopsis*-type branching with opposite laterals and delayed cross wall formation (Setchell & Gardner 1924: pl. 13, fig. 16). Thallus architecture, branching mode and cell dimensions of the holotype are in agreement with *Valoniopsis pachynema* (G. Martens) Børgesen. Most records of *Cladophoropsis robusta* (Taylor 1945: 51; Dawson 1961: 404; Wysor 2002: 96, fig. 8, as *Struveopsis*) are to be regarded as misapplied names for *Willeella mexicana* Dawson. The only record of *C. robusta* outside the eastern Pacific (Islam 1976: Bangladesh) represents an unidentifiable *Cladophora* species.

DISCUSSION

Species concepts in *Cladophoropsis*

In this paper, six *Cladophoropsis* species are characterized based on the morphological species concept, which recognizes species by discontinuities in morphological characters. A major predicament in doing so lies in the fact that *Cladophoropsis* plants are relatively simple and that there is only a limited range of morphological characters available for delimitation of species. It is therefore likely that, when applying other features such as characters associated with nucleic acids, physiology, breeding relations or ecology, discrepancies will be found between the morphological and other species concepts (such as the biological and phylogenetic species concept). Indeed, based on inferences from ITS sequence divergence, differential microsatellite amplification and thermal ecotypes,

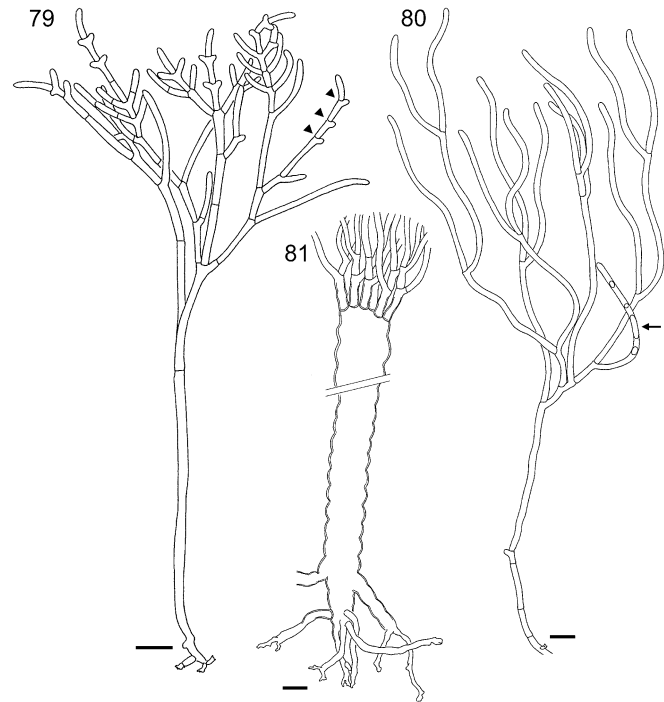
van der Strate *et al.* (2002) revealed that *Cladophoropsis membranacea* consists of at least three cryptic species in the Atlantic Ocean. Comparable data are unavailable now for the other *Cladophoropsis* morphospecies, but the existence of additional cryptic species is not unlikely. On the other hand, it is just as possible that the phenotypic plasticity in some of the recognized morphospecies is in fact larger than presently assumed and consequently that different morphospecies belong to a single genetic entity (phylogenetic species). For example, *C. philippinensis* is here distinguished from *C. membranacea* based on discontinuities of cell dimensions. Still, we cannot rule out the possibility that the range of cell dimensions in *C. membranacea* is more extensive than previously considered and, consequently, that *C. philippinensis* represents a growth form of the latter. The identity of other morphospecies, like *C. magna*, is more solid because they are clearly distinguished by multiple morphological features. Elucidation of (cryptic) genetic diversity within the different *Cladophoropsis* species could be addressed by phylogenetic analysis of additional ITS sequence data or by assessment of genealogical concordance of multiple independent loci.

