Cryptogamie, Algol., 2000, 21 (2): 111-131

S0181156800)001070/FLA

Taxonomic observations on *Hypoglossum* (Delesseriaceae, Rhodophyta) in the Indian Ocean and Malayan region, including the description of two new species[1]

Michael J. WYNNE[a]* & *Olivier DE CLERCK*[b]

[a] *Department of Biology, University of Michigan, Ann Arbor, MI 48109, USA*

[b] *Laboratory of Botany, University of Ghent, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium*

(Received 2 August 1999, accepted 20 January 2000)

Abstract — Two new species of the genus *Hypoglossum* Kützing (Delesseriaceae, Rhodophyta) are described: *H. androlamellare* sp. nov. from Zanzibar Island, Tanzania, and *H. annae* sp. nov. from the Malay Archipelago. The former is the first species of *Hypoglossum* to be reported from Tanzania and is distinguished by a combination of its overall habit, the chevron-like arrangement of the spermatangial sori, and the non-participation of lateral pericentral cells in sporangium formation within the tetrasporangia sori. The latter species is based on the material identified by Weber-van Bosse as "*Hypoglossum spathulatum* Kützing" (Kützing, 1849; 1869, as *Delesseria spathulata* Sonder), which has been recognized as having nothing to do with the present taxonomic placement of that species, *Apoglossum spathulatum* (Sonder) Womersley *et* Shepley. *H. annae* is distinguished by the restriction of its reproductive structures to relatively small final-order, or penultimate-order, bladelets. *Hypoglossum simulans* M.J. Wynne, I.R. Price *et* D.L. Ballantine is newly reported for Zanzibar. © 2000 Adac/Éditions scientifiques et médicales Elsevier SAS

Delesseriaceae / *Hypoglossum* / *H. androlamellare* / *H. annae* / *H. simulans* / Malay Archipelago / marine red algae / Tanzania / Rhodophyta / Zanzibar Island

Résumé — Quelques observations taxinomiques sur le genre *Hypoglossum* (Delesseriaceae, Rhodophyta) dans l'océan Indien et la région malaise, comprenant la description de deux nouvelles espèces. Deux espèces nouvelles du genre *Hypoglossum* Kützing (Delesseriaceae, Rhodophyta) sont décrites : *H. androlamellare* sp. nov. de l'île Zanzibar, Tanzanie, et *H. annae* sp. nov. de l'archipel malais. *H. androlamellare* est la première espèce d'*Hypoglossum* rapportée de Tanzanie ; elle se distingue des autres par son aspect général, la disposition en chevron de ses sores de sporocystes et la non-participation des cellules péricentrales latérales à la formation des sporocystes à l'intérieur des sores de tétrasporocystes. La seconde espèce, *H. annae*, est fondée sur le matériel identifié par Weber-van Bosse sous le nom « *Hypoglossum spathulatum* Kützing » (Kützing, 1849 ; 1869, *sub Delesseria spathulata* Sonder). On a en effet montré que le matériel identifié par Weber-van Bosse n'a rien à voir avec cette espèce, actuellement connue sous le nom de *Apoglossum spathulatum* (Sonder) Womersley *et* Shepley. *H. annae* se distingue par des structures reproductrices restreintes aux petits rameaux foliacés de dernier ou d'avant-dernier ordre.

* Correspondence and reprints: mwynne@umich.edu

[1] This paper is dedicated to Professor Francis Magne to honour his 75th birthday.

Hypoglossum simulans M.J. Wynne, I.R. Price *et* D.L. Ballantine est rapportée pour la première fois de Zanzibar.

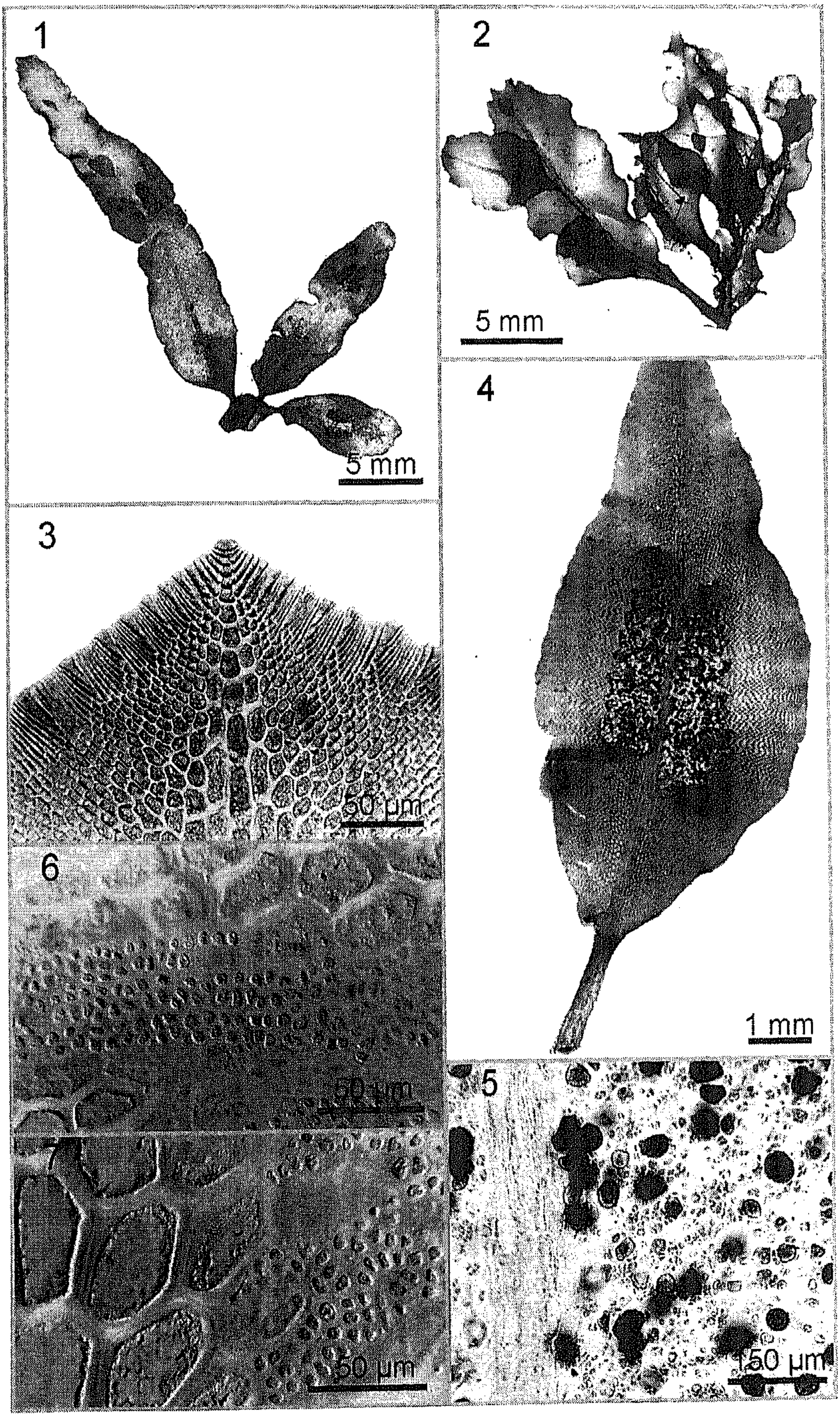
algue rouge marine / archipel malais / Delesseriaceae / *Hypoglossum* / *H. androlamellare* / *H. annae* / *H. simulans* / Tanzanie / Rhodophyta / île Zanzibar

INTRODUCTION

This study is based on recent collections of *Hypoglossum* from East Africa, including an undescribed species, and a re-examination of collections of a *Hypoglossum* made by Weber-van Bosse in the Malay Archipelago during the Siboga Expedition of 1899–1900. The only previous record of the delesseriacean genus *Hypoglossum* from East Africa was that made by Lawson (1980) as "*Hypoglossum* sp." from Zanzibar, Tanzania. Weber-van Bosse (1923) reported *H. spathulatum* (Kützing) J. Agardh from four collections in Malaya [see De Clerck & Coppejans (1997) for a map of the Malay Archipelago]. Similarly, this same species has been reported from India (Børgesen, 1932; Krishnamurthy & Varadarajan, 1990), the Red Sea (Nasr, 1947), and the Persian Gulf (Nizamuddin & Gessner, 1970). Womersley & Shepley (1982), however, found that the Western Australian type of this species (Sonder, 1845, as *Delesseria spathulata*) belongs to *Apoglossum* and transferred it to that genus. Because some of the reported "*Hypoglossum spathulatum*" appear to be assignable to *Hypoglossum*, such as *H. heterocystideum* (J. Agardh) J. Agardh (Silva *et al.*, 1996), it was desirable to re-study voucher material to determine the status of these collections. Weber-van Bosse's Malayan collections of "*Hypoglossum spathulatum*" in Leiden provide the basis for the description of a new species, *H. annae*.

