

**SEAWEEDS OF THE SNELLIUS-II EXPEDITION
CHLOROPHYTA: CAULERPALES
(EXCEPT CAULERPA AND HALIMEDA)**

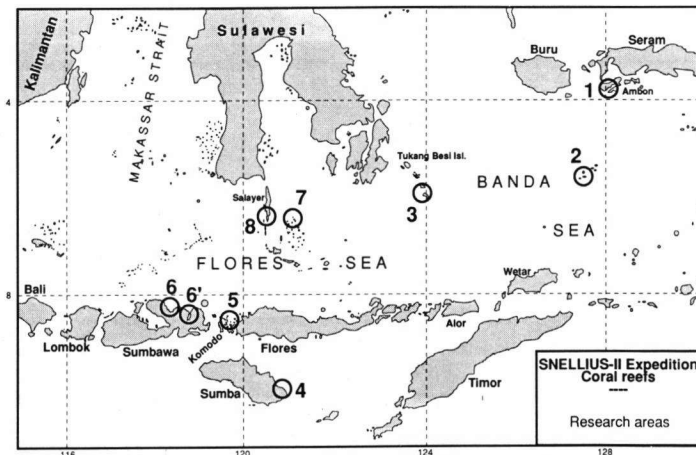
E. COPPEJANS* & W.F. PRUD'HOMME VAN REINE**

SUMMARY

In the present paper a survey is given of species belonging to the genera *Avrainvillea*, *Chlorodesmis*, *Rhipilia*, *Rhipiliopsis*, *Tydemania*, and *Udotea* collected during the Indonesian-Dutch Snellius-II Expedition (1984) in the Banda, Sawu and Flores Seas. The morphology and anatomy of these seaweeds are discussed, biogeographical data are added and some comparison is made with the material from the earlier Siboga Expedition (1899-1900).

INTRODUCTION

In the Indonesian-Dutch Snellius-II Expedition marine algae were collected during one month (September 1984) in the eastern part of the Indonesian archipelago exclusively. Approximately 1750 numbers of seaweed herbarium specimens were collected (see map, below) at Ambon (1), Pulau Maisel (2), Tukang Besi Is. (3), Sumba (4), Komodo (5), Sumbawa (6), Taka Bone Rate (7), and Salayer (8).



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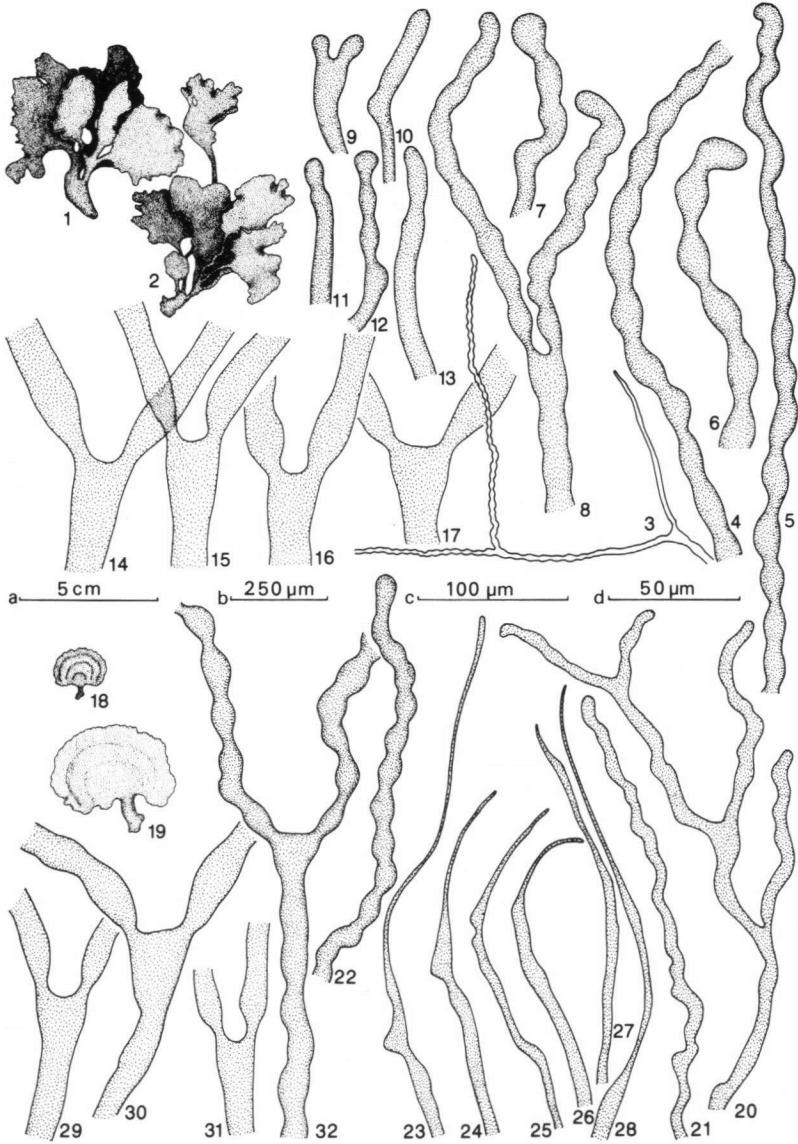


Plate 1 (the letter between brackets refers to the scale bar). — *Avrainvillea amadelpha* (Mont.) A. & E. S. Gepp: 1, 2: Habit (SN 11085 A) (a), 2 (SN 11543 A) (a). 3: Partly straight, partly sinuous filament (SN 11543 E) (b). 4–13: Details of apical parts of filaments: 4, 5, 8 (SN 11085 A) (c), 6 (SN 11085 A) (d) 7 (SN 11543 E) (d), 9–13 (SN 11509 A) (c). 14–17: Dichotomies with constrictions: 14, 15 (SN 11509 A) (c), 16 (SN 11543 E) (c), 17 (SN 11085 A) (c). — *Avrainvillea longicaulis* (Kütz.) Murr. & Boodle: 18, 19: Habit (SN 11496 A) (a). 20–22: Filaments with rounded apices: 20 (SN 10664 A) (c), 21 (SN 11496 A) (c), 22 (SN 10846 A) (c). 23–28: Filaments with pointed apices (SN 11496 A) (c). 29–32: Dichotomies with constrictions: 30, 32 (SN 10160 A) (c), 31 (SN 10664 A) (c).

MATERIALS AND METHODS

Collecting was done by walking and wading in the supra- and intertidal zones and by snorkeling and scuba-diving in the subtidal biotopes. As many different biotopes as possible have been sampled such as reef flat, reef pools, sea-side slope of the reef, lagoon, beach, mangrove. Duplicate herbarium specimens were prepared, according to the available specimens. They have been deposited in different series: A and C in Leiden (L), B and D in the Centre for Oceanological Research and Development in Indonesian Institute of Sciences, in Jakarta (JAK) and in Ambon (AMB) respectively, and the E-series in the Botanical Institute of the University of Ghent, Belgium (GENT). In some cases different specimens of the same series belong to different species; the series has then been split up into a & b.

The Chlorophyta are currently being studied; the Dasycladales have recently been published (Coppejans & Prud'homme van Reine, 1989a). All the drawings are original and made by the first author except for figure 1 on plate 8 (Mr. J.H. van Os); anatomical details are by camera lucida. In 'specimens examined' the abbreviation 'st.' means station.

DESCRIPTIONS

Avrainvillea Decaisne

Plants erect, composed of a stipe and a compressed flabellum; stipe sometimes very short, the blade then being sessile. Flabellum composed of uncalcified, intricately, dichotomously branching filaments with constrictions above the forks but without lateral branchlets or appendages and therefore without true cortex.

In spite of the monograph by Olsen-Stojkovich (1985) some of the specimens from this expedition were difficult to assign definitely to a species. Sometimes this was due to the limited development of the specimens or to the fact that some of the morphological and/or anatomical characters were contradictory.

Avrainvillea amadelpha (Montagne) Gepp & Gepp – Plate 1, figs. 1–17

Well developed specimens gregarious, with slender branched stipes (figs. 1, 2), each branch bearing a single terminal blade, but most of the specimens from the Snellius-II collection solitary. Stipe generally 2–3 cm long, but smaller in solitary specimens or up to 6 cm in well branched ones (fig. 2). Blade thin and spongy (not papery as in *A. lacerata*), brown olive, 1–2(–3.5) cm wide; solitary blades roundish with smooth growing margin, gregarious specimens with eroded or lacerate margins; never zonate. Siphons cylindrical in medullary parts (fig. 3 p.p., 9–11, 13), 19–25 µm in diameter, becoming increasingly torulose and tapering in surface layers (down to 12 µm in diameter) (figs. 3 p.p.–8, 12); dichotomies deeply constricted (figs. 14–17); apices rounded (figs. 5–13).