Systematic position of *Cladophoropsis*

The close relationship between *Cladophoropsis* and the genera *Struvea*, *Phyllocladon*, *Boodlea*, *Struveopsis* and *Chamaedoris* has been demonstrated by morphological as well as molecular evidence (Olsen-Stojkovich 1986; Kooistra *et al.* 1993; Wysor 2002; Leliaert *et al.* 2003, 2006), and several authors have commented on the vague morphological boundaries between these genera (Børgesen 1913; Egerod 1952, 1975; Leliaert *et al.* 1998, 2003). As a result of these fuzzy morphological delineations, there are a number of species crossing generic boundaries (Table 3). For example, *Boodlea composita* can easily be distinguished from *Cladophoropsis* species by the formation of regular opposite lateral branches and the abundant tenacular cells resulting in reticulate thalli. However, in sheltered habitats and in culture conditions, the cells in *Boodlea* only form a single lateral, and tenacular cells are lacking, giving the plants a typical *Cladophoropsis* appearance (Fig. 79). On the other hand, some *Cladophoropsis* species in the field frequently produce opposite laterals (e.g. *C. magna* and *C. philippinensis*) or form tenacular cells (*C. membranacea*). Under certain culture conditions (elevated temperatures and calm conditions), *C. membranacea* may even form reticulate thalli (Wysor 2002). The genera *Struvea* and *Chamaedoris* can easily be distinguished from most *Cladophoropsis* species by the typical annulated stipe cells (Fig. 81). Yet one *Cladophoropsis* species, *C. magna*, produces similar stipes and may therefore be more closely allied to one of the above-mentioned genera than to the other *Cladophoropsis* species. A number of morphological characters are shared between the different genera (Table 3). For example, the typical unilateral branching pattern in *Cladophoropsis* also characterizes the genus *Chamaedoris* (Fig. 80), and simultaneous cell division, occurring in *C. membranacea* and *C. philippinensis*, has also been observed in the genera *Boodlea* (Fig. 79, arrowheads), *Struveopsis* and *Struvea* (Leliaert 2004). The variety of calcium oxalate crystals found in the six *Cladophoropsis* species are also found in species of the other genera. The elongate prismatic crystals found in *C. macromeres*, *C. mem-*

Table 3. Comparison of morphological characters between two *Cladophoropsis* species (*C. magna* and *C. membranacea*) and representatives of the genera *Boodlea*, *Struveopsis*, *Phyllo-dictyon* and *Chamaedoris*.

	<i>Cladophoropsis magna</i>	<i>Cladophoropsis membranacea</i>	<i>Boodlea composita</i>	<i>Struveopsis siamensis</i>	<i>Phyllo-dictyon anastomosans</i>	<i>Chamaedoris peniculum</i>
Thallus morphology	mat-forming thalli composed of loosely entangling filaments	mat-forming thalli composed of loosely entangling filaments	cushion-forming thalli composed of tightly interwoven filaments	stipitate thalli, single or grouped into cushion-like thalli	stipitate, reticulate blades clustering into cushion-like thalli	stipitate capitula
Mode of cell division	lateral single or opposite	lateral single	lateral opposite or occasionally single, older cells producing additional branches	lateral opposite or occasionally single, older cells producing additional branches	lateral opposite or occasionally single, older cells producing additional branches	CI (occasionally SCD) lateral single
Organization of branch systems	site	lateral single	lateral opposite or occasionally single, older cells producing additional branches	lateral opposite or occasionally single, older cells producing additional branches	lateral opposite or occasionally single, older cells producing additional branches	lateral single
Simultaneous cell division	frequent	frequent	frequent	frequent	frequent	occasional
Cross walls at the base of the laterals	absent	present in some older branches	present (except in newly formed laterals)	present (except in newly formed laterals)	present (except in newly formed laterals)	present in some older branches
Stipe cell	present, with annular constrictions	absent	absent (or sometimes present in young plants)	present, with or without annular constrictions	present, without annular constrictions	present, with annular constrictions
Mode of thallus reinforcement	loosely entangling of filaments; anastomosis occasionally by type-3 tenacular cells	tightly interweaving of filaments; anastomosis occasionally by type-3 tenacular cells	tightly interweaving of filaments; anastomosis by type-1 and -3 tenacular cells	loosely entangling of filaments; tenacular cells absent	tightly interweaving of filaments; anastomosis by abundant type-1 and -3 tenacular cells	loosely entangling of filaments; anastomosis occasionally by type-3 tenacular cells
Shape of the prismatic calcium oxalate crystals	diamond-shaped	hexagonal, trapeziform or rectangular	elongate hexagonal or trapeziform to needle-shaped	elongate hexagonal or trapeziform to needle-shaped	elongate hexagonal or trapeziform to needle-shaped	diamond-shaped