MATERIALS AND METHODS

Hypoglossum androlamellare and *H. simulans* were collected using SCUBA or snorkelling and were processed as herbarium specimens as well as a part being preserved in 4 % Formalin/seawater. Slide material was stained in a mixture of 1 g aniline blue powder, 70 ml Karo®, 30 ml distilled water, 5 ml acetic acid and was deposited in GENT and MICH. Collections of *H. annae*, received on loan from L, were collected during the Siboga Expedition in Indonesia and the Philippines. Børgesen's collections of *H. spathulatum* from India were received on loan from C and examined. For comparative purposes a paratype specimen of *H. abyssicolum* W.R. Taylor and a topotype specimen of *H. guineense* G.W. Lawson *et* D.M. John (from Vernon Bank, Ghana) both in MICH were also examined. Line-drawings were prepared using a camera lucida mounted on a Leitz Diaplan microscope. Photographs were taken on a Leitz Diaplan microscope with both brightfield and Nomarski interference contrast optics. Agfa APX25 was used in making black and white photographs. Abbreviations of herbaria follow those of Holmgren *et al.* (1990).



Figs 1–7. *Hypoglossum androlamellare.* Fig. 1. Holotype (ODC 634). Fig. 2. Habit of a wet-preserved specimen. Fig. 3. Detail of a blade apex. Fig. 4. Tetrasporangial blade. Fig. 5. Detail of a tetrasporangial sorus. Fig. 6. Detail of a spermatangial sorus. Fig. 7. Detail of a spermatangial sorus close to the midrib.

OBSERVATIONS

Hypoglossum androlamellare M.J. Wynne *et* De Clerck sp. nov. (Figs 1–10)

Vegetative Structure

The alga consists of undulate blades with an erect habit, up to 4 cm tall, arising from a single holdfast (Fig. 1). The blades are monostromatic except along the midrib, which becomes well corticated in the lower portion of the thallus (375–600 µm in diameter). The blades are alternately branched to three or four orders from the midrib. Individual blades are lanceolate-ligulate (Fig. 1) to obovate (Fig. 4), with rounded to obtuse apices, up to 4 mm wide and 18 mm long. Blade margins are smooth and undulating (Fig. 2). Growth takes place by a transversely dividing apical cell terminating each blade (Fig. 3), with lateral pericentral cells formed prior to the transverse pericentral cells. All cells of the second-order rows produce third-order cell rows (Fig. 10). Cells comprising the alae are polygonal near the midrib (40–53 µm long and 17–22 µm wide), becoming more linear in shape closer to the blade margins (*ca* 30 µm long and 8–10 µm wide). Alar cells are not arranged in longitudinal rows.

Reproductive Structure

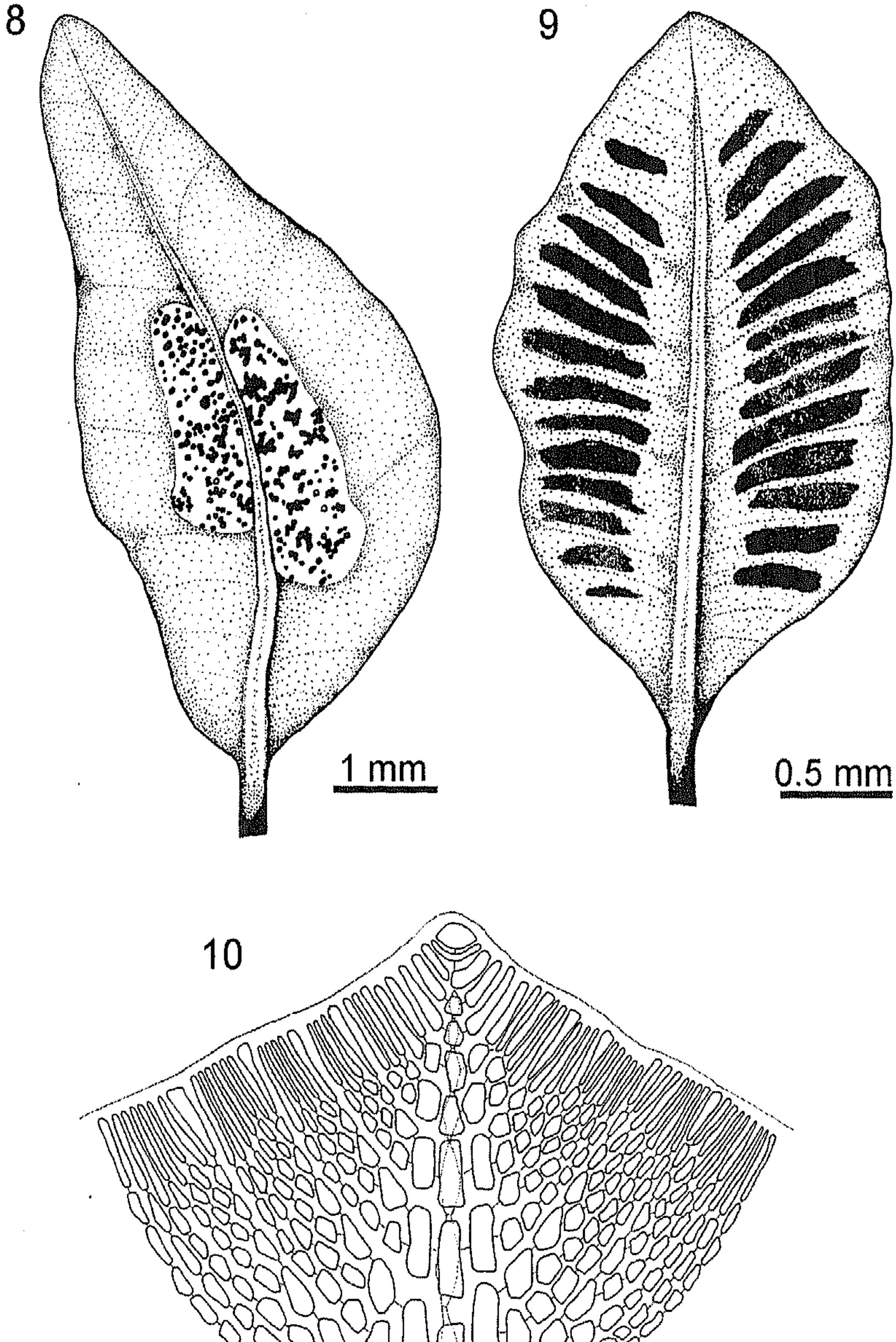
Tetrasporangial thalli produce discrete 'twin' sori, symmetrically placed on both sides of the midrib in the mid-region or the upper half of ultimate- or penultimate-order blades (Fig. 4). Mature sori are up to 1.5 mm long and 0.6 mm wide. The number of sori per blade varies, some blades producing a single pair of sori and other blades producing two pairs of sori. Lateral pericentral cells do not participate in the production of tetrasporangia (Figs 5 and 8). The combination of the two sori gives a cordate aspect to the soral region. Tetrasporangia are tetrahedrally divided and measure 30–37 µm in diameter at maturity.

Male thalli bear spermatangial sori arranged in conspicuous chevrons, diagonally arranged along both sides of the midrib (Fig. 9), with about 10 to 26 chevrons being produced per blade. Each chevron is 90–105 µm wide and 300–700 µm long, separated from one another by a sterile region 50–80 µm wide (Fig. 6). Spermatangial sori are separated from the midrib by a sterile zone, about 100–130 µm wide, and do not reach the blade margins (Fig. 7).

Female thalli were not observed.