Specimens examined. 11085 A, E: st. 4.114, N of Sumbawa, Bay of Sanggar, lagoon side of reef barrier, c. 20 m deep; 11286 Aa: st. 4.140, NE Taka

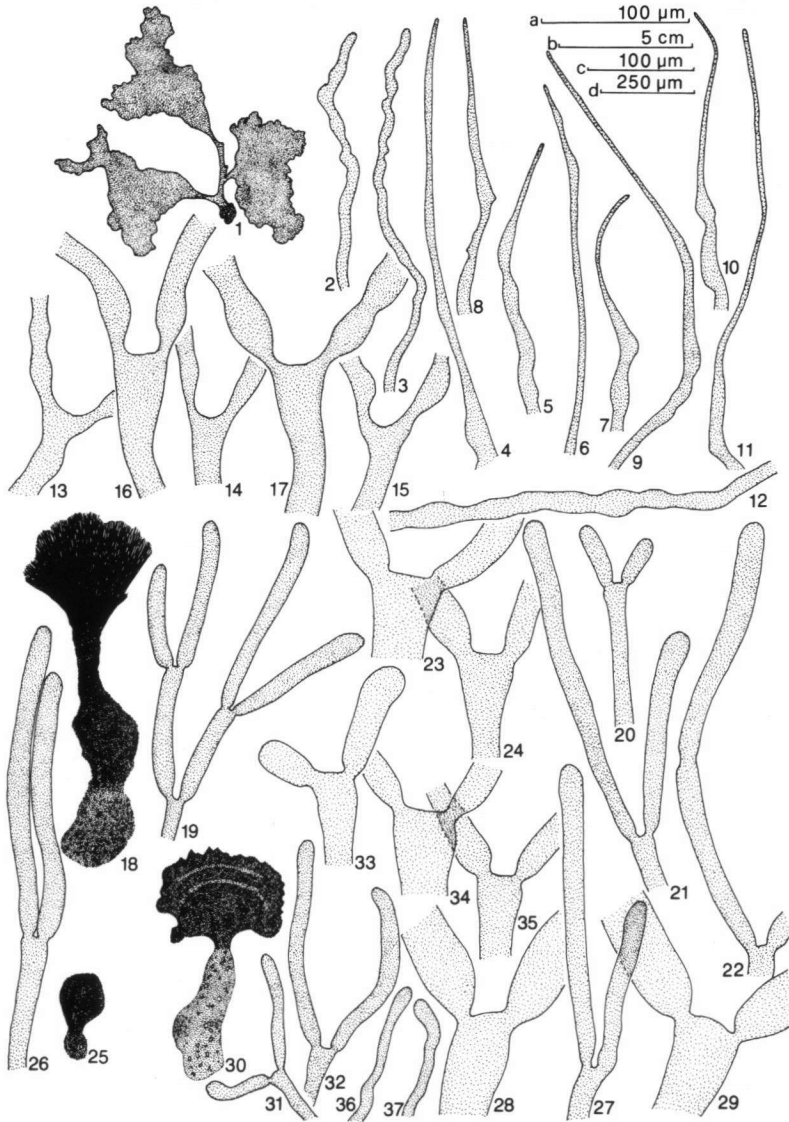


Plate 2 (the letter between brackets refers to the scale bar). — *Avrainvillea lacerata* J. Ag.: 1: Habit (SN 11321 A) (b) 2, 3: Filaments with rounded apices (SN 11321 A) (a). 4–11: Filaments with pointed apices: 4–7 (SN 11286 Ab) (a), 8–11 (SN 11321 A) (a). 12: Central part of a filament (SN 11321 A) (a). 13–17: Dichotomies with constrictions: 13–15 (SN 11321 A) (a), 16, 17 (SN 11286 Ab) (a). — *Avrainvillea erecta* (Berk.) A. & E.S. Gepp–*A. obscura* (C. Ag.) J. Ag. complex: 18, 25, 30: Habit: 18 (SN 10873 A) (b), 25 (SN 10641 A) (b), 30 (SN 11490 A) (b). 19–22: More or less clavate filament apices (SN 10873 A) (d). 23, 24: Dichotomies with constrictions (SN 10873 A) (a). 26, 27: Cylindrical and clavate filament apices (SN 10641 A) (d). 28, 29: Dichotomies with constrictions (SN 10641 A) (d). 31, 32, 36–38: More or less clavate filament apices (SN 11490 A) (d). 33–35: Dichotomies with constrictions (SN 11490 A) (a).

Bone Rate, E of Tarupa Besar, outer reef, c. 30 m deep; 11360 A, E: st. 4.151, NE Taka Bone Rate, Taka Garlarang atoll, reef flat, silty substrate; 11509 A, E, 11543 A, E: st. 4.161, SW Salayer, coral sand, seagrasses, reef crest.

Geographic distribution. Red Sea, Indian Ocean (mostly eastern part), Pacific Ocean: E Micronesia, N Polynesia (Olsen-Stojkovich, 1985: 38).

Discussion. Anatomically all the specimens agree very well with Gepp's (1911) and Olsen-Stojkovich's (1985) descriptions except for the presence of a pseudocortex mentioned by the former. Gepp & Gepp (1911: 43) mention that "this pseudocortex is not so well developed" in some of the collections. Basson (1979) did not notice it either in the material from the Arabian Gulf. However, the morphology of our material is more or less aberrant: the "holdfast developed into an extensive emergent mat from which many stipes arise" (Olsen-Stojkovich, 1985: 36) has never been observed in the Snellius-II material; on the contrary: solitary, shortly stipitate blades are frequent.

Avrainvillea erecta (Berkeley) Gepp & Gepp – *A. obscura* (C. Ag.) J. Agardh complex – Plate 2, figs. 18–37

Specimens SN 10641 A, C

Plants small (2 cm high), flabellum thick, cuneate with rounded margin, sessile on the small 'pseudobulbous' holdfast (= densely intricated mass of rhizoids, heavily embedded with sand and silt). Siphons mostly cylindrical (fig. 26) but some clavate (fig 23), 50–60 μm in diameter, green, greenish brown to greenish orange; dichotomies deeply constricted (figs. 26–29); apices rounded.

Specimen SN 10873 A

Stipe stout, 2 cm long, unbranched, gradually expanding in the cuneate blade of 4 cm high, 5 cm wide, rather thin (filaments distinguishable with the naked eye) in the upper part (2 cm) not zonate; upper margin more or less ciliate; dark brownish green. Fixation by a very large [7×2.5 (1.5) cm] 'pseudobulbous' holdfast. Siphons mostly clavate (figs. 19–22), 40–65 μm in diameter, brownish red; dichotomies deeply constricted (figs. 19–24); apices rounded.

Specimen SN 11490 A

Plant solitary, with a very short, stout, unbranched stipe (fig. 30), bearing a single blade. Blade reniform (3.5 cm high, 5 cm wide), thick spongy, upper margin slightly eroded; markedly zonate, light brownish green. Fixation by a large [5×1 (1.5) cm] submerged 'pseudobulb'. Siphons cylindrical (figs. 31, 32) or clavate (figs. 33, 36, 37), 50 μm in diameter, olive-green to brownish; dichotomies deeply constricted (figs. 31–35), apices rounded.

Specimens examined. *SN 10641 A, C*: st. 4.059, NE coast of Sumba, Melolo, stony littoral; *SN 10873 A*: st. 4.090, E of Komodo Is., Selat Linta, coastal reef flat; *SN 11490 A*: st. 4.161, SW Salayer, coral sand, seagrasses, reef crest.

Geographic distribution. Indo-Pacific, from East Africa to Philippines and Micronesia (Olsen-Stojkovich, 1985).

Discussion. Morphologically two entities could be distinguished: *SN 11490*

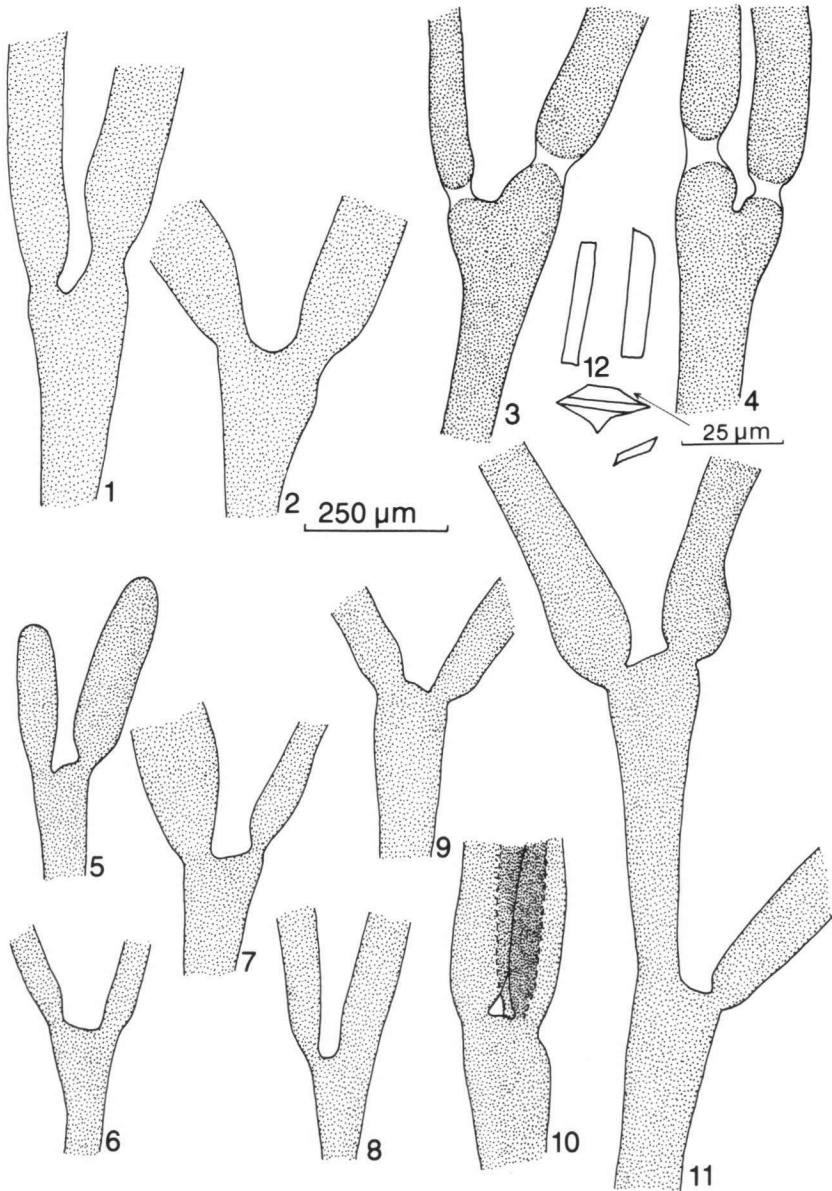


Plate 3. *Chlorodesmis fastigiata* (C. Ag.) Ducker: 1–4: Details of dichotomies: supporting segment convex at the top, supra-dichotomic constrictions very unequally situated (SN 10621 E). 12: Crystals (SN 10612 E). — *Chlorodesmis hildenbrandtii* A. & E.S. Gepp: 5–11: Details of di- (and tri-)chotomies: supporting segment truncated at the top; supradichotomic constrictions on the same level: 5–8 (SN 11332 E), 9–11 (SN 10782 E).