**Fig. 79.** *Boodlea composita* (L 936.181.459). Young stipitate plant with opposite and unilaterally organized branch systems, lacking tenacular cells. Arrowheads indicating simultaneous cell division by centripetal invagination of the cell walls followed by equally developing laterals. Scale = 500 μ m.**Figs 80, 81.** *Chamaedoris peniculum* (HOD RD2-02-45).**Fig. 80.** Unilaterally branching capitulum filaments. Arrow indicating a cell undergoing segregative cell division. Scale = 500 μ m.**Fig. 81.** Stipe cell with numerous annular constrictions; capitulum filaments produced at the distal pole and rhizoidal cells at the proximal pole. Scale = 500 μ m.

branacea, *C. philippinensis* and *C. sundanensis* are similar to those found in the *Boodlea composita* and *Phyllo-dictyon anastomosans*, while the diamond-shaped crystals occurring in *C. magna* resemble the crystals in *Chamaedoris peniculum*, *Phyllo-dictyon orientale*, *P. pulcherrimum*, *Struvea gardineri* and *S. plumosa* (Leliaert & Coppejans 2004).

The genus complex *Boodlea-Chamaedoris-Cladophoropsis-Phyllo-dictyon-Struvea-Struveopsis* can be characterized by a number of shared derived morphological characters: (1) Thalli are composed of densely branched, entangling filaments. (2) Reinforcement of the thallus is generally achieved by tenacular cells, with the exception of *Struveopsis* and some *Cladophoropsis* species where this feature may have been lost secondarily. (3) Prismatic calcium oxalate crystals are found in the cells of most taxa; this type of crystals presumably evolved on a single occasion and was subsequently lost in *Struvea elegans* Børgesen, *Chamaedoris auriculata* Børgesen and *Chamaedoris delphinii* (Harriot) Feldmann & Børgesen. (4) Laterals are produced almost immediately after the division of an apical or intercalary cell, singly or in opposite pairs. Cross wall formation at the base of the laterals is markedly delayed, and in most *Cladophoropsis* species cross walls are even never formed. (5) Segregative cell division, either organized as in *Struvea plumosa* or through cell wounding as

in *Cladophoropsis membranacea*, has been documented in most representatives.

Based on these morphological observations, it seems unlikely that *Cladophoropsis* would form a natural group within the genus complex. Indeed, phylogenetic analyses inferred from ITS, SSU and LSU rDNA sequences indicate that *Cladophoropsis macromeres*, *C. membranacea* and *C. philippinensis* are more closely related to *Boodlea composita*, *B. montagnei*, *Phyllocladon anastomosans* and *Struveopsis siamensis* than to *Cladophoropsis sundanensis*. *Cladophoropsis vaucheriiformis* has been found to be more closely allied to *Chamaedoris peniculum* than to *C. membranacea* (Kooistra *et al.* 1993; Hanyuda *et al.* 2002), although taxon sampling in these studies was rather low. No sequence data are yet available for *Cladophoropsis magna*.

The extremely close relationship between the above-mentioned genera, the nonmonophyly of most of the included genera (*Boodlea*, *Cladophoropsis*, *Chamaedoris*, *Phyllocladon* and *Struvea*), in combination with the fuzzy morphological boundaries and the presence of a number of shared derived morphological characters could support the recognition of a single genus. Biological classifications are meant to represent the best current estimate of phylogeny, but, for the sake of utility, they should not drift and evolve slavishly in response to every newly proposed phylogeny. Therefore, for the sake of taxonomic stability, we choose at this stage to maintain the genus *Cladophoropsis* as presently circumscribed and await further molecular phylogenetic studies before undertaking taxonomic changes.

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Appendix 1. Specimens examined.