Description

Alga ex laminis undulatis cum habitu erecto consistens, usque 4 cm altis, e singulari fundamento enascentibus; costa media ad basem thalli (375–600 µm in diam.) bene corticatescens; ramificatio laminarum alterna in tres aut quattuor ordines; singulae laminae oblongae, usque 4 mm latae, 18 mm longae, cum apicibus rotundis aut obtusis; margines laminarum leves, undulantes; omnes cellulae serierum cellularum secundi ordinis series cellularum tertii ordinis procreantes; alae propre costam ex cellulis polygonis (ca 40–53 µm long. et 17–22 µm lat.) consistentes, propre margines laminae ex cellulis linearioribus (ca 30 µm long. et 8–10 µm lat.) consistentes; cellulae alae in



Figs 8–10. *Hypoglossum androlamellare*. Fig. 8. Habit of a blade with tetrasporangial sori. Fig. 9. Habit of a blade with spermatangial sori. Fig. 10. Detail of the apical organization of a blade.

seriebus longitudinalibus non dispositae; thalli tetrasporangiales soros discretos geminatos procreant similiter positos in ambo lateribus mediae costa in dimidio supero laminarum ultimi vel penultimi ordinis; sori maturi usque 1.5 mm longi, 0.6 mm lati; cellulae laterales pericentrales tetrasporangia non formantes; tetrasporangia matura 30–37 µm in diametro; thalli masculi cum soris spermatangialibus in lamellis conspicuis ordinatis, secundum ambo latera costae media diagonaliter dispositis; ca 10–26 lamellae per laminam productae; omnis lamellae 90–105 µm latae, 300–700 µm longae, alia ab alia separata regione sterili 50–80 µm latae; sori spermatangiales a costa separati zona sterili, ca 100–130 µm latae, margines laminae non contingentes; thalli feminei non observati.

Etymology: the specific epithet, Gr. *andro*, male; L. *lamellaris*, gill-like, alludes to the chevron- or gill-like arrangement of the spermatangial sori.

Holotype: *legit O. De Clerck* (ODC 634), 10.vii.1997, Kunduchi, Fungu Reef, Zanzibar Island, Tanzania; epilithic, 15 m depth; tetrasporic. Deposited in GENT (Fig. 1).
Isotype: Deposited in MICH.

Hypoglossum simulans M.J. Wynne, I.R. Price *et* D.L. Ballantine (Figs 11–17)

TANZANIA. Chwaka Bay, Zanzibar Island: 17.vii.1997, *legit* Olivier De Clerck (ODC 711), mangrove tide channel; male, female and tetrasporangiate; in GENT and MICH. Nungwi, Zanzibar Island: 26.vii.1997, *legit* Tim Roels (RT 85); male, female and tetrasporangiate; in GENT and MICH.

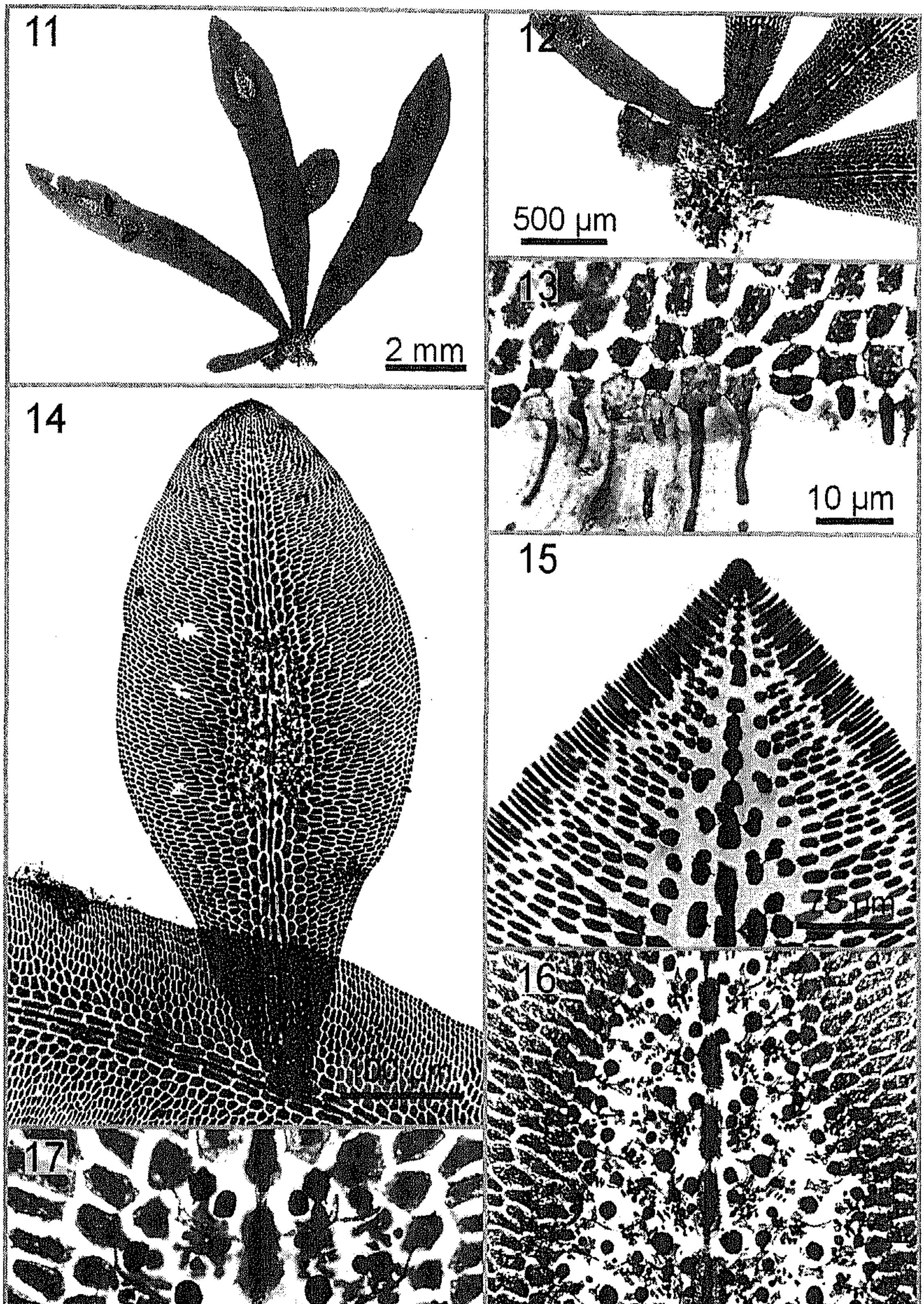
Vegetative Structure

Thalli form small creeping tufts on leaves of the seagrass *Thalassodendron ciliatum* (Forrskål) Den Hartog, up to 12 mm long (Fig. 11). Thalli are attached primarily at a single point (Fig. 12), from which several first-order blades arise. These blades are attached often at several points to the substratum by means of small groups of rhizoids which arise from the margins (Fig. 13). Thalli generally branch only up to the second order, third-order blades being rare. Branches are formed endogenously and arise predominantly on the adaxial surface, less frequently from both surfaces. Often a new branch is formed from the basal axial cell of a young blade.

Blade apices are acute or rounded. The lateral pericentral cells cut off second-order rows, but not all of the second-order cells bear third-order rows (type 2 apex) (Fig. 15). All apical cells of third-order rows reach the blade margin. The midrib remains uncorticated throughout.

Reproductive Structure

Tetrasporangia are formed in discrete, narrow, elongate sori (450–750 µm long, 240–300 µm wide) on both sides of the midrib (Fig. 14). Up to two soral pairs have been observed on a single blade. The lateral but not the transverse pericentral cells are involved in the formation of tetrasporangia. Apart from the lateral pericentral cells and cells from the second-order and third-order cell rows close to the midrib, tetrasporangia are also formed by cortical cells (Fig. 16). Mature tetrasporangia measure 45–60 µm in diameter (Fig. 17).