with a reniform, zonate blade, agreeing with *A. erecta*, SN 10641 and SN 10873 with a cuneate, not zonate blade, looking like *A. obscura*. Clavate apices of the filaments are, however, present in all specimens: they are rare in SN 10641, more common in SN 10873 and SN 11490. This character points to *A. obscura*, because *A. erecta* exclusively has cylindrical siphons (Gepp & Gepp, 1911: 33; Olsen-Stojkovich, 1985: 22).

Specimens described by Meñez (1961) from the Philippines and by Egerod (1975) from Thailand have clavate siphons but have been identified as *A. erecta* by both authors, on the basis of their morphology. The siphons should be bright yellow to orange-brown in *A. erecta* and olive to light brown in *A. obscura* (Olsen-Stojkovich, 1985: 22, 19). None of the specimens from the Snellius-II collection has yellow siphons, the colour varying from olive to brownish red.

On the basis of the anatomy all specimens should therefore be considered as *A. obscura*, but we are not convinced that *A. obscura* and *A. erecta* are separate species. It appears that there are intermediates. We recently collected a large number of specimens belonging to this group from Kenya and from Papua New Guinea. Detailed analysis of these specimens might elucidate this problem.

Avrainvillea lacerata J. Agardh – Plate 2, figs. 1–17

Stipe slender and irregularly ramified, up to 3 cm long, each branch bearing a single terminal blade (fig. 1). Blade thin, papery (not spongy as in *A. amadelpha*), light brownish green, cuneate with distinctly eroded-lacerate growing margins; never zonate. Siphons cylindrical in medullary parts (fig. 12), 19–23 μm in diameter, becoming more or less torulose in surface layers (figs. 2, 3, 5) and tapering (12–6 μm); dichotomies deeply constricted (figs. 14–16), more rarely shallowly constricted (fig. 13); apices generally pointed (figs. 4–11) but sometimes rounded (figs. 2, 3).

S p e c i m e n s e x a m i n e d. *11286 Ab*: st. 4.140, NE Taka Bone Rate, E of Tarupa Besar, outer reef, c. 30 m deep; *11321 A*: st. 4.150, NE Taka Bone Rata, Taka Garlarang Atoll, edge of reef flat.

G e o g r a p h i c d i s t r i b u t i o n. Indo-Pacific from East Africa to Malaysian and Indonesian archipelagos, Melanesia, Polynesia (Olsen-Stojkovich, 1985: 36).

D i s c u s s i o n. The specimen SN 11321 is anatomically aberrant in having some siphon apices rounded. According to Olsen-Stojkovich (1985: 33) they should be pointed (or torn away). Gepp & Gepp (1911: figs. 106, 108) do not describe the siphon apices but illustrate them as being rounded!

Avrainvillea longicaulis (Kützing) Murray & Boodle – Plate 1, figs. 18–32

Plants solitary (rarely by two's or three's); stipe short (0.5–1.5 cm), unbranched, bearing a single terminal blade (figs. 18, 19). Blade thin, velutinous, brownish green, rotundate to reniform, more rarely cuneate, 2–3(–4.5) cm wide, sometimes zonate (figs. 18, 19). Siphons cylindrical in the medullary parts (fig. 20), (38–)25–20 μm in diameter, becoming torulose, tortuous and tapered in cortical parts (figs. 20–22, 32), (14–)10(–8) μm in diameter; dichotomies generally deeply constricted

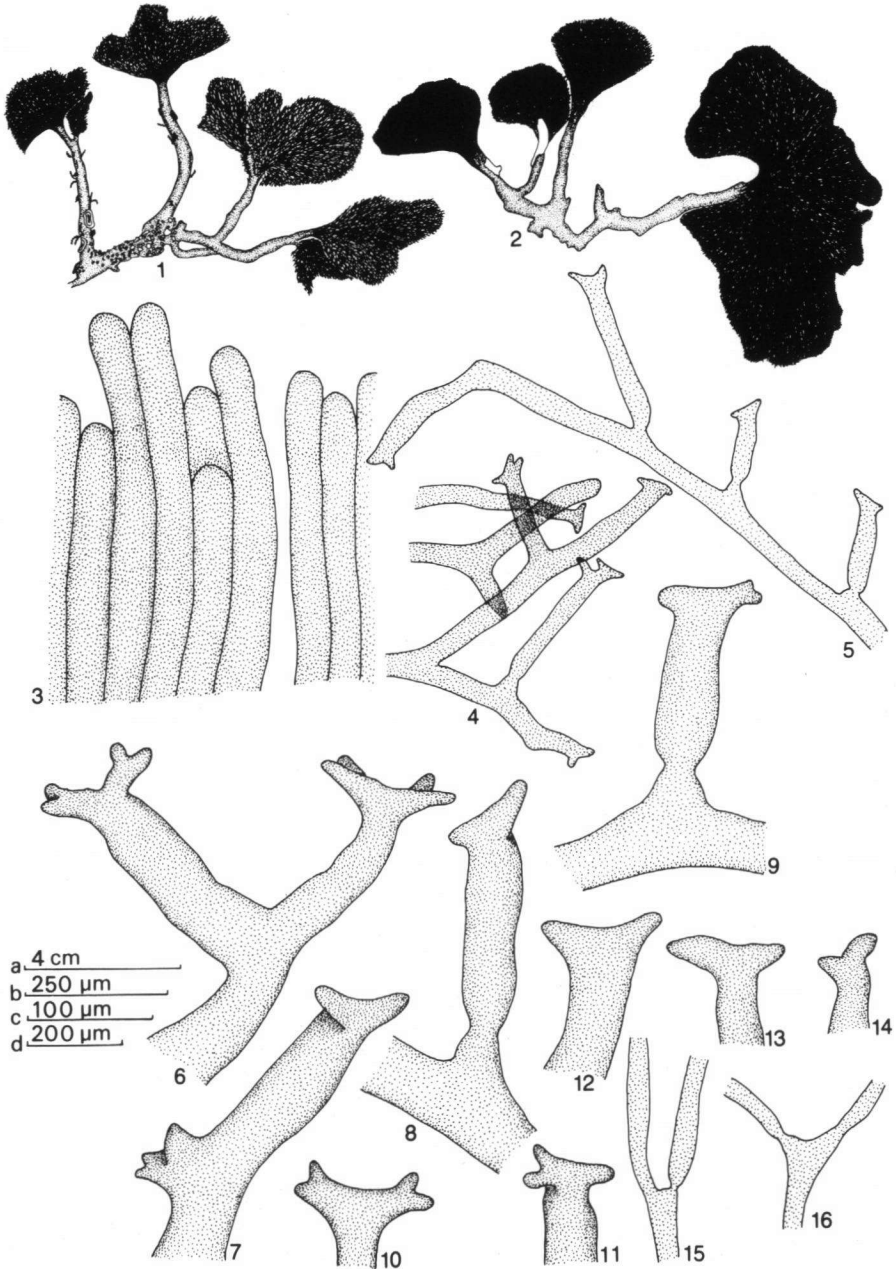


Plate 4 (the letter between brackets refers to the scale bar). — *Rhipilia diaphana* W.R. Taylor: 1, 2: Habit: 1 (SN 10284 A) (a), 2 (SN 10284 E) (a). 3: Thallus margin (SN 10284 E) (d). 4–14: Details of tenacula with prongs, side branchlets frequently constricted at the base (4, 5, 8, 9); 4, 5 (SN 10284 C) (b), 6–14 (SN 10284 E) (c). 15, 16: Dichotomies with constrictions (SN 10284 E) (b).

(figs. 29–32), sometimes only shallowly constricted (fig. 20); apices mostly rounded (figs. 20–22) but also pointed (figs. 23–28).

Specimens examined. *10160 A, C*: st. 4.013, Maisel Islands, N of Mai, reef edge, c. 20 m deep; *10280 A*: st. 4.030, Tukang Besi Islands, W coast Binongko, reef slope, c. 20 m deep; *10385 A*: st. 4.013, see *10160* above, reef flat; *10664 A*: st. 4.059, NE coast of Sumba, Melolo, stony littoral; *10864 A*: st. 4.084, E of Komodo Is., Selat Linta, coastal reef flat; *11496 A*: st. 4.161, SW Salayer, coral sand, seagrasses, reef crest.

Geographic distribution. Caribbean, Gulf of Mexico, Philippines (Olsen-Stojkovich, 1985: 29), Indonesia.