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

Cladophoropsis magna Womersley: **Pacific Ocean: Australia.** Denial Bay, South Australia (leg. Tieskens s.n., MEL 3011); Smoky Bay, Eyre Peninsula, South Australia (leg. Womersley, 21 Jan. 1951, A13615, ADU, holotype; nos. A13615 and A13616: MEL 3012, MEL 666096, MEL 666097 and NY, isotypes).

Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen: **Atlantic Ocean: Canary Islands.** Fare de Maspalomas, Gran Canaria (leg. van der Strate CmCI GC MP1 & CmCI GC MP2, Jan. 1998, GENT); Punta del Hidalgo, Tenerife (leg. van der Strate CmCI TF PdH1 & CmCI TF PdH2, Jan. 1998, GENT); Punta del Rincón, Fuerteventura (leg. van der Strate CmCI FV PdR1 & CmCI FV PdR2, Jan. 1998, GENT); Faro de Orchilla, Hierro (leg. Cancap 2 Expedition 455, 6 Sep. 1977, L 996 225 796); **Cape Verde Islands.** Sal Island, Pedra da Lume (leg. van der Strate CmCVI Sal PdL1 and CmCVI Sal PdL2, Jul. 1998, GENT); Branco, north coast (leg. Cancap 7 Expedition 9621, 5 Sep. 1986, L 996 222 039); Branco, south coast (leg. Cancap 7 Expedition 9697, 5 Sep. 1986, L 996 222 055); **Caribbean Sea: Barbados.** Hasting Rocks (leg. Vickers, s.n., 16 Dec. 1898, BR); unknown locality (leg. Vickers 26, 1905, PC); **Bermuda.** Shark Hole, Harrington Sound: shallow subtidal (leg. Schneider 92–4–2, 20 Jun. 1992, NY); Hungry Bay, Hamilton Island (leg. Taylor & Bernotowicz 49–463, 26 Mar. 1949, BR); Hungry Bay, Hamilton Island (leg. Collins 7021, Apr. 1912, BR); **Curaçao.** Boco Grandi (leg. van den Hoek 68/62, 23 May 1968, L 993 113 339); Sint Michiels-baai (leg. van den Hoek 68/22bis, 14 May 1968, L 993 113 322); Playa Chikitu: infralittoral fringe (leg. van den Hoek 68/17, 11 May 1968, L, 993 113 308); **Guadeloupe.** Petit Havre (leg. Wynne 8209, 25 Feb. 1987, MICH); **Martinique.** Pointe des Nègres (leg. Hamel & Hamel-Joukov 61, Apr. 1930, B 34440, L 939 028 260); **Puerto Rico.** Caja de Muertos (leg. Howe 7471, 8 Jul. 1915, NY); Cayo Icacos (leg. Pagan 5252, 22 Jan. 1966, NY); Guanica Harbor, low intertidal (leg. Howe s.n., 1 Jul. 1915, L 938 095 652); Playa Talloboa, south coast of Guayanilla (leg. Diaz-Piñer 1333, 1959, L 996 224 552); Salinas Bay, near Guánica (leg. Howe 2680, 29 Jun. 1903, BR); **Virgin Islands.