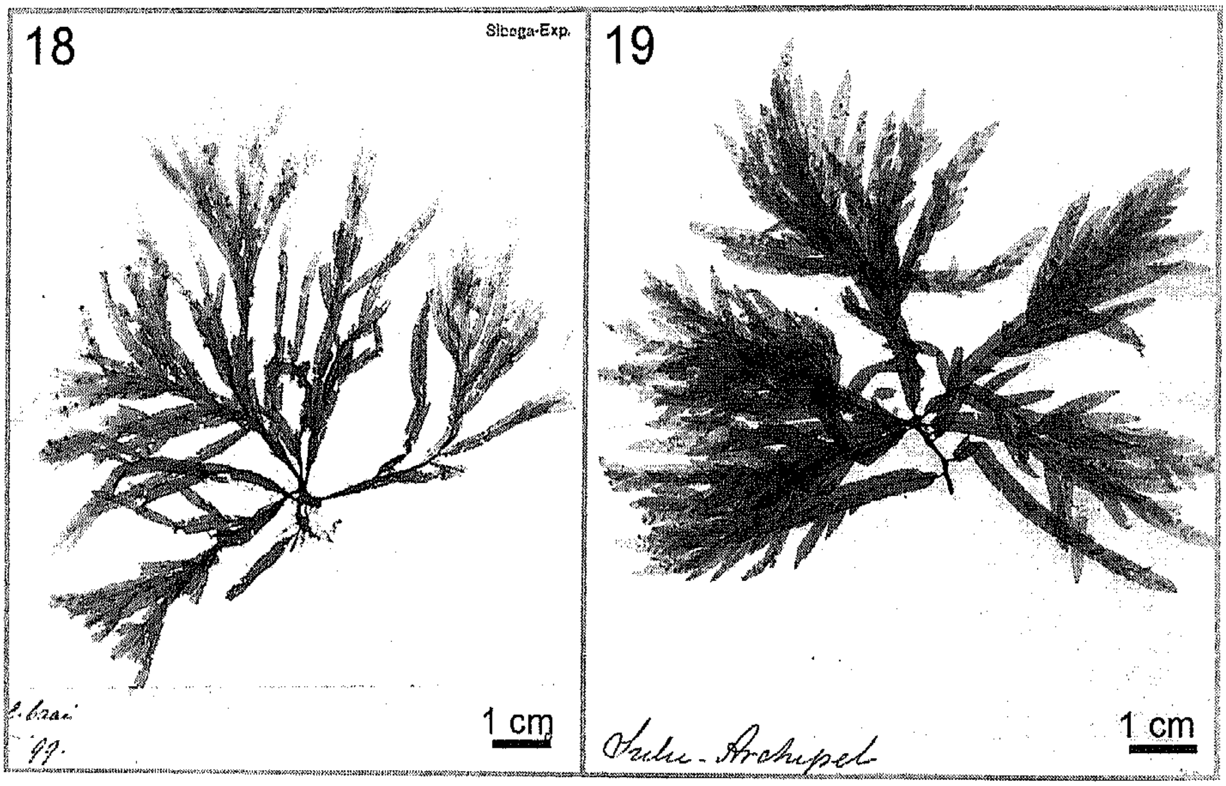
Figs 11–17. *Hypoglossum simulans*. Fig. 11. Habit. Fig. 12. Base. Fig. 13. Detail of marginal rhizoids. Fig. 14. Detail of a young blade with an immature sporangial sorus [notice the wing cells orientated in longitudinal rows]. Fig. 15. Detail of the apical organization. Figs 16–17. Details of tetrasporangial sori.

Spermatangia are produced in small discrete sori scattered over both surfaces of the blade. Individual sori are often produced from a single cell of the alae.

Hypoglossum annae M.J. Wynne *et* De Clerck sp. nov. (Figs 18–22)

Vegetative Structure

The alga consists of from one to several principal axes arising from a conspicuous base. Fronds are 8–14 cm long, and primary blades are 4–6 mm wide. Thalli are branched to three or four orders (Figs 18 and 19). Secondary blades are produced mainly alternately, rarely in an opposite manner. All orders of branching exhibit the same structure. Principal blades become denuded below, leaving the corticated midrib as a stipe-like portion, 1–2 cm long. Blade margins are smooth; projections or teeth formed by the simple extension of marginal cells have not been observed.

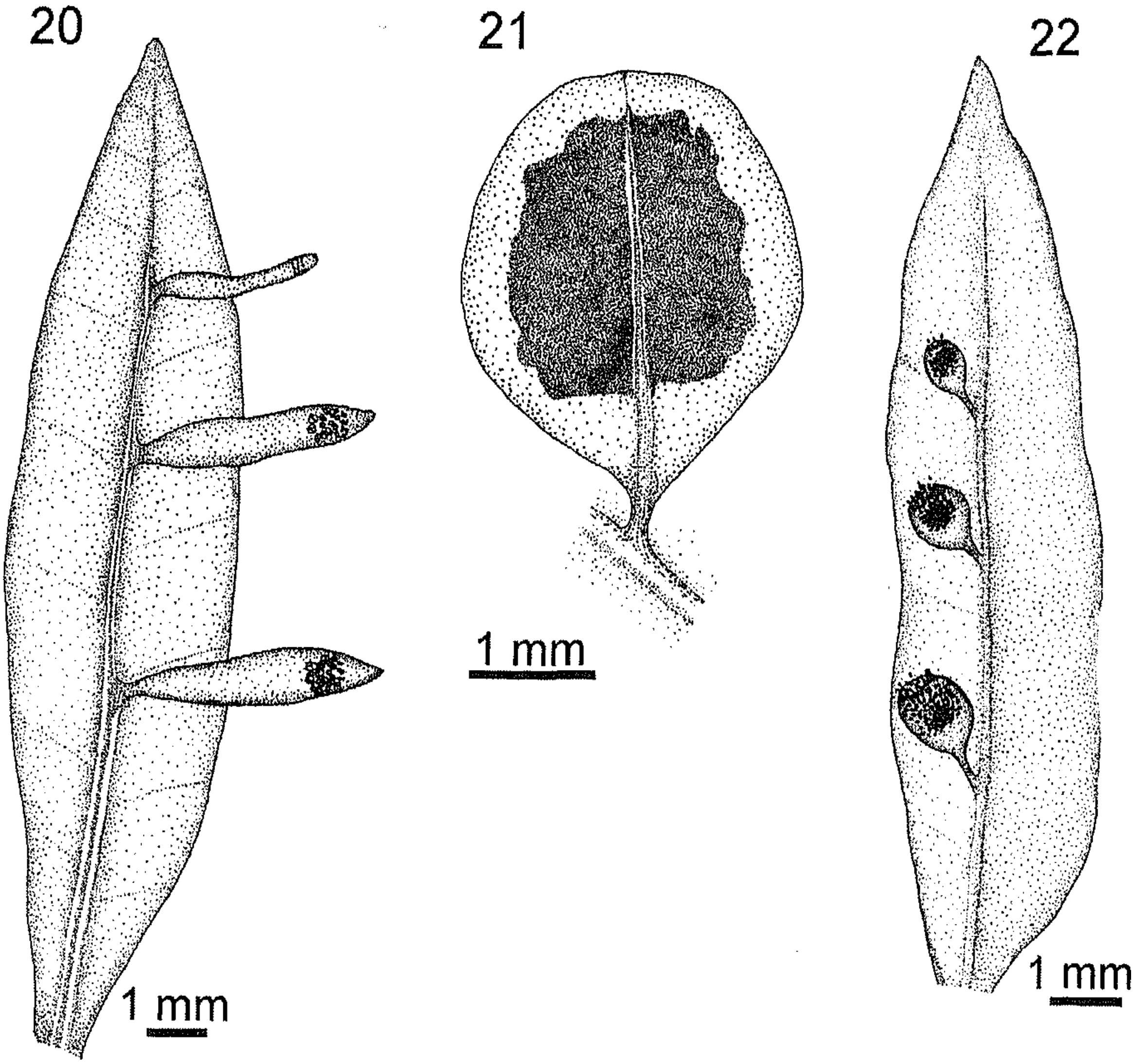


Figs 18–19. *Hypoglossum annae*. Fig. 18. Holotype (L 941.98-52). Fig. 19. Paratype (L 941.98-55).

Growth takes place by means of a transversely dividing apical cell. The lateral and transverse pericentral cells start to develop 4–8 segments from the apex. Only the inner 4–5 cells of the second-order rows produce third-order rows (Type 2 apex, Wynne *et al.*, 1989). The terminal cells of both second- and third-order rows are typically narrow and elongate in young parts of the apices. Lower down, marginal cells are similar in appearance to the other wing cells.

Reproductive Structure

Tetrasporangia develop in small lanceolate final-order bladelets (2.0–3.5 mm long, 400–600 µm wide) (Fig. 20). Tetrasporangia are produced in an acropetal sequence. In older bladelets sporangia appear to be formed only in the upper half of the bladelet, but this is merely due to the fact that sporangia in the lower portions of the bladelet have already been released. The relatively narrow width and the abundant formation of sporangia cause the tetrasporangial bladelets to become terete and have a stichidium-like appearance.



Figs 20–22. *Hypoglossum annae*. Fig. 20. A blade bearing three sporangial bladelets. Fig. 21. A spermatangial blade. Fig. 22. A blade bearing three stalked cystocarps.

Transverse as well as lateral pericentral cells and second-order cell rows are involved in the formation of sporangia. Probably only a single row of cells develops from the lateral pericentral cells. There is no direct evidence that cortex cells are involved in the formation of tetrasporangia in that all sporangia in a single segment appear to be at a similar stage of development. Mature tetrasporangia measure 100–130 µm in diameter.