Discussion. Most of the specimens from the Snellius-II Expedition are morphologically different from Olsen-Stojkovich's description (1985: 29); they never have a long stipe and although the blade is cuneate in some cases (*SN 10280 A, 10385 A, 10664 A p.p., 10846 A p.p.*), a large number of specimens are rotundate or reniform; moreover the specimens *11496 A* (figs. 18, 19) are distinctly zonate. The anatomy, on the contrary, agrees in all characters with Olsen-Stojkovich's (l.c.) description.

Chlorodesmis Bailey & Harvey

Thallus uncalcified, composed of an entangled creeping mass of filaments attached by rhizoids as well as tufted but free erect filaments, subdichotomous with constrictions above the dichotomies.

Chlorodesmis fastigiata (C. Agardh) Ducker – Plate 3, figs. 1–4, 12

Forming dense, souple brownish green tufts; base like a spongy cushion because of the densely interwoven filaments; upright filaments 7–8 cm long, 120–150 μm in diameter; branching (sub)dichotomous; supporting segment of the dichotomy not truncated but convex at level of branch constrictions, dichotomy not symmetrical (constrictions on different levels: figs. 1–4), giving rise to a bifurcate top of the supporting segment; intercalary constrictions rare. Crystals extremely scarce in the rehydrated herbarium specimens.

Specimens examined. *SN 10621 A, E*: st. 4.059, NE coast of Sumba, Melolo, stony littoral.

Geographic distribution. Indo-Pacific (Ducker, 1967: 161–162, as *C. comosa* Harvey & Bailey).

Discussion. Ducker (1967: 161) mentions filament diameters of (72–)90–110(–150) μm ; the Snellius-II specimens have filaments ranging into the widest filament diameters reported for this species, but they are still markedly different from *C. baculifera* (J. Ag.) Ducker with filament diameters over 200 μm . The biacicular crystals which “are always sparse but rarely completely absent” (Ducker, l.c.) have not been observed in these specimens. Only a few crystals with very divergent form were present (fig. 12).

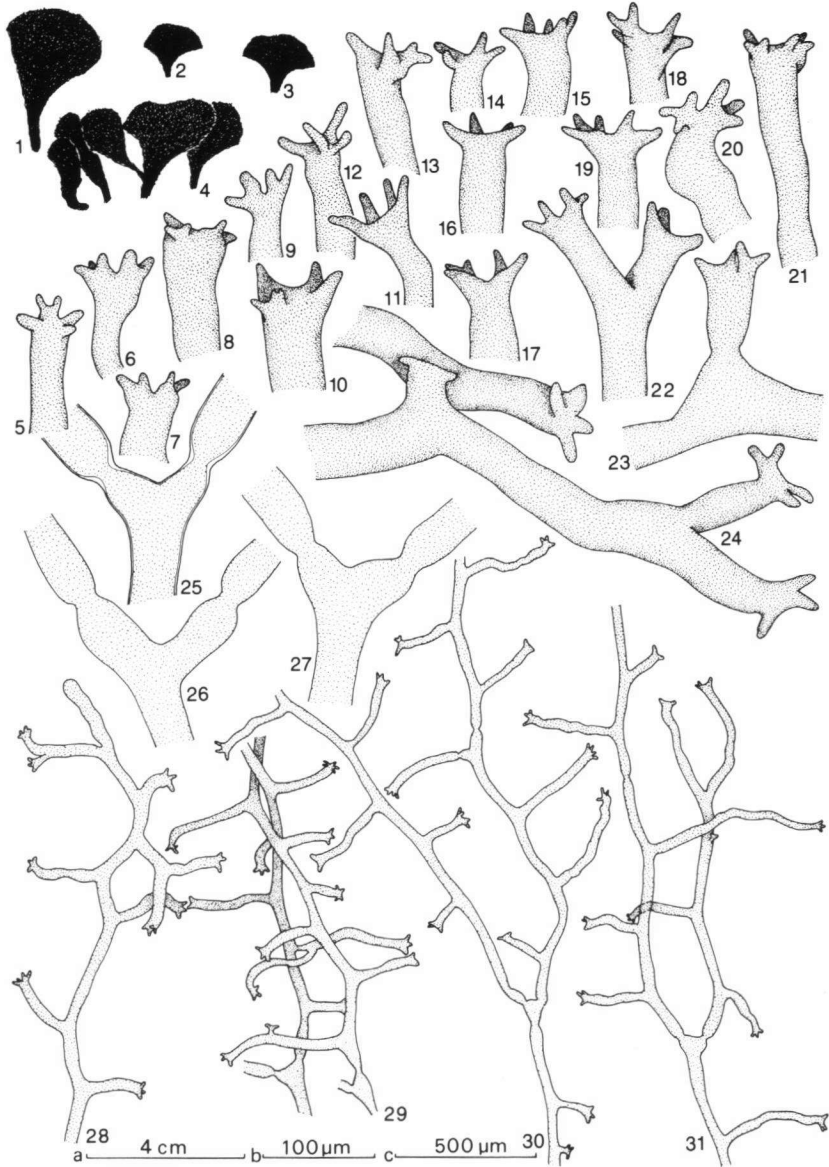


Plate 5 (the letter between brackets refers to the scale bar). — *Rhipilia nigrescens* Coppejans & Prud'homme van Reine: 1-4: Habit: 1 (SN 10285 A) (a), 2-4 (SN 11223 Ea) (a). 5-23: Details of tenacula with prongs: 5, 6, 23 (SN 11322 A) (b), 7-9 (SN 10285 E) (b), 10 (SN 10932 C) (b), 11-13 (SN 11368 Eb) (b), 14-17 (SN 11623 Aa) (b), 18-22 (SN 11223 Ea) (b). 24: Two filaments with reciprocal attachment of tenacula (SN 11322 A) (b). 25-27: Dichotomies with constrictions: 25 (SN 11322 A) (b), 26 (SN 10285 Ab) (b), 27 (SN 11623 Aa) (b). 28-31: Sympodial arrangement of the lateral branchlets with tenacula: 28 (SN 11223 Ea) (c), 29 (SN 11623 Eb) (c), 30-31 (SN 10285 Ab) (c).

Chlorodesmis hildenbrandtii Gepp & Gepp – Plate 3, figs. 5–11

Forming dense, souple, bright green (sometimes iridescent) tufts; base very intricated; upright filaments 3–5 cm long, 60–80 μm (*SN 11332*) to 80–100 μm (*SN 10782*) in diameter; branching (sub)dichotomous; supporting segment of the dichotomy truncated, dichotomy symmetrical, constrictions very close to the supporting segment (figs. 5–11); intercalary constrictions rarely observed, crystals absent.

Specimens examined. *SN 10782 A, E*: st. 4.079, E of Komodo Is., Selat Linta, reef slope, c. 16 m deep; *SN 11332 A, E*: st. 4.150, NE Taka Bone Rate, Taka Garlarang atoll, reef edge.

Geographic distribution. Indo-Pacific (Ducker, 1967: 165–168).

Discussion. The specimens of the Snellius-II collection agree very well with Ducker's (l.c.) description except for the filament diameter which is rather small, especially in *SN 11332* (60–80 μm); Ducker mentions 95–123 (mean 96) μm .

Rhipilia Kützing

A worldwide monographic study of this genus is in preparation by Millar & Kraft and not yet available.

The genus is characterized by its uncalcified spongy habit, its intricated filaments provided with pseudo-lateral tenaculiferous branchlets with prongs and the absence of a cortex.

Rhipilia diaphana W.R. Taylor (Plate 4, figs. 1–16)

Plants brownish green, presenting distinct solid stipes which can be ramified, up to 5–6 cm long with a single terminal blade; flabellum asymmetrically cuneate, flabellate, peltate, or infundibuliform, with entire or undulated margin, 3–4 (–9) cm wide, thick and spongy, sometimes transparent, composed of filaments, 35–50 μm in diameter, interconnected by short pseudolateral tenaculiferous 150–250 (–400) μm long branchlets, frequently constricted at their base (figs. 4–6, 8, 9); tenacula with 2–3 (–4) prongs (figs. 5–14); main filaments slightly constricted above the dichotomies (figs. 15, 16); growing apices rounded (fig. 3).

Specimens examined. *SN 10284 A, E*: st. 4.030, Tukan Besi Is., W coast of Binongko, reef slope, c. 20 m deep.

Geographic distribution. Indo-Pacific (Marshall Is., Indonesia).

Discussion. The specimens of the Snellius-II expedition agree well with Taylor's (1950: 72, 73) description except for their ecology (epilithic, not epiphytic) and for the thickness of the flabellum: Taylor (l.c.) described them as "exceedingly soft, thin, diaphanous and sometimes practically reticulate, the margin even thinner, often filament-fringed." *SN 10284 A* agrees with this description, *SN 10284 E* is markedly thicker.