** St. Croix (leg. collector unknown s.n., Herbarium Agardh, LD 7287: lectotype of *C. membranacea*); St. Croix (leg. collector unknown, LD 7285 & 7307); **Gulf of Mexico: USA.** West Summerland Key, Florida (leg. Prud'homme van Reine 2508, 30 Jul. 1991, L 992 035 589); Key West, Florida (leg. Messina 225, PC); **Indian Ocean: Seychelles.** La Digue Island, near Anse Union: intertidal granite boulders (leg. Coppejans *et al.*, 23 Dec. 1992, SEY 306); **Sri Lanka.** Beruwela, intertidal rock platform, in front of Confiffi Beach Hotel: sheltered and exposed side of the reef crest, epilithic on horizontal substratum (leg. Coppejans, 25 Jan. 1997, HEC 11813b); Hikkaduwa, in front of Reefcomber Hotel: intertidal fossil reef, exposed to strong surf, epilithic on horizontal rock substratum (leg. Coppejans, 12 Jan. 1997, HEC 11671); Midigama beach, west of Weligama: infralittoral fringe, epilithic on horizontal substratum (leg. Coppejans, 10 Jan. 1997, HEC 11641); **Mediterranean Sea: Israel.** Shave-Zion (leg. Rayss, 27 Oct. 1949, BM); **Spain.** Balearium minorum (leg. Wittrock & Nordstedt 317, 1870, NY); **Tunesia.** Zarzis, 18 km S of El Kantara, exposed sandy beach (leg. Meñez & Cherif, 30 Apr. 1975, EGM 28, BM); **Pacific Ocean: Caroline Islands.** Unknown locality (leg. Hallier s.n., B 09451, M); reef between Falu and Moen Island, Truk Group (leg. Meñez, Doty no. D23458.2, 29 Jul. 1960, BISH! 510376: holotype of *Boodlea trukensis*); **Hawaii.** Hanaua Bay, Oahu (leg. Eubank 704, 12 Jan. 1942, UC 940 373); Kae-nana point (leg. Tilden 146, B 09449: holotype of *Boodlea kaenana*; B 09450: isotype); **Indonesia.** Flores (leg. Weber-van Bosse 1068, Dec. 1888, L 937 279 433); **Marshall Islands.** Parry Island, Eniwetok Atoll: seaward reef flat (leg. Dawson 13669, 20 Aug. 1955, AKU, VWL13669); **Philippines.** Bingag, Danis, Panglao Island, Bohol: intertidal, epilithic or epiphytic, loosely attached to substratum (leg. Leliaert *et al.*, 10 Aug. 1998, PH 115); Hilangagan, Punta Maria, Borongan, Samar, epilithic (leg. Cordero, Yamba & de la Cruz PNH 124807, 30 Nov. 1977, L 366099); Malibago Bluewater Resort, Mac-