Spermatangia are produced in small, ovate final-order bladelets (3.0–3.7 mm long, 2.2.–2.8 mm wide), forming a pair of sori on both sides of the primary cell row

(Fig. 21). Lateral pericentral cells generally participate in spermatangial production. Transverse pericentral cells remain undivided except one or two cells near the distal end of the bladelet, forming a connection between the sori. Lateral pericentral cells in spermatangial bladelets produce only two rows of second-order rows.

Cystocarp-bearing bladelets occur sporadically along the midrib of penultimate blades. These fertile bladelets are 1.0–1.5 mm long and are narrowly stipitate (Fig. 22). The stalk is 400–500 μm long and 150 μm in diameter. The mature cystocarps measure 900–1000 μm wide and 1100–1300 μm long and are ostiolate and spherical. The carposporangia are 40–60 μm long and 25–35 μm broad.

Description

Alga ex uno ad aliquot axibus principalibus e base conspicua enascentibus constans; thalli 8–14 cm longi; laminae primariae 4–6 mm latae, ad tres vel quattuor ordines ramificatione; laminae secundae praecipue alternatim productae, raro in modo opposito; laminae principales infra denudatae, costa corticata sic parte stipitata, 1–2 cm longa; margines laminae laeves; solae interiores 4–5 cellulae serierum secundi ordinis series cellularum tertii ordinis procreantes (Typus 2 apex); tetrasporangia in sequentia acropeta in laminis ultimae ordinis parvis lanceolatis evoluta (2.0–3.5 mm longis, 400–600 μm latis); hae laminae tetrasporangiales teretes et aspectu simili stichido; cellulae pericentrales laterales et transversales sporangia facientes; tetrasporangia 100–130 μm in diametro; spermatangia in laminis parvis ovatis ultimae ordinis producta, parem sororum in ambo lateribus serei cellularum primariarum; cellulae pericentrales laterales spermatangia facientes; cellulae pericentrales laterales in laminis spermatangialibus solum duo series serierum secundae ordinis procreantes; cystocarpias-ferentes laminae passim in costa laminarum penultimatae ordinis, 1.0–1.5 mm longae et anguste stipitatae; cystocarpiae maturae 900–1000 μm in latae, 1100–1300 μm longae, ostiolo et sphericae.

Etymology: the specific epithet honors the collector, Anna Weber-van Bosse of Eerbeck, The Netherlands.

Holotype: *legit* Anna Weber-van Bosse (L 941.98-52). Station 33. Pidjot Bay [situated 6°02'S 115°47'E, on Lombok, Indonesia], 25.iii.1899 (male, cystocarpic, and tetrasporic). A total of six cards, consisting of male, female, and tetrasporic specimens, are in Leiden under this number. A cystocarpic specimen (Fig. 18) is designated the Holotype; the other cards are treated as Isotypes, all remaining in L.

Additional paratype collections (all Weber-van Bosse collections in L): L941.98-29. Station 64. Tanah Djampea [situated 7°00'S 120°34'E, current name Tanahjampea, Indonesia]; 30 m, sterile.

L941.98-55. Station 80. Banc de Bornéo, Sulu Archipelago [situated approx. 6°N 120°E, now belongs to the Philippines], 7–13 fathoms, tetrasporic.

L941.98-30. Station 99. North Ubian [situated 6°07'N 120°26'E, an island in the Sulu Archipelago, Philippines]; 9 fathoms, sterile. (Fig. 19).

DISCUSSION

Hypoglossum is currently recognized to contain about 26 species (Womersley & Shepley, 1982; Wynne, 1994; Yoshida, 1998). The more significant taxonomic criteria include pattern of growth (monopodial or sympodial), habit (erect or prostrate), apical organization (Type 1 or Type 2), participation or lack of participation of lateral pericentral cells in the formation of tetrasporangia, shape and arrangement of the spermatangial and tetrasporangial sori, and the restriction of tetrasporangial production to a single (primary) layer or several layers of the blade (see Table 1 in Appendix). Less important criteria include branching pattern (opposite or alternate), blade margins (entire or dentate), blade colour, and arrangement of the cells of the alae (in longitudinal rows or not so). It is usually a unique combination of these traits that is used to distinguish individual species within the genus. A Key to species[2] is herein presented:

1a. A 3rd-order row produced from every cell of the 2nd-order rows 2

1b. A 3rd-order row not produced from every cell of the 2nd-order rows 21

2a. Branching of the thallus regularly sympodial, blades usually revolute .... *H. revolutum*

2b. Branching of the thallus regularly monopodial 3

3a. Branching arising and emerging from the midline of the midrib of parent blade.... 4

3b. Branches arising and emerging at points between the blade margin and midline (midrib) of the parent blade .... *H. anomalum*

4a. Blade margins smooth (sometimes with marginal rhizoids but never serrate/dentate) 5

4b. Blade margins not smooth (minutely dentate, serrate, or strongly fimbriate.. 18

5a. Habit mostly prostrate or decumbent, with multiple attachments to substrate or host. 6

5b. Habit essentially erect, attached by a discrete holdfast 11

6a. Prostrate axis very narrow, rhizomatous, giving rise to erect simple (potentially fertile) blades .... *H. rhizophorum*

6b. Prostrate axis not narrow but blade-like 7

7a. Prostrate axis regularly constricted, nodal regions forming attachment organs, oppositely arising more prostrate axes, and erect simple (potentially fertile) blades .... *H. caloglossoides*

7b. Thallus lacking such an organization 8

8a. Branching regularly and strictly opposite .... *H. geminatum*

8b. Branching alternate, often with a branch arising from the basal segment of parent blade, giving the false impression of opposite branching 9

9a. Lateral pericentral cells participating in formation of tetrasporangia 10

9b. Lateral pericentral cells not participating in formation of tetrasporangia .... *H. nipponicum*

10a. Blades with acute apices and more narrow (to 1.5 mm wide); little branched; blades often marginal rhizoids or forming a dense apical tuft; tetrasporangial sori oblong .... *H. barbatum*

10b. Blades with broadly rounded to truncate apices and broader (to 2 mm wide); a greater degree of branching; blades with some marginal rhizoids and also formed when injured; tetrasporangial sori short and ovate .... *H. wynnei*

11a. (comes from 5b). Stature of thallus small, 1 cm tall or less; one or more (sub-) simple blades arising from a single discoid holdfast 12

11b. Stature of thallus tall, at least 3 cm tall (or much taller); usually 2 or more orders of branching 13

12a. Tetrasporangial sori running indefinitely distally .... *H. subsimplex*

12b. Tetrasporangial sori small, discrete, ovate .... *H. minimum*

13a. Lateral pericentral cells participating in formation of tetrasporangia 14

13b. Lateral pericentral cells not participating in formation of tetrasporangia 17

[1] *H. retusum* and *H. tortile* have not been included in this key because of the lack of data on their anatomy and reproductive features.

14a. Thallus fastigiate; blade apices strongly involute; bullations along the blade margins .... *H. involvens*
14b. Not as above 15
15a. Tetrasporangial sori restricted to proximal portions of blades .... *H. parvulum*
15b. Tetrasporangial sori not so restricted 16
16a. Thallus tufted, densely branched; midrib slightly to moderately developed; spermatangial sori rounded, elongate or irregular, on both sides of midrib .... *H. heterocystideum*
16b. Thallus sparsely branched; midrib inconspicuous; spermatangial sori [based on var. *abyssicolum*] in chevron arrangement on both sides of midrib .... *H. attenuatum*
17a. (comes from 13b) Spermatangial sori in chevron arrangement on both sides of midrib .... *H. androlamellare*
17b. Spermatangial sori forming continuous (or occasionally interrupted) bands on both sides of midrib .... *H. hypoglossoides*
18a. (comes from 4b) Thallus with only one order of blades arising from a terete, stipitate base .... *H. guineense*
18b. Thallus profusely branched, to several orders 19
19a. Tetrasporangial sori restricted to a median narrow elongate region on small ultimate and penultimate blades .... *H. serratifolium*
19b. Tetrasporangial sori occupying a broader, ovate central region on the fertile blades 20
20a. Marginal serration of blade derived from outgrowth of second-order cell rows .... *H. harveyanum*
20b. Marginal serration of blade derived from outgrowth of third- and some fourth-order cell rows .... *H. armatum*
21a. (comes from 1b) Habit mostly prostrate or decumbent, with multiple attachments to substrate or host .... *H. simulans*
21b. Habit essentially erect, attached by a discrete holdfast 22
22a. Branching strictly dichotomous 23
22b. Branching alternate 24
23a. Thallus robust, to 30 cm tall, with well developed midrib; intercalary cell divisions in 2nd-order rows absent .... *H. dendroides*
23b. Thallus smaller, to 4 cm tall, with slightly developed midrib; intercalary cell divisions in 2nd-order rows present .... *H. sagamianum*
24a. Some marginal cells of blades forming 2–3-celled outgrowths; tetrasporanial sori covering the approximate central half of fertile flat blade .. *H. protendens*
24b. Marginal cells of blades not forming any outgrowths; tetrasporangial sori forming more restricted regions 25
25a. Reproductive organs restricted to ultimate blades, which are conspicuously smaller and specialized in appearance; tetrasporangia formed in narrow stichidium-like proliferations .... *H. annae*
25b. Reproductive organs produced on ordinary ultimate and penultimate blades .... *H. tenuifolium*