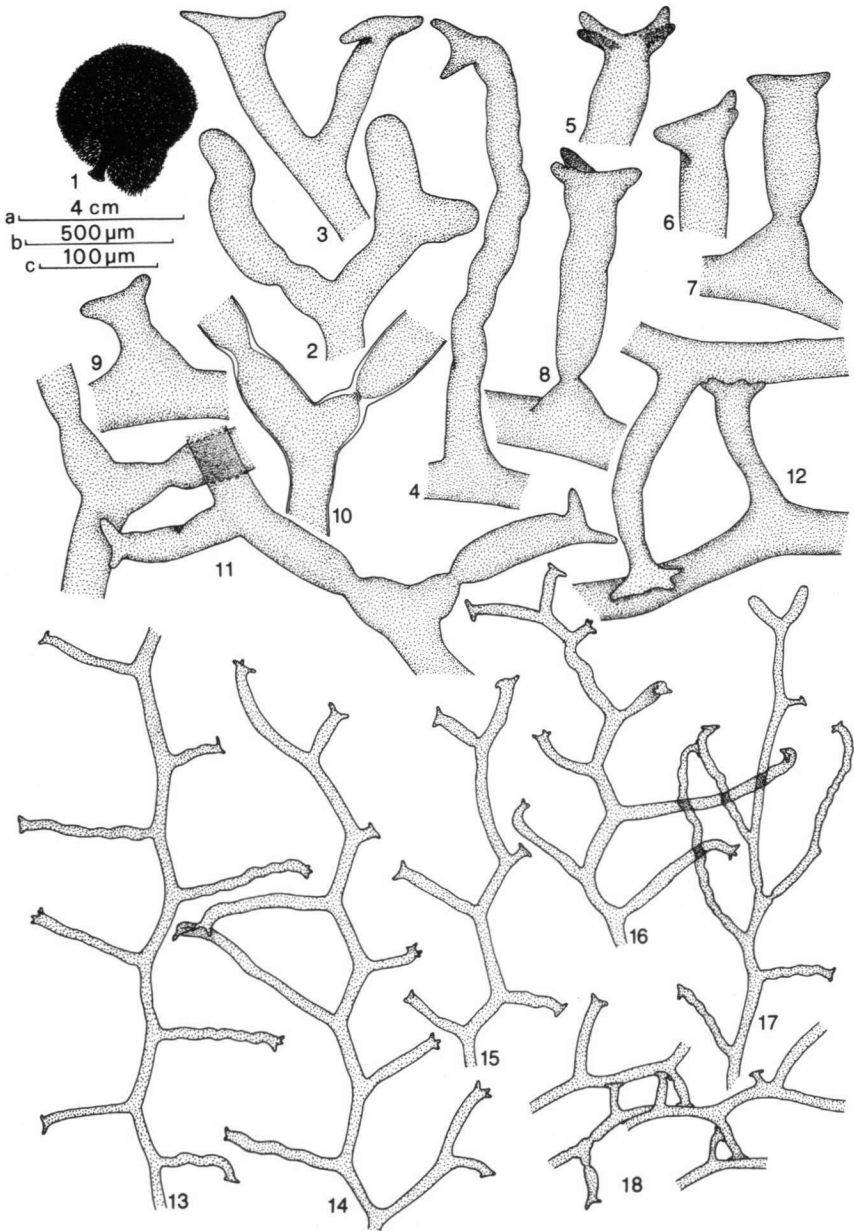


Plate 6 (the letter between brackets refers to the scale bar). — *Rhipilia orientalis* A. & E.S. Gepp: 1: Habit (SN 11223 A) (a). 2: Growing apices with rounded apices (SN 11223 A) (c). 3-9: Details of tenacula with prongs: 3, 5-9 (SN 10283 A) (c), 4 (SN 11223 Eb) (c). 10, 11: Dichotomies with constrictions: 10 (SN 10284 Ab) (c), 11 (SN 11623 Ea) (c). 12: Two filaments with reciprocal attachment of tenacula (SN 11223 A) (c). 13-18: Sympodial arrangement of the lateral branchlets with tenacula: 13-16 (SN 10284 Ab) (b), 17 (SN 11223 Eb) (b), 18 (SN 11623 Ea) (b).

***Rhipilia nigrescens* Coppejans & Prud'homme van Reine – Plate 5, figs. 1–31**

This species has recently been described after material from the Snellius-I Expedition (Coppejans & Prud'homme van Reine, 1989b).

Plants (1–)2(–3.5) cm high, dark brownish green, erect, generally clavate and gregarious, frequently anastomosing in the widest part (fig. 4) [more rarely solitary and turbinate, peltate, infundibuliform or flabellate (figs. 1–3), but even then thick and spongy, not transparent], never zonate. Main filaments (35–)40–50(–60) μm in diameter, densely interwoven, dichotomous, constricted above the dichotomies (figs. 25–27), bearing numerous sympodially placed tenaculiferous branchlets (figs. 28–31), (75–)250–400(–750) μm long, rarely branched, generally not constricted at the base and tenaculate at the tip; tenacula (2–)4–5(–6) pronged (figs. 5–24). Specimens becoming blackish green upon drying, even staining the paper brownish.

Specimens examined. *SN 10285 A, E:* st. 4.030, Tukang Besi Is., W coast of Binongko, coastal reef, slope, c. 20 m deep; *SN 10932 Aa, C:* st. 4.096, Komodo Is., NE cape, from steep reef slope, c. 25 m deep; *SN 11223 Ea:* st. 4.139, NE Taka Bone Rate, S of Tarupa Kecil, seagrass meadow, c. 10 m deep; *SN 11322 A, E:* st. 4.150, NE Taka Bone Rate, Taka Garlarang atoll, edge of reef flat, 0.5–3 m deep; *SN 11368 A, Ea:* st. 4.151, NE Taka Bone Rate, Taka Garlarang atoll, middle part of silty reef flat, 0.5–3 m deep; *SN 11623 Aa:* st. 4.169, SW Salayer, reef N of Pulau Bahuluang, edge of offshore reef, 2–5 m deep.

Geographic distribution. Indonesia.

Discussion. Differing from *R. crassa*, a new species that will be described by Millar & Kraft by the smaller diameter of the filaments and from all the other described *Rhipilia* species by the numerous prongs of the tenacula.

***Rhipilia orientalis* Gepp & Gepp – Plate 6, figs. 1–18**

Plants (1–)2(–3) cm high, dark brownish green, sessile or with a short, mostly indistinct stipe which gradually widens to the blade; flabellum frequently infundibuliform, sometimes flabelliform or very irregular in outline; frond varying from more or less thick spongy to thin translucent. Main filaments dichotomous (fig. 17), 30–50 μm in diameter, provided with numerous sympodially placed tenaculiferous branchlets (figs. 13–18), (150–)250–500(–650) μm long, sometimes constricted at the base (figs. 7, 8, 11); tenacula with 2–3(–4) prongs (fig. 3–12); main filaments constricted above the dichotomies (figs. 10, 11), in some cases with cell wall thickenings at the constrictions (fig. 10); growing apices rounded (figs. 2, 17).

Specimens examined. *SN 10283 A:* st. 4.030, Tukang Besi Is., W coast Binongko, reef slope, till c. 20 m deep; *SN 10932 A, E:* st. 4.096, Komodo Is., NE cape, steep reef slope, till c. 30 m deep; *SN 11223 A, Ea:* st. 4.139, NE Taka Bone Rate, S of Tarupa Kecil, seagrass meadow, reef flat; *SN 11623 Cb:* st. 4.169, SW Salayer, reef N of Pulau Bahuluang, edge of offshore reef, 2–5 m deep.

Geographic distribution. Indo-Pacific (Caroline Is., Marshall Is., Solomon Is., Australia, Indonesia).



Plate 7 (the letter between brackets refers to the scale bar). — *Rhipiliopsis gracilis* Kraft (SN 10164 A): 1: Habit (the uncorticated, monosiphonous base of the stipe is lacking) (a). 2, 3: Concentric bands of filament laterals (2: b; 3: c). 4: Regularly sinuous longitudinal filaments with some laterals (c). 5: Dichotomies with constrictions (c).

D i s c u s s i o n. The Snellius-II specimens differ from Gepp & Gepp's (1911: 57) and Taylor's (1950: 72) descriptions in the length of the tenaculiferous branchlets. They mention (70–)170(–350) μm ; in our specimens they are longer. After the study of herbarium material from different parts of the world Millar (pers. comm.) considers *R. diaphana* and *R. orientalis* as one entity. On the other hand the specimens from the Snellius-I expedition, occurring in a single region, can easily be split up in 3 morphological entities, i.e., no intermediates being present between *R. diaphana*, *R. orientalis*, or *R. nigrescens* although they were sometimes growing next to each other. Therefore we still consider them as distinct species.

Rhipiliopsis Gepp & Gepp

Uncalcified thallus composed of a mono- or polysiphonous stalk (corticated or not) and a mono- or polystromatic flabellum; siphons radially arranged, cohering directly at scattered sites or attached by lateral processes without pronged tenaculae.

Rhipiliopsis gracilis Kraft – Plate 7, figs. 1–5

Plants 4–5 mm, dark green, sessile to shortly stipitate (up to 1 mm), basal part of stipe not seen, upper part densely corticated; flabellum excentrically peltate, markedly zoned, polystromatic close to the stipe, monostromatic for the major part, composed of parallel regularly sinuous filaments radiating from stipe to thallus margin, 12–16 μm in diameter; filament dichotomies constricted (fig. 5) or not (fig. 2). Lateral cohesions between the filaments by direct contact of adjacent filaments or by papillar outgrowths, but without any thickened rings, tenaculae or prongs. Zoned pattern of the flabellum due to the concentrically ordered bands of filament laterals which in the Snellius-II material are dominantly directed in one direction in one zone and in the opposite direction in the former and the following zones (fig. 2).

S p e c i m e n s e x a m i n e d. *SN 10164 A, C*: st. 4.013, Maisel Is., N of Mai, reef edge, till c. 20 m deep.

G e o g r a p h i c d i s t r i b u t i o n. E Australia (Kraft, 1986), Indonesia.