tan Island: intertidal sandy reef flat with dead coral boulders, unattached (leg. Leliaert *et al.*, 27 Aug. 1998, PH 569b); Tulapos, Enrique Villanueva, Siquijor: intertidal reef flat, loosely attached to substratum (leg. Leliaert *et al.*, 7 Aug. 1998, PH 670); **Solomon Islands.** Guadalcanal, Kapiu, on reef rim (leg. Bailey 737, 5 Oct. 1965, L 211518); New Georgia, Matiu Island, lower intertidal (leg. Womersley & Bailey 396, 28 Aug. 1965, L 211513); **Tahiti.** Papevi Pass (leg. Setchell & Parks 5214, 24 Jun. 1922, NY); **Tonga.** Unknown locality (leg. Graefte s.n., S).

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

Cladophoropsis sundanensis Reinbold: **Indian Ocean: Kenya.** Between English Point and Mc Kenzie Point, Mombasa (leg. Coppejans, Jan. 1986, HEC 5839); Gazi Bay: *Sonneratia* mangrove (leg. Coppejans, 7 Aug. 1989, HEC 8275); Iwantine Bay, Mombasa: high intertidal rock pools (leg. Coppejans *et al.*, 11 Sep. 1992, HEC 9401); Kanamai, Mombasa (leg. Coppejans, Jun. 1985, HEC 5623); Tiwi (leg. Coppejans, 13 Jul. 1987, HEC 6837); **Oman.** Mangroves of Shaghaf Island, Masirah Island: mid-intertidal (leg. Schils, MAS 463b); **Rodrigues.** Graviers: epilithic on horizontal sand-covered rock substratum (leg. Coppejans, 19 Sep. 2001, HEC 14673); **Seychelles.** Bird Island, East coast: epilithic on coral boulders covered by *Thalassodendron ciliatum* (leg. Coppejans *et al.*, 20 Dec. 1992, SEY 244); Ile Desnoeuvs: steep sandy beach with large isolated flat rocks, epilithic on horizontal surface (leg. Coppejans *et al.*, 2 Jan. 1993, SEY 618); Ile du Sel, Poivre Atoll: lower intertidal, rocky substratum (leg. Coppejans *et al.*, 1 Jan. 1993, SEY 616); Le Corsaire, NW coast of Mahé Island: mid-intertidal, rocky platform of an artificially built dike (leg. Coppejans *et al.*, 12 Dec. 1992, SEY 61, 66); St. François Atoll, Bijoutier Island: subtidal coral slope (leg. Coppejans *et al.*, 5 Jan. 1993, SEY 732); **South Africa.** 1/4 Mile Reef, Sodwana Bay, KwaZulu-Natal: subtidal, – 9 m (leg. De Clerck *et al.*, 11 Feb. 2001, KZN 2148); Isipingo Beach, KwaZulu-Natal: high intertidal pools, epilithic on vertical and overhanging rockwalls (leg. Coppejans, 21 Jan. 1995, HEC 10944); Island Rock, KwaZulu-Natal: intertidal rock pools (leg. De Clerck & Cocquyt, 14 Aug. 2000, KZN 1693); Mabibi, KwaZulu-Natal: intertidal pools and infralittoral fringe (leg. Coppejans *et al.*, 9 Aug. 1999, KZN 395); Treasure Beach, The Bluff, Durban, KwaZulu-Natal (leg. Coppejans *et al.*, 3 Aug. 1999, KZN 0072a); **Sri Lanka.** Beruwela, intertidal rock platform, in front of Confiffi Beach Hotel: sheltered and exposed side of the reef crest, epilithic on horizontal substratum (leg. Coppejans, 25 Jan. 1997, HEC 11813a); **Tanzania.** Kunduchi, in front of Bahari Beach Hotel: shallow subtidal, epiphytic on *Amansia dietrichiana* (leg. Coppejans & De Clerck, 3 Jan. 1996, HEC 11062); Kunduchi, Bahari Beach: mid- to low intertidal, epilithic (leg. Leliaert & Coppejans, 10 Jul. 2001, FL 901); Mbudya Island, west coast: supralittoral fringe, epilithic on vertical substratum, mixed with *Boodleopsis* sp. (leg. Leliaert & Coppejans, 11 Jul. 2001, FL 919); Chwaka Bay, Zanzibar: intertidal seagrass bed, on sponge (leg. Leliaert & Coppejans, 18 Jul. 2001, FL 975); Fishermen's resort, Mbweni Cliffs, Zanzibar: epilithic on coral boulder, intertidal (leg. Leliaert, 15 Jul. 1997, FL 606); Mana Hawanja Island close to Nangerera, Mnazi Bay, Mtwara area: high intertidal, epilithic on horizontal rock, under overhanging fossil coral cliff (leg. Coppejans *et al.*, 29 Jul. 2000, HEC 12976); Matemwe, in front of Matemwe Beach Village, Zanzibar: mid-intertidal reef flat, epiphytic on *Gelidiella acerosa* and *Turbinaria* sp. (leg. Leliaert & Coppejans, 16 Jul. 2001, FL 949 and FL 953); Nungwi, Zanzibar: drift (leg. Leliaert &