The arrangement of spermatangial sori in chevron-like patches running diagonally on either side of the midrib in *Hypoglossum androlamellare* is shared by at least two other species in the genus. It is a pattern also seen in other genera of the family: *Apoglossum ruscifolium* (Turner) J. Agardh (Kylin, 1923; Wynne, 1984) and *Branchioglossum pygmaeum* M.J. Wynne *et* R.E. Norris (Wynne & Norris, 1991). The male soral pattern in *H. androlamellare* in combination with such features as its erect habit, blades with their smooth, undulating margins and well developed midribs, the Type 1 apical organization, and the paired tetrasporangial sori allow separation from known species in the genus.

The most distinctive feature of *Hypoglossum annae* is the restriction of its reproductive structures (male, female, and tetrasporangial) to relatively small final-order, or penultimate-order, bladelets. The stature of *H. annae* (up to 14 cm tall) places it in the category of moderate-sized species in the genus.

Thalli of *Hypoglossum harveyanum* (J. Agardh) Womersley *et* Shepley (1982) are robust, reaching 40 cm in height and with four to five orders of branching. Similarities with *H. androlamellare* include the arrangement of the spermatangial sori as series of diagonally oriented bands on either side of the blade, with a relatively broad sterile region along the midrib, and the tetrasporangial sori being in relatively continuous bands with a broad sterile region along the midrib, although the sori are broader in the new species. A major difference is that the blades in *H. harveyanum* are conspicuously serrate or fimbriate (Harvey, 1858, pl. 59, as *Delesseria serrulata*; Womersley & Shepley, 1982; Wynne, 1989).

Similarly, *Hypoglossum guineense*, described from Ghana, West Africa, by Lawson & John (1982), resembles *H. androlamellare* in its overall habit of erect axes bearing oblong blades with alternate branching and the heavily corticated, denuded basal axes but differs by the minute marginal serrations of the blades. Topotype material of *H. guineense* in MICH has a Type 1 apex, a feature previously not stated for this species. Female plants of *H. guineense* bear cystocarps on a reduced foliar stipiate appendage, similar to the small, final-order cystocarpic blades of *H. annae*. But the type of apex and the finely serrate blade margins in *H. guineense* separate it from *H. annae*. Male plants are unknown for *H. guineense*. Another species for which male plants are unknown is *H. armatum* (J. Agardh) J. Agardh (1898), but it can also be eliminated from consideration because its blades have dentate margins (Womerlsey & Shepley, 1982).

Mikami (1985) showed that the tetrasporangial sori in *Hypoglossum serratifolium* Okamura (1936) are produced as a single narrow continuous patch per final-order bladelet. But this differs from both of the new species by its blade having strongly serrate margins.

A paratype specimen in MICH of *Hypoglossum abyssicolum* W.R. Taylor, which was depicted by Taylor (1945, pl. 89, fig. 1) as 'sterile', has been re-examined and found to be male. The spermatangial sori are in the same distinctive chevron arrangement as in *H. androlamellare*. Dawson (1962) treated Taylor's Galapagos species at the varietal level within *H. attenuatum* N.L. Gardn. (1927), namely, *H. attenuatum* var. *abyssicolum* (W.R. Taylor) E.Y. Dawson. Thalli in this species and in the variety reach 12 cm in height and have a Type 1 apex. The fact that the lateral pericentral cells appear to be involved in the formation of tetrasporangia in *H. attenuatum* (Gardner, 1927) separates it from *H. androlamellare*.

Hypoglossum heterocystideum (J. Agardh) J. Agardh was depicted by Womersley & Shepley (1982, as *H. hypoglossoides*) as having an erect habit reaching up to 6 cm in height and with blades with entire margins. It differs from *H. androlamellare* by its tetrasporangial sori having the lateral pericentral cells involved in sporangium formation and the spermatangia being formed in elongate or irregular sori, not in a chevron arrangement. Also, the midline of the blades does not become heavily corticated as in *H. androlamellare*. *Hypoglossum heterocystideum* is distinguishable from *H. annae* in that cystocarps in the former species are not placed on stalk-like branches and tetrasporangia occur in sori of young blades that are otherwise like ordinary vegetative blades unlike the ultimate, narrow tetrasporangial bladelets in *H. annae*, which resemble stichidia in the Dasyaceae.

Hypoglossum hypoglossoides (Stackhouse) Collins *et* Hervey, the type of the genus, has tetrasporangia in linear sori running along both sides of the midrib of ordinary blades, with the sori separated from the midrib by sterile cells (Harvey, 1846, as *Delesseria hypoglossum*; Maggs & Hommersand, 1993). This feature along with others distinguish it from *H. androlamellare* and *H. annae*.

Notoya (1986) made observations on *H. nipponicum* Yamada, a relatively poorly known species, based on cultured plants, and he obtained all reproductive stages. Spermatangial sori were present as scattered, discrete spots arising from isolated cells of the blade, which occasionally were coalesced into few-celled sori. The midline of the blades was not corticated. These differences distinguish *H. nipponicum* from *H. androlamellare*.

Several points of similarity exist between *H. androlamellare* and *H. parvulum* Levring (1941): the same approximate height (*ca* 4 cm) and blade width (3 mm), a Type 1 apex, alternate branching, oval to lanceolate blades with the broadest portion usually being above the middle of the blade. Although he indicated that the midrib was weakly developed, his figures show the same sort of midrib present in *H. androlamellare*, which we would regard as relatively well developed. Although Levring did not describe sexual plants, he depicted the tetrasporangial sori to be located in the proximal part of the blades and to have the paired sori in close proximity to the midline, these two features differing from those in *H. androlamellare*.

Womersley & Shepley (1982) described the spermatangial sori in *Hypoglossum dendroides* (Harvey) J. Agardh as having a paired arrangement with the transverse pericentral cells not forming spermatangia, whereas some of the lateral pericentral cells were involved in forming spermatangia, and others remained sterile. But this species has a Type 2 apex and also has regularly opposite branching (Harvey, 1860, as *Delesseria dendroides*) unlike the alternate pattern in *H. androlamellare*. *Hypoglossum dendroides* resembles *H. annae* in its production of small fertile blades (Wynne, 1989), the cystocarpic blades also being narrowly stalked. But these two species are easily separable by the highly branched nature of *H. dendroides* versus the more laxly branched thallus in *H. annae*, the opposite branching versus alternate branching, and the Type 2 apex in *H. dendroides*.

Some traits of *Hypoglossum sagamianum* as described by Yamada (1941) are shared with *H. androlamellare*, such as the general habit, being "stem-like near the base", and the overall height and width dimensions of the blades. But the acute apices of the blades and the presence of both alternate and opposite branching in *H. sagamianum* do not occur in *H. androlamellare*. Mikami (1987) provided more information on *H. sagamianum*, such as the restriction of tetrasporangial sori to small ultimate bladelets and participation of lateral pericentral cells involved in sporangial production, which serve to separate this species from *H. androlamellare*.

Tetrasporangial sori in *Hypoglossum tenuifolium* (Harvey) J. Agardh occur in narrow bands close to and often depicted as overlying the midline of the blades (Harvey, 1853, as *Delesseria tenuifolia*; Børgesen, 1919, as *D. tenuifolia*; Wynne & Ballantine, 1986; Schneider & Searles, 1991). Male plants bear the spermatangia in linear sori on either side of the midline (Børgesen, 1919), in a manner reminiscent of *H. androlamellare*. But the Type 2 apex of *H. tenuifolium* (Wynne & Ballantine, 1986) and the absence of a corticated midline clearly distinguish this species from *H. androlamellare*.

The Australian species *H. protendens* (J. Agardh) J. Agardh is a robust plant, reaching 20 cm in height, with a well developed midrib and axes becoming denuded below (Womersley & Shepley, 1982). The blades in this species bear distinctive 1–2-celled marginal projections. Other differences from *H. androlamellare* include the fairly continuous nature of the spermatangial sorus, with a sterile midrib region and some sterile second-order cell rows. The lateral pericentral cells participate in sporangium formation within the tetrasporangial sori.