D i s c u s s i o n. The specimens completely agree with Kraft's description (1986: 55). It is not possible to identify this species by using the identification key for *Rhipiliopsis* of Farghaly & Denizot (1979: 173) because their main differentiating characters are: blade polystromatic versus monostromatic, stipe monosiphonous versus polysiphonous. *Rhipiliopsis gracilis* has a polystromatic blade at the base, monostromatic higher up; the stipe is polysiphonous in the upper part, monosiphonous at the base. This monosiphonous part of the stipe is not present in the Snellius-II material, probably because of incomplete sampling: this part is always embedded in the coralline crusts in which the plant is anchored.

Tydemania Weber-van Bosse

Plant calcified but souple, composed of simple or branched monosiphonous main axis, bearing flabella and/or dense glomeruli of dichotomously branched ramelli.

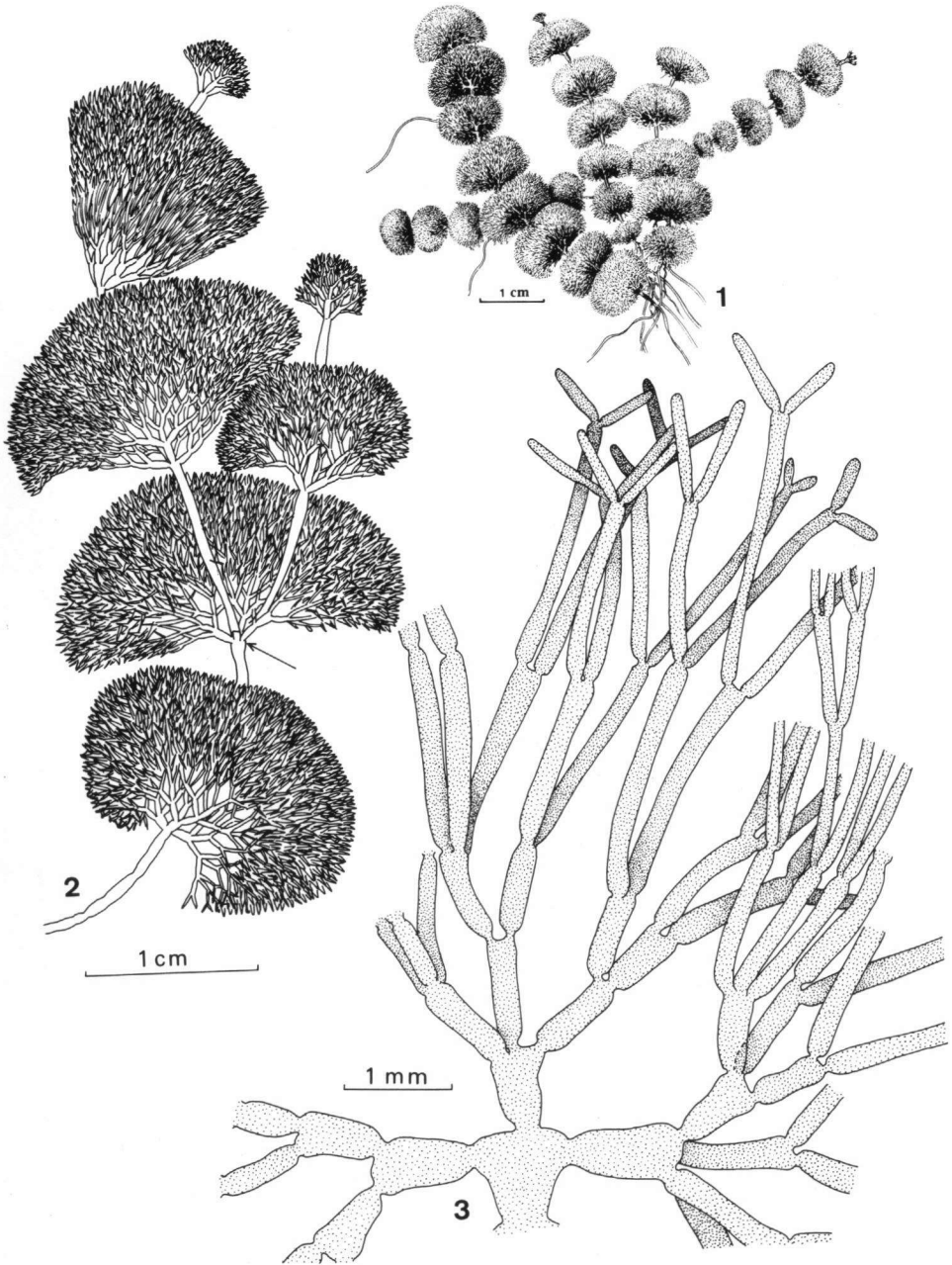


Plate 8. *Tydemania expeditionis* Weber-van Bosse: 1: Habit. 2: Detail of a branch with sidebranch and clusters of verticillate branchlets [one branchlet (arrow) has been taken away (fig. 3), uncovering the main axis]. 3: Detail of a whorl branch.

Tydemanian expeditionis Weber-van Bosse – Plate 8, figs. 1–3

Plants greyish green because of the calcification, growing as smaller isolated specimens (c. 5 cm) or forming tufts of up to 30 cm diameter (*SN 10894*). Main axis partly prostrate, partly erect, 400–450 μm in diameter, bearing contiguous glomeruli of branchlets giving a beadlike aspect to the thallus; branchlets arising from the main axis in verticils of 5–4 and dividing divaricately in alternate planes, tetra- and trichotomously at the base, dichotomously higher up; suprabasal segments of the branchlets 450 μm in diameter tapering to 100–140 μm at apices; some of the branchlets touching the substratum produce rhizoids. No flabellate branchlets in any of the Snellius-II specimens.

Specimens examined. *SN 10785 A, E:* st. 4.079, E of Komodo Is., Selat Linta, reef slope, till c. 16 m deep; *SN 10894 A, E:* st. 4.096, Komodo Is., NE cape, steep reef slope, till c. 30 m deep; *SN 10998 A, E:* st. 4.121, N of Sumbawa, Bay of Sanggar, coastal reef and sea grass; *SN 11324 A, E:* st. 4.150, NE Taka Bone Rate, Taka Garlarang atoll, edge of reef flat; *SN 11396 A, E:* st. 4.157, SW Salayer, E of Pulau Guang, sheltered sandflat, covered by seagrasses; *SN 11624 A, E:* st. 4.171, SW Salayer, N point of Pulau Bahuluang, seagrass bed; *SN 11647 A, E:* st. 4.175, SW of Salayer, N of Pulau Bahuluang, reef flat.

Geographic distribution. Indonesia, Philippines (Trono, 1969), Solomon Is. (Womersley & Bailey, 1970), Marshall & Caroline Is. (Gilmartin, 1966; Tsuda, 1972), Papua New Guinea (Coppejans, unpublished), India (Srinivasan, 1954), Maldives (Coppejans, unpublished), Red Sea (Meinesz, 1981).

Discussion. Meinesz (1981: 64) concludes from the study of material from the Red Sea that the presence or absence of flabellate branchlets might be due to ecological factors and that therefore *Tydemanian mabahithae* Nasr (without flabella) and *T. gardineri* Gepp & Gepp (with exclusively flabella) should be regarded as growth forms of *T. expeditionis*. Our recent observations in Papua New Guinea (Madang Province) corroborate this conclusion: specimens growing under overhanging coral walls are richly provided with flabellate branches (but it is rare to find this species under such conditions in that area), well lighted specimens do not have any. An experiment was done to confirm Meinesz' observation, by bringing a specimen lacking flabellae in a rather shaded aquarium (Christensen Research Institute, Malang); some weeks later a series of flabella were formed on the main axis, above the glomeruli of dichotomous branchlets. A vaucher specimen in GENT is numbered *HEC 8148*. All Snellius-II specimens were devoid of flabellate branches.

Udotea Lamouroux

Plants erect from a more or less well developed rhizoidal base, stipitate. Stipe short or long, mono- or polysiphonous, with or without cortication. Blade flabellate, sometimes proliferous or lacerate, often concentrically zonated, sometimes longitudinally striated; colour depending on the degree of calcification (which can be totally absent in some species). Thallus composed of dichotomously branched filaments, with constrictions above the dichotomies, with or without lateral appendages which can become elaborate and form a cortical layer.