Coppejans, 21 Jul. 2001, FL 1000); Nungwi, Zanzibar: supralittoral fringe, epilithic on vertical fossil reef substratum (leg. Leliaert & Coppejans, 21 Jul. 2001, FL 995); Uroa, Zanzibar: high intertidal, epilithic, sand trapping (leg. Coppejans, 2 Aug. 1993, HEC 9833); Chwaka, Zanzibar: high intertidal mangrove creek, epilithic (leg. Coppejans & De Clerck, 27 Aug. 1994, HEC 10714); Kizinkazi, Zanzibar: epiphytic on *Cystoseira myrica* (leg. Coppejans & De Clerck, 26 Aug. 1994, HEC 10669); in front of Mafia Island Lodge, Mafia Island: mid-intertidal, epiphytic on *Sonneratia-pneumatophores* (leg. Coppejans & De Clerck, 12 Jan. 1996, HEC 11224a); seaward side of Juani Island, Mafia Island: lower intertidal, epilithic on horizontal rock (leg. Coppejans & De Clerck, 11 Jan. 1996, HEC 11211); **Yemen**. Ra's Hamadara, NE coast of Socotra: shallow subtidal, – 3 m, epilithic on dead coral (leg. Leliaert, 23 Feb. 1999, SOC 152); **Mediterranean Sea: Greece**. Saron Gulf, Attika (leg. Schiffner 965, 6 Dec. 1928, NY); **Pacific Ocean: Caroline Islands**. Reef flat near Utwa Village, Kusaie Island (leg. E.G. Meñez, Doty no. D23616, 7 Jul. 1960, BISH 586970: holotype of *Cladophoropsis carolinensis*); **Japan**. Yokohama (leg. FR. Kjellman, Vega-expedition, 18 Sep. 1879, UPS: holotype of *Siphonocladus fasciculatus*); **Indonesia**. Kangean (leg. Weber-van Bosse, Siboga Expedition s.n., L 937.279.372: lectotype of *Cladophoropsis sundanensis*); **Papua New Guinea**. Medibur, Madang Province (leg. Coppejans & Prud'homme van Reine, 23 Jul. 1990, Copp & PvR 13365a); **Tahiti**. Arue Reef (leg. Setchell & Parks 5048, 23 May 1922, UC 261237); Reef at Tahara Mountain (leg. Setchell & Parks 5155 and 5160, 17 Jul. 1922, UC 261238 and 261303); **The Philippines**. Bantayan Island: epilithic (leg. Dargent & Bel, 5 Aug. 1999, HOD PH 99-30); Lumangcapan, Enrique Villanueva, Siquijor: high intertidal sandy reef flat, epiphytic on seagrasses (leg. Leliaert *et al.*, 7 Aug. 1998, PH 42); Punta Engano, Mactan Island: high intertidal reef flat, epiphytic (leg. Leliaert *et al.*, 5 Aug. 1998, PH 628); **Persian Gulf: Saudi Arabia**. Abu Ali Island, N of Jubail: infralittoral fringe, epilithic on beach rock, salinity 44 pm, temperature 31°C (leg. Coppejans, 1 Aug. 1992, HEC 9291); Abu Ali Island, N of Jubail: intertidal, shallow rock pools, epiphytic on *Digenea* (leg. De Clerck, 2 Nov. 1992, ODC 40); Abu Ali Island, N of Jubail: mid-intertidal, in rock crevices (leg. De Clerck, 1 Nov. 1992, ODC 21); close to Bomb Crater Bay, N of Jubail: lower intertidal rock pool, epiphytic or epizoic on sponges (leg. Coppejans, 23 Jan. 1992, HEC 8929); Fisherman's Bay, Abu Ali Island, N of Jubail: lower intertidal, in crevices of the coastal beach rock exposed to surf, salinity 44 pm, seawater temperature 30°C (leg. Coppejans, 20 Jul. 1992, HEC 9190); N of Jubail: infralittoral fringe between *Digenea*, unattached (leg. De Clerck, 11 Nov. 1992, ODC 125); Ras Al Bukhara, N of Jubail: mid-intertidal, epiphytic on *Digenea* sp., salinity 44 pm, seawater temperature 27°C (leg. Coppejans, 27 Jul. 1992, HEC 9256); Ras Al-Zawr, N of Jubail: epilithic in crevices of the infralittoral fringe, salinity 44 pm, seawater temperature 28°C (leg. Coppejans, 24 Jul. 1992, HEC 9220).

Cladophoropsis vaucheriiformis (Areschoug) Papenfuss: **Indian Ocean: Kenya**. Kanamai, Mombasa (leg. Coppejans, Jan. 1986, HEC 6064); Mc Kenzie Point, Mombasa (leg. Coppejans, Jan. 1986, HEC 5976); Mwamba Beach, Mombasa: mid- to lower intertidal rock pools, seagrass bed, epiphytic on *Halimeda opuntia* (leg. Coppejans, 12 Sep.