Wynne (1994) described *Hypoglossum subsimplex* as consisting of an erect simple or subsimple blade arising from a discoid holdfast. It differs from the pair of new species by its blade midlines not being corticated, its tetrasporangial sori occurring in indefinitely running pairs close to the midline, the lateral pericentral cells participating in sporangium formation, and its spermatangial sori occurring as scattered small patches over the fertile blade surface.

Another small-statured species is *Hypoglossum minimum* Yamada, which consists of a tuft of simple blades arising from a common discoid holdfast. Reproductive plants have been described by Yoshida & Mikami (1986) and Wynne *et al.* (1989). The male plant bears spermatangial sori in an arrangement similar to that of *H. androlamellare*, although the diagonal sori are more divided and patch-like in *H. minimum*. The tetrasporangial sori, however, in *H. minimum* are small and restricted in extent, occurring close to the midline and involving the lateral pericentral cells in sporangium formation.

Species with a decumbent habit include *Hypoglossum barbatum* Okamura (1901), *H. nipponicum* Yamada (1930), and *H. wynnei* I.A. Abbott (1996) can be eliminated from further comparison with either of the two new species. It should be mentioned that the alga depicted as *H. barbatum* by Wynne *et al.* (1989) was actually *H. nipponicum*. These two species share many similarities, but in the former species the lateral pericentral cells participate in tetrasporangium formation, not so in the latter species (Yoshida, 1998, Schneider, in press). Other species of *Hypoglossum* with a strongly creeping habit, such as *H. caloglossoides* M.J. Wynne *et* Kraft (1985), *H. rhizophorum* D.L. Ballantine *et* M.J. Wynne (1988), *H. simulans* M.J. Wynne, I.R. Price *et* D.L. Ballantine (1989), and *H. geminatum* Okamura (1908) can likewise be discounted. Male plants of *H. rhizophorum* bear spermatangial sori in oblique bands extending out from the lateral pericentral cells, whereas in the tetrasporangial plants the lateral pericentral cells participate in sporangium formation. Plants of *H. revolutum* (Harvey) J. Agardh consist of dichotomously branched blades with sharply serrate margins, the axes showing a conspicuous sympodial development (Harvey, 1860, as *Delesseria revoluta*; Womersley & Shepley, 1992), unlike the monopodial development of the two new species.

Our records of *Hypoglossum simulans* are the first reports from East Africa. When the species was first described from Guadeloupe, French West Indies, its distribution was also reported to include Caribbean Central America, the South Pacific, Hawaii, and eastern Australia (Wynne *et al.*, 1989). It was later reported from the Maldives (Wynne, 1993).

Note added in proof. Since this paper was accepted for publication, the following publication has come to our attention: Zheng-Yi, 1998 — *Hypoglossum fujianensis* sp. nov (Delesseriaceae, Rhodophyta) from Fujian coast, China. *Chinese Journal of Oceanology and Limnology* 16: 369–372.

Acknowledgements. Olivier De Clerck was research assistant of the Fund for Scientific Research-Flanders (Belgium) (FWO). Financial support was provided by FWO-project G002496. We wish to acknowledge the following persons: Prof. Dr Eric Coppejans for providing funding; Dr Ngoile, director of the Institute of Marine Sciences, Zanzibar, and Dr Matt Richmond for the hospitality during the field work; and Dr Peter Audiffred (L) and Dr Ruth Nielsen (C) for loans of specimens.

REFERENCES

ABBOTT I.A., 1996 — *New species and notes on marine algae from Hawai'i.* Pacific Science 50: 142–156.

ABBOTT I.A., 1999 — *Marine Red Algae of the Hawaiian Islands.* Stanford, California, Stanford University Press, xv + 477 p.

AGARDH J.G., 1898 — *Species, genera et ordines algarum.* Vol. 3: 3. Lund, Gleerups.

BALLANTINE D.L. & WYNNE M.J., 1988 — The life history and development of *Hypoglossum rhizophorum* (Delesseriaceae, Rhodophyta) in culture, a new deep-water species from the Caribbean. *Journal of Phycology* 24: 8–12.

BØRGESEN F., 1919 — The marine algae of the Danish West Indies. Rhodophyceae 5. *Dansk Botanisk Arkiv* 3 (1e): 305–368.

BØRGESEN, F., 1932 — Some Indian Rhodophyceae, especially from the shores of the Presidency of Bombay. II. *Bulletin Miscellaneous Information Kew* 1932: 113–134.

DAWSON E.Y., 1962 — Marine red algae of Pacific Mexico. Part 7. Ceramiales: Ceramiaceae, Delesseriaceae. *Allan Hancock Pacific Expeditions* 26: 1–207.

DE CLERCK O. & COPPEJANS E., 1997 — The genus *Dictyota* (Dictyotaceae, Phaeophyta) from Indonesia in the Herbarium Weber-van Bosse, including the description of *Dictyota canaliculata* spec. nov. *Blumea* 42: 407–420.

GARDNER N.L., 1927 — New Rhodophyceae from the Pacific coast of North America. VI. *University of California Publications in Botany* 14: 99–138.

HARVEY W.H., 1846 — *Phycologia Britannica.* Pls I-LXXII. London.

HARVEY W.H., 1853 — Nereis Boreali-Americana. II. Rhodospermae. *Smithsonian Contributions to Knowledge* 5 (5): 258 p., 36 pls.

HARVEY W.H., 1858 — *Phycologia australica.* Vol. I. London.

HARVEY W.H., 1860 — *Phycologia australica.* Vol. III. London.

HOLMGREN P.K., HOLMGREN N.H. & BARNETT L.C., 1990 — *Index Herbariorum, Part I. The Herbaria of the World.* N. Y., New York Botanical Garden, Bronx [*Regnum Vegetabile* vol. 120], x + 693 p.

KRISHNAMURTHY V. & VARADARAJAN K., 1990 — Studies on some Indian Delesseriaceae. *Seaweed Research & Utilization* 12: 101–114.

KÜTZING F.T., 1849 — *Species Algarum.* Lipsiae, Brockhaus.

KÜTZING F.T., 1869 — *Tabulae Phycologicae.* Vol. XIX. Nordhausen.

KYLIN H., 1923 — Studien über die Entwicklungsgeschichte der Florideen. *Kungl. Svenska Vetenskapsakadeniens Handlingar* 63 (11). 139 p.

LAWSON G.W., 1980 — A check-list of East African seaweeds (Djibouti to Tanzania). Lagos, Nigeria, Department of Biological Sciences, University of Lagos, 65 p. (Mimeographed.)

LAWSON G.W. & JOHN D.M., 1982 — The marine algae and coastal environment of tropical West Africa. *Nova Hedwigia Beihefte* 70: 455 p. Vaduz, J. Cramer.

LEVRING T., 1941 — Die Meeresalgen der Juan Fernandez-Inseln. In: Skottsberg C. (ed.), *The Natural History of Juan Fernandez and Easter Island.* Vol. II. Uppsala, Almqvist & Wiksells, pp. 601–670, pls 49–53.

MAGGS C.A. & HOMMERSAND M.H., 1993. *Seaweeds of the British Isles. Vol. 1 Rhodophyta. Part 3A Ceramiales.* xiii + 444 p., 1 map. London, The Natural History Museum, HMSO Publications.

MIKAMI H., 1985 — On *Hypoglossum serratifolium* Okamura, a delesseriaceous red alga from Japan. *Japanese Journal of Phycology* 33: 51–56.

MIKAMI H., 1987 — On *Erythroglossum pulchrum* Yamada and *Hypoglossum sagamianum* Yamada (Rhodophyta, Delesseriaceae). *Japanese Journal of Phycology* 35: 124–129.

NASR A.H. 1947 — Synopsis of the marine algae of the Egyptian Red Sea coast. *Bulletin of the Faculty of Science, Fouad I University* No. 26: 1–155, pls 1–14.

NIZAMUDDIN M. & GESSNER F., 1970 — The marine algae of the northern part of the Arabian Sea and of the Persian Gulf. *"Meteor" Forschungsergebnisse*, Reihe D, Biologie, 6: 1–42.

NOTOYA M., 1986 — *Hypoglossum nipponicum* Yamada (Delesseriaceae, Rhodophyta) in culture. *Japanese Journal of Phycology* 34: 28–30.