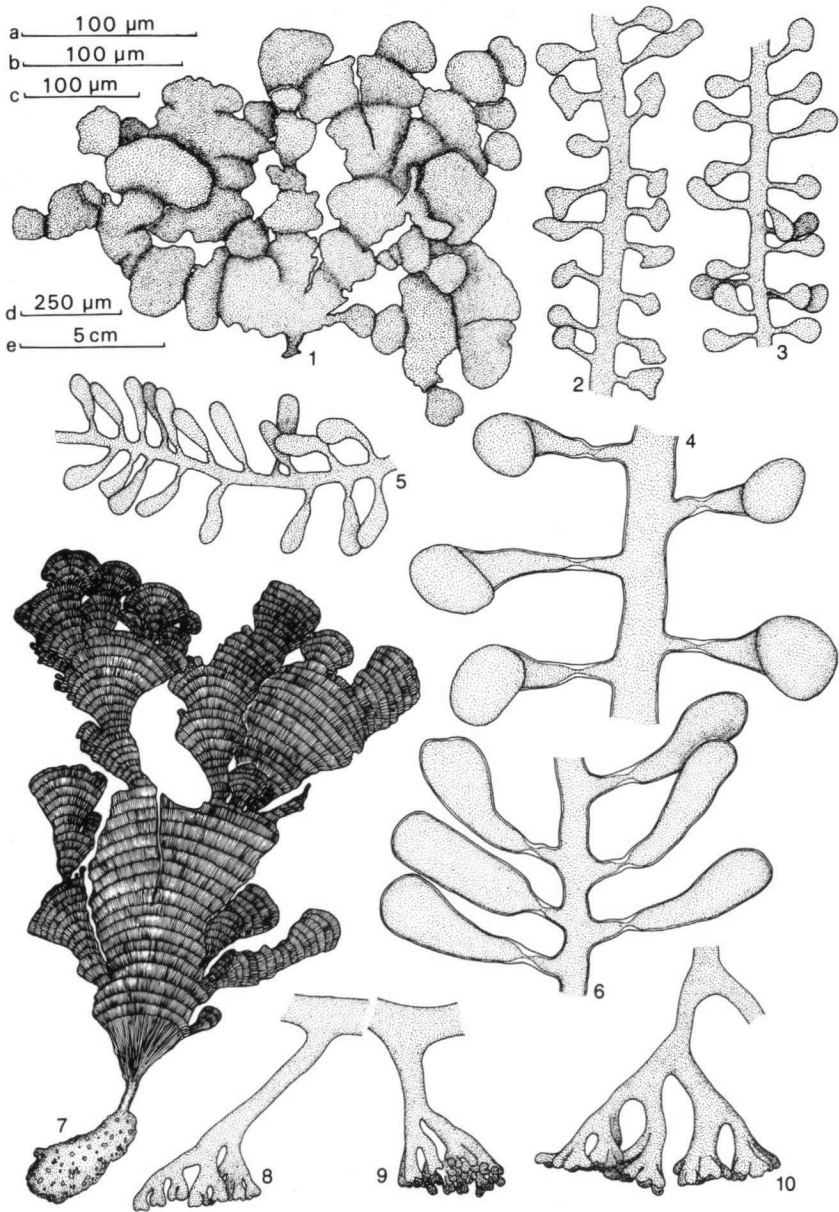


Plate 9. Anatomical details after rehydrated, decalcified herbarium specimens (the letter between brackets refers to the scale bar). — *Udotea argentea* Zanard. var. *spumosa* A. & E.S. Gepp: 1: Habit (SN 11504 A) (e). 2–6: Filaments with distichously placed, pear-shaped or oblongate lateral branchlets: 2 (SN 11355 A) (d), 3, 4 (SN 11545 E) (d), 5, 6 (SN 11505 A) (d). — *Udotea flabellum* Howe: 7: Habit (SN 11334 A) (e). 8–10: Filaments with fasciculate lateral branches: 8, 9 (SN 11285 E) (b), 10 (SN 11285 A) (a).

Udotea argentea Zanardini var. **spumosa** Gepp & Gepp – Plate 9, figs. 1–6

Plants greyish-ashy green and extremely stiff because of pronounced calcification. Stipe very short (a few mm), generally fixed by a compact mass of rhizoids, sometimes forming a pseudobulbous holdfast when growing on sand. Flabellum reaching 15 cm in height and width, rather thick, composed of superposed sub-reniform-rotundate-flabellate segments, abundantly proliferous, sometimes laterate (fig. 1), the surface minutely spumose but frequently strongly covered by small epiphytic algae. Frond filaments 30–50 μm in diameter, parallel, in 2 or more layers, sparingly dichotomous, very unevenly constricted above each dichotomy, bearing distichously, numerous, short, lateral branchlets of nearly equal length (150–200 μm) (figs. 2–6), each constricted above the base (figs. 4, 6) and elongate-pyriform with more (figs. 3, 4) or less (figs. 5, 6) pronounced head or of more irregular form (fig. 2); the branchlets contiguous, forming a cortex, concealing the main filaments.

Specimens examined. *SN 11355 A, E:* st. 4.151, NE Taka Bone Rate, Taka Garlarang atoll, silty reef flat; *SN 11504 A, SN 11505 A, E, SN 11506 A, SN 11507 A:* st. 4.161, SW Salayer, from reef crest; *SN 11545 A, E:* same station, sandy reef flat with seagrasses.

Geographic distribution. Eastern Indian Ocean, SW Pacific (Philippines).

Discussion. The Snellius-II specimens agree perfectly well with Gepp & Gepp's description (1911: 126). The typical variety differs from it by the markedly lobed heads of the lateral branchlets.

Udotea flabellum Howe – Plate 9, figs. 7–10

Plants bright green and extremely stiff and tough because of the strong calcification. Fixation by a well developed pseudobulbous holdfast. Stipe short (up to 1 cm) and compressed towards the flabellum. Blade cuneate at the base, fan-shaped, repeatedly and irregularly proliferous from the margin, the proliferations often superposed and plicated as to form a bushy plant, reaching 20 cm in height; surface markedly concentrically zonated and longitudinally striated (fig. 7). Frond filaments bearing lateral branchlets of unequal length, at irregular intervals, densely and fasciculately branched at the apex (figs. 8–10); these apices contiguous and forming a dense cortex which is very difficult to disentangle, even after decalcification.

Specimens examined. *SN 10225 A, E:* st. 4.016, Tukang Besi Is., Kaledupa reef, gently sloping reef, till c. 10 m deep; *SN 10255 A:* st. 4.027, Tukang Besi Is., Kaledupa reef, inner part of SW reef, till c. 8 m deep; *SN 11245 A, E:* st. 4.139, NE Taka Bone Rate, S of Tarupa Kecil, edge of reef flat, in *Thalassodendron*-meadow; *SN 11266 A, E:* same station; *SN 11285 A, E:* st. 4.133, NE Taka Bone Rate, E coast of Tarupa Kecil, in front of the village, sandy slope, till c. 11 m deep; *SN 11334, A, E, SN 11335 A, E:* st. 4.150, NE Taka Bone Rate, Taka Garlarang atoll, edge of reef flat; *SN 11356 A, E:* st. 4.151, NE Taka Bone Rate, Taka Garlarang atoll, silty reef flat.

Geographic distribution. In all tropical seas.

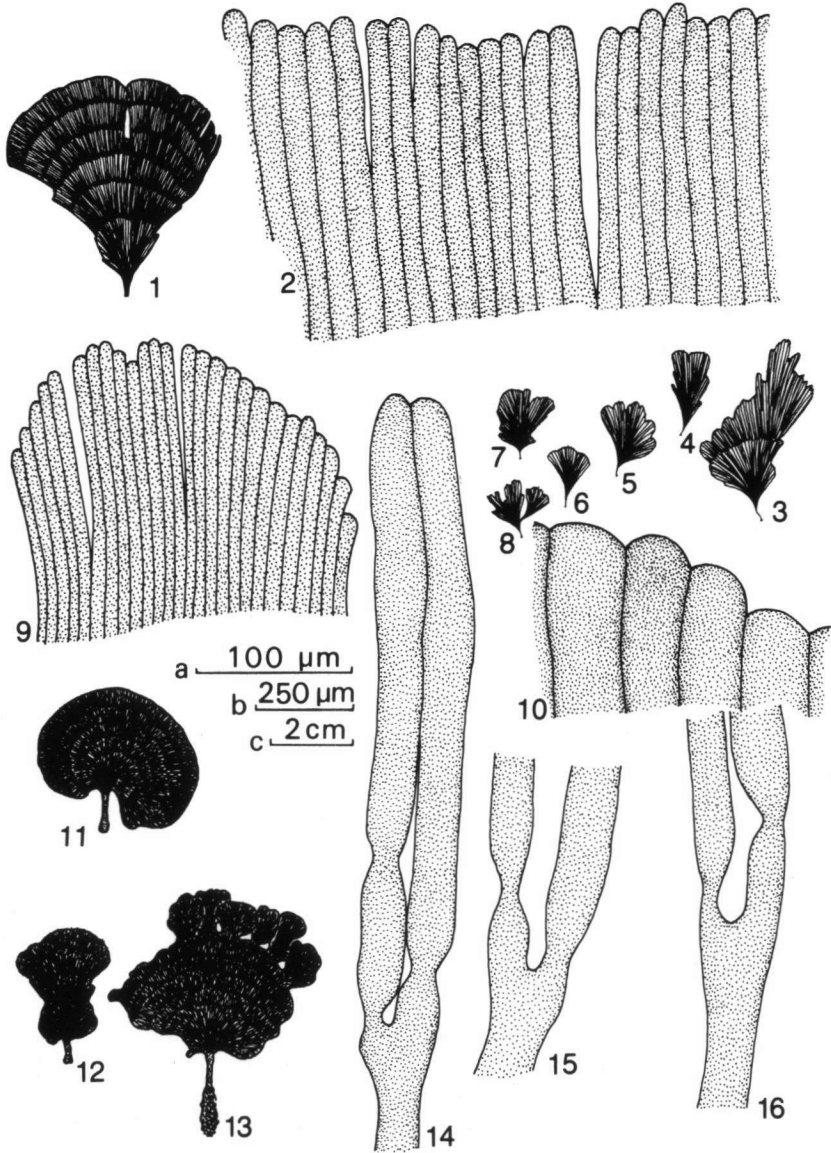


Plate 10. Anatomical details after rehydrated, decalcified herbarium specimens (the letter between brackets refers to the scale bar). — *Udotea glaucescens* Harv.: 1: Habit (SN 11247 E) (c). 2: Margin of the flabellum (SN 11247 E) (b). — *Udotea javensis* A. & E.S. Gepp: 3–8: Habit: 3–5 (SN 11667 A) (c), 6–8 (SN 11618 A) (c). 9, 10: Margin of the flabellum (SN 11508 A): 9 (b), 10 (a). — *Udotea orientalis* A. & E.S. Gepp: 11–13: Habitat (SN 11544 A) (c). 14–16: Dichotomies; supradichotomic constrictions very unequally situated: 14 (SN 10296 A) (a), 15, 16 (SN 10281 A) (a).