1991, HEC 8724); Shimoni, Kisite Island (leg. Coppejans, 9 Mar. 1988, HEC 7278); Tiwi, between Mombasa and Diani: lower intertidal, epilithic on horizontal substratum (leg. Coppejans *et al.*, 13 Sep. 1992, HEC 9423); Vipingo, 35 km N of Mombasa (leg. Coppejans, 29 Jul. 1989, HEC 8181); **Mauritius**. Unknown locality (leg. Areschoug or Pike, S A2572: lectotype of *Spongocladia vaucheriiformis*; syntypes: S A2569, A2570 & A2571); **Singapore**. Unknown locality (leg. collector unknown, MEL 6835); **Tanzania**. Fungu Achungu, Mnazi Bay, Mtwara area: shallow subtidal, – 8 m, on coral rubble on sand (leg. Coppejans *et al.*, 11 Aug. 2000, HEC 14221); Mana Hwanja Island, Mnazi Bay, Mtwara area: subtidal reef slope, – 15 m, epilithic (leg. Coppejans *et al.*, 5 Aug. 2000, HEC 14186); Ruvula beach, Mnazi Bay, Mtwara area: shallow subtidal, – 5 m (leg. Coppejans *et al.*, 26 Jul. 2000, HEC 12912); S of Ras Ruvula, Mnazi Bay, Mtwara area: low intertidal rock pools (leg. Coppejans *et al.*, 23 Jul. 2000, HEC 12843); Chapwani Island, in front of Zanzibar Town, Zanzibar: lower intertidal, epilithic (leg. Coppejans, 27 Jul. 1993, HEC 9754); Chwaka Bay, Zanzibar: lower intertidal, shallow rock pools, epilithic (leg. Coppejans, 24 Jul. 1993, HEC 9702); Fishermen's resort, Mbweni Cliffs, Zanzibar: drift, epizoic on sponge (leg. Leliaert, 15 Jul. 1997, FL 607b); Matemwe, in front of Matemwe Beach Village, Zanzibar: mid-intertidal reef flat (leg. Leliaert & Coppejans, 16 Jul. 2001, FL 954); Paje, Zanzibar: fringing reef, epizoic on sponge (leg. Leliaert, 23 Jul. 1997, FL 683); Uroa, Zanzibar: mid-intertidal reef flat (leg. Leliaert & Coppejans, 19 Jul. 2001, FL 989); Nungwi, Zanzibar: infralittoral fringe, seaward side of the reef flat, exposed to strong surf, epilithic (leg. Coppejans & De Clerck, 23 Aug. 1994, HEC 10570); Mafia Island, Chole Bay in front of Mafia Island Lodge: shallow subtidal seagrass bed, epilithic (leg. Coppejans & De Clerck, 8 Jan. 1996, HEC 11135); Misali Island, NE coast (W of Pemba Island): shallow intertidal rock pool, epilithic on horizontal substratum (leg. Coppejans & De Clerck, 21 Jan. 1996, HEC 11394); **Pacific Ocean: Australia**. Goode Island, Queensland (leg. Powell s.n., MEL 6828); **Indonesia**. Sorong, W Irian Jaya (leg. Beccari, May 1872, BM: lectotype of *Spongodendron crassum*); Sorong, W Irian Jaya (leg. Beccari, May 1872, BM: lectotype of *Spongodendron dichotomum*); Ambon Bay, near Tawiri (leg. Coppejans *et al.*, 6 Sep. 1984, Snellius-II 10037 and 10078); NE cape of Komodo Island (leg. Coppejans *et al.*, 26 Oct. 1984, Snellius-II 10891 and 19 Sep. 1984, Snellius-II 10908); Taka Garlarang Atoll, NE Taka Bone Rate (Tiger Island) (leg. Coppejans *et al.*, 27 Sep. 1984, Snellius-II 11347); **Japan**. Iriomote Island–Nadara (leg. Coppejans, 16 Sep. 1993, HEC 10097); **New Caledonia**. Poro (leg. Grunow 3558, 9 Oct. 1884, W: holotype of *Spongocladia neocaledonica*, isotype in BM); **Papua New Guinea**. Baga-bag, SE point of Christmas Bay, Madang Province (leg. Coppejans & Prud'homme van Reine, 8 Aug. 1990, Copp & PvR 13621); Kranket Island, Madang Province (leg. Coppejans, 23 Jun. 1988, HEC 7571); Malagere Island, Potsdam Harbour, Madang Province (leg. Coppejans, 6 Jul. 1988, HEC 7697); Manam, Madang Province (leg. Coppejans, 16 Jul. 1988, HEC 7811); Nagada harbour, on opposite side of CRI buildings, Madang Province (leg. Coppejans & Prud'homme van Reine, 9 Jul. 1990, Copp & PvR 13050); Wangat Island, Madang Province (leg. Coppejans, 22 Jun. 1988, HEC 7547); **Philippines**. Mactan Island (leg. Leliaert *et al.*, 6 Aug. 1998, PH 654).