Discussion. Agreeing very well with Gepp & Gepp's description (1911: 132).

Udotea glaucescens Harvey – Plate 10, figs. 1, 2

Plants greyish green because of the calcification, souple. Fixation by rhizoids; stipe up to 7 mm, densely corticated; blade cuneate to flabellate, entire, sometimes partly split up lengthwise (fig. 1), monostromatic, some specimens markedly zonated (levels of dichotomies), others not zonated, up to 5 cm high. Filaments (60–)65–75 μm in diameter, radiating from the stipe to the margin, contiguous, laterally coherent by means of calcification, sometimes somewhat split up in groups at the margin (fig. 2), dichotomous, unequally constricted above the dichotomies; with appendages in the stipe, without appendages in the flabellum.

Specimens examined. SN 11247 A, E: st. 4.139, NE Taka Bone Rate, S of Tarupa Kecil, edge of reef flat, *Thalassodendron*-meadow.

Geographic distribution. Indian Ocean and tropical Pacific.

Discussion. Gepp & Gepp (1911: 113) report filament diameters of 65–105 μm in the flabellum; this dimension range is less variable in the Snellius-II material: (60–)65–75 μm and just like Harvey's specimens (in Gepp & Gepp, 1911: 114): 65–70 μm or in Gilbert & Doty's specimens (1969): "up to 85 μm ."

Udotea javensis Gepp & Gepp – Plate 10, figs. 3–9

Plants green to greyish green, souple. Monosiphonous stipe, up to 3 mm long, fixed by a lobed holdfast or by small rhizoids arising from the basal part, no cortication. Flabellum cuneate, entire or more frequently irregularly lacerate, monostromatic, in most collections up to 5 mm high, in SN 11618 up to 15 mm (figs. 6–8), and in SN 11667 even up to 40 mm (figs. 3–5). Filaments smooth, disposed as in *U. glaucescens* but 40–45 μm in diameter.

Specimens examined. SN 10874 A: st. 4.090, E of Komodo Is., Selat Linta, coastal reef flat; SN 11032 A, E: st. 4.125, N of Sumbawa, Bay of Sanggar, shallow sandy area; SN 11089 A: st. 4.114, N of Sumbawa, Bay of Sanggar, lagoon side of reef barrier, till 20 m deep; SN 11415 A: st. 4.157, SW Salayer, E of Pulau Guang, sheltered sandflat; SN 11508 A, E: st. 4.161, SW Salayer, reef crest; SN 11618 A: st. 4.158, SW Salayer, near cape Batu Kerapo, sheltered bay; SN 11661 A: st. 4.175, SW Salayer, N of Pulau Bahuluang, reef flat; SN 11667 A: st. 4.176, SW Salayer, N of Pulau Bahuluang, reef flat.

Geographic distribution. Tropical Indian and Western Pacific Oceans; S Japan.

Discussion. The small green (almost uncalcified) specimens fully agree with Gepp & Gepp's description (1911: 110); the larger ones rather look like *U. glaucescens* especially because of their typical greyish green colour. But the monosiphonous, uncorticated stipe and the small diameter of the filaments confirm their identification as *U. javensis*. Egerod (1975: 59) also discusses the fact that *U. javensis* sometimes is calcified but may remain uncalcified under certain circumstances.

Udotea orientalis Gepp & Gepp – Plate 10, figs. 11–16

Plants greyish green, rather thick and somewhat stiff. Fixation by a more or less bulbous group of rhizoids (fig. 13). Stipe simple, 1–2 cm high, 1–2 mm thick, corticated; blade flabellate, mostly with cordate to auriculate base (figs. 11–13), 2–3 cm in diameter, sometimes proliferous at the upper margin (fig. 13), surface longitudinally filamentous-striate, markedly zoned, pluristromatic. Frond filaments (27–)30 (–35) μm in diameter, dichotomous, supradichotomic constrictions very unequally situated (figs. 14–16), smooth, without lateral branchlets or appendages, closely interwoven in several layers, conglutinated by the calcification.

Specimens examined. *SN 10281 A*: st. 4.030, Tukang Besi Is., W coast Binongko, reef slope, till c. 20 m deep; *SN 10296 A*: st. 4.030, Tukang Besi Is., W coast Binongko, reef flat; *SN 11034 A, E*: st. 4.123, N of Sumbawa, Bay of Sanggar; *SN 11510 A*: st. 4.161, SW Salayer, reef crest; *SN 11544 A, E*: st. 4.161, SW Salayer, sandy reef flat; *SN 11615 A, E*: st. 4.158, SW Salayer, near Cape Batu Kerapo, sheltered bay.

Geographic distribution. Indo-Pacific.

Discussion. Agreeing with Gepp & Gepp's description (1911: 119) in all characters.

IDENTIFICATION KEY OF THE CAULERPALES

(except *Caulerpa*, *Halimeda*)

This key of the Caulerpales from the Snellius-II expedition comprises all species of this group recorded from Indonesia (Gepp & Gepp, 1911; Taylor, 1966; Weber-van Bosse, 1913), except the seldomly recorded *Boodleopsis siphonacea* Gepp & Gepp, *Penicillus nodulosus* Blainville, *P. sibogae* Gepp & Gepp, *Udotea explanata* Gepp & Gepp, and *U. papillosa* Gepp & Gepp. These five species are not known to occur in the Philippines (Silva et al., 1987), or, except the two *Penicillus* species, in Northern Australia (Lewis, 1987).

- 1a. Thallus composed of free filaments 2
- b. Thallus composed of intricated or conglutinated filaments 4
- 2a. Thallus composed of a monosiphonous axis provided with glomeruli (verticils of mainly dichotomously branching filaments) . . . **Tydemanian expeditionis**
- b. No main axis, no verticils, all erect filaments alike **Chlorodesmis** 3
- 3a. Supporting segment of the dichotomy convex (not truncated), supradichotomic constrictions very unequally situated **Chlorodesmis fastigiata**
- b. Supporting segment of the dichotomy truncated, supradichotomic constrictions at same level **Chlorodesmis hildenbrandtii**
- 4a. Thallus calcified 5
- b. Thallus not calcified 10
- 5a. Thallus composed of a monosiphonous axis provided with glomeruli (verticils of mainly dichotomously branching filaments) . . **Tydemanian expeditionis**
- b. Thallus composed of a stipitate blade 6
- 6a. Blade filaments without appendages 7
- b. Blade filaments with appendages 9

- 7a. Filaments in several layers (blade polystromatic) **Udotea orientalis**
- b. Filaments in a single layer (blade monostromatic) 8
- 8a. Filament diameter 40–45 μm **Udotea javensis**
- b. Filament diameter 60–75 μm **Udotea glaucescens**
- 9a. Blade filament appendages pear-shaped or oblong (not ramified)
 - Udotea argentea var. spumosa**
 - b. Blade filament appendages fasciculately ramified **Udotea flabellum**
- 10a. Filaments without special appendages 11
- b. Filaments with special appendages (tenacula with prongs) 16
- 11a. Blade monostromatic 12
- b. Blade polystromatic **Avrainvillea** 13
- 12a. Blade without concentric zonation, filaments straight, contiguous, stipe monosiphonous, uncorticated **Udotea javensis**
- b. Blade with concentric zonation, filaments sinuous, stipe monosiphonous, corticated **Rhipiliopsis gracilis**
- 13a. Thallus fixed with a pseudobulbous holdfast, filaments straight, neither torulose nor tortuous **Avrainvillea erecta/obscura**
- b. No pseudobulbous holdfast, filaments torulose or tortuous, at least towards the apices 14
- 14a. Filament apices always rounded **Avrainvillea amadelpa**
- b. Some filaments rounded, others pointed or all of them exclusively pointed 15
- 15a. Filament apices partly rounded and partly pointed; blade surface velutinous
 - Avrainvillea longicaulis**
 - b. Filament apices generally pointed but occasionally also some rounded ones occur; blade surface smooth (papery) **Avrainvillea lacerata**
- 16a. Flabella supported by well developed, sometimes branched, solid stipes
 - Rhipilia diaphana**
 - b. No such stipe 17
- 17a. Tenacula with 2–3 prongs **Rhipilia orientalis**
- b. Tenacula with (2–)4–5(–6) prongs **Rhipilia nigrescens**

DISCUSSION

As we already argued (Coppejans & Prud'homme van Reine, 1989a) it is not correct to compare the number of species collected during the Siboga Expedition, where phycological collecting was done during a whole year and all over the Indonesian archipelago, with the number of species from the Snellius-II Expedition where phycologists collected during one month and exclusively in the eastern part of Indonesia. From our collections a new species of *Rhipilia* is described (*R. nigrescens*) and *Rhipiliopsis gracilis*, only recently described from Australia (Kraft, 1986) was also collected. *Tydemania expeditionis* seems to be a rather common species in this area as it has been collected at numerous study sites. We did not collect *Boodleopsis siphonacea*, *Penicillus sibogae*, *Udotea explanata*, and *U. papillosa*, all described from Siboga material, nor *Penicillus nodulosus*, recorded by Gepp & Gepp (1911) from the Moluccas.

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