OKAMURA K.,1901 — *Illustrations of the Marine Algae of Japan*. Vol. 1, no. 2, p. 15–27 (in English) + pp. 19–37 (in Japanese), pls. VI–X. Keigyosha, Tokyo.

OKAMURA K., 1908 — *Icones of Japanese algae*. Vol. 1 (7), 147–177, pls. 31–35. Tokyo.

OKAMURA K., 1936 — *Nippon Kaisoshi*. Frontispiece + 9 + 6 + 964 + 11 p. Tokyo. [In Japanese].

SCHNEIDER C.W., [In press] — Notes on the marine algae of the Bermudas. 5. Some Delesseriaceae (Ceramiales, Rhodophyta), including the first record of *Hypoglossum barbatum* Okamura from the Atlantic Ocean. *Botanica Marina* 43.

SCHNEIDER C.W. & SEARLES R.B., 1991 — *Seaweeds of the southeastern United States. Cape Hatteras to Cape Canaveral*. Durham, North Carolina, Duke Univ. Press, xiv + 553 p.

SILVA P.C., BASSON P.W. & MOE R.L., 1996 — Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 179: xiv + 1,259 p.

SONDER O.W., 1845 — Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae collegit L. Preiss, Ph. Dr. *Botanische Zeitung* 3: 49–57.

TAYLOR W.R., 1945 — Pacific marine algae of the Allan Hancock Expeditions to the Galápagos Islands. *Allan Hancock Pacific Expeditions* 12, iv + 528 p.

WEBER-VAN BOSSE A., 1923 — Liste des algues du Siboga. III. Rhodophyceae. Seconde partie. Ceramiales. *Siboga-Expeditie Monographie* 59c. Leiden, E.J. Brill, pp. 311–392, pls IX–X.

WOMERSLEY H.B.S. & SHEPLEY E.A., 1982 — Southern Australian species of *Hypoglossum* (Delesseriaceae, Rhodophyta). *Australian Journal of Botany* 30: 321–346.

WYNNE M.J., 1984 — The occurrence of *Apoglossum* and *Delesseria* (Ceramiales, Rhodophyta) in South Africa. *South African Journal of Botany* 3: 136–145.

WYNNE M.J., 1989 — A reassessment of the *Hypoglossum* group (Delesseriaceae, Rhodophyta), with a critique of its genera. *Helgoländer Meeresuntersuchungen* 42: 511–534.

WYNNE, M.J., 1993 — Benthic marine algae from the Maldives, Indian Ocean, collected during the R/V *Te Vega* Expedition. *Contributions from the University of Michigan Herbarium* 19: 5–30.

WYNNE M.J., 1994 — The description of *Hypoglossum subsimplex* sp. nov. (Delesseriaceae, Rhodophyta) from the Florida Keys, Gulf of Mexico. *Cryptogamie, Algologie* 15: 253–262.

WYNNE M.J. & BALLANTINE D.L., 1986 — The genus *Hypoglossum* Kützing (Delesseriaceae, Rhodophyta) in the tropical western Atlantic, including *H. anomalum* sp. nov. *Journal of Phycology* 22: 185–193.

WYNNE M.J. & KRAFT G.T., 1985 — *Hypoglossum caloglossoides* sp. nov. (Delesseriaceae, Rhodophyta) from Lord Howe Island, South Pacific. *British Phycological Journal* 20: 9–19.

WYNNE M.J. & NORRIS R.E., 1991 — *Branchioglossum pygmaeum* sp. nov. and new records of other delesseriaceous algae (Rhodophyta) from Natal, South Africa. *Phycologia* 30: 262–271.

WYNNE M.J., PRICE I.R. & BALLANTINE D.L., 1989 — Distinctions between *Hypoglossum barbatum* Okamura, *H. minimum* Yamada, and *H. simulans* sp. nov. (Delesseriaceae, Rhodophyta). *Phycologia* 28: 28–38.

YAMADA Y., 1941 — Notes on some Japanese algae IX. *Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido Imperial University* 2: 195–215, pls 41–48.

YOSHIDA T., 1998 — *Marine Algae of Japan*. Tokyo. Uchida Rokakuho Publishing Co., Ltd, 1,222 p. [In Japanese].

YOSHIDA T. & MIKAMI H., 1986 — Observations on morphology of *Hypoglossum minimum* Yamada and *H. geminatum* Okamura (Delesseriaceae, Rhodophyta). *Japanese Journal of Phycology* 34: 177–184.

Tab. 1. Comparison of species of *Hypoglossum*.

	Habit	*Branching pattern*	*Type of apex*[1]	*Blade margin*	*Cortication*	*Male sori*
H. androlamellare	erect, to 4 cm tall	alternate, 3-4 orders	1	smooth, undulate	in lower portions	in chevrons on both sides of midline
H. annae	erect, to 14 cm tall	alternate (rarely opposite), 3-4 orders	2	smooth	present- stipe-like older portions	paired sori, restricted to small ultimate blades
H. anomalum	mostly prostrate, 10-30 mm long	almost entirely opposite, emerging between midrib and blade margins	1	smooth	present, well developed	round/ovate, paired, fused distally
H. armatum	erect, 10-25 cm tall	alternate, mainly abaxial, profusely branched	1	serrate	present, well developed proximally	?
H. attenuatum	erect, 3-4 cm tall (12 cm for var. *abyssicolum*)	alternate; sparsely branched	1	smooth	inconspicuous	in chevrons on both sides of midline
H. barbatum	mostly prostrate, to 20 mm long	alternate, often arising from basal segment of parent blade	1	smooth (occasional marginal rhizoids)	absent	?
H. caloglossoides	mostly prostrate, to 12 mm long	almost entirely opposite	1	smooth	absent	paired, rounded, flanking midline & lateral pericentral cells
H. dendroides	erect, to 30 cm tall	opposite, 5-6 orders	2	smooth	well developed	paired, flanking midline, on small blades
H. geminatum	prostrate blades giving rise to free, erect blades	always opposite	1	smooth	absent	paired, at distal end of ultimate & penultimate blades
H. guineense	erect, 4-10 cm tall	irregular	1	minutely serrate	present, stipitate base	?
H. harveyanum	erect, to 40 cm tall	profusely branched, 4-5 orders	1	serrate (to fimbriate)	present	in chevrons on both sides of midline
H. heterocystideum	erect, densely tufted (small discoid holdfast)	irregular	1	smooth, undulate	present (slight to moderate)	rounded/elongate or irregular, both sides of midline
H. hypoglossoides	erect, 2-30 cm tall	alternate or opposite	1	smooth (rarely dentate)	usually present	mostly continuous over length of blade on both sides of midrib
H. involvens	erect, 5-9 cm tall	alternate, fastigiate	1	smooth	absent	?

[1] *Type 1 apex: all cells of 2nd-order rows bearing 3rd-order rows; Type 2 apex: not all cells of 2nd-order rows bearing 3rd-order row (Wynne et al. (1989). See first dichotomy in Key.*

Tab. 1 (contd.). Comparison of species of *Hypoglossum*.

	Habit	*Branching pattern*	*Type of apex*[1]	*Blade margin*	*Cortication*	*Male sori*
H. minimum	cluster of erect, simple blades (to 9 mm tall), from discoid holdfast	simple	1	smooth	absent	in irregular chevrons, on both sides of midline
H. nipponicum	decumbent, pulvinate, 9 cm in overall extent	alternate, often arising from basal segment of parent blade	1	smooth (marginal rhizoids)	absent	discrete, scattered
H. parvulum	erect, to 4 cm tall	alternate, 2 orders	1	smooth	present, weakly developed	?
H. protendens	erect, to 20 cm tall	alternate, mainly abaxial, much branched	2	smooth	present, stipitate basal portion	broad (sterile margins and adjacent to midline)
H. retusum	erect, to 2.7 cm tall	simple blades arising from fleshy stipe	?	smooth	present, stipitate basal portion	?
H. revolutum	erect, bushy clump, 6-8 cm tall	alternate, adaxial, ramisympodial	1	serrate	present	?
H. rhizophorum	narrow prostrate axes, erect simple blades (to 3 mm tall)	alternate	1	smooth	absent	in chevrons
H. sagamianum	erect, 2-4 cm tall	opposite	2	smooth	slightly developed	?
H. serratifolium	erect, 15-17 (-25) cm tall	alternate and opposite, to several orders	1	strongly serrate	well developed	?
H. simulans	mostly decumbent, up to 15 mm long	alternate, often arising from basal segment of parent blade	2	smooth (marginal rhizoids)	absent	small, discrete, scattered
H. subsimplex	erect blades, to 6 mm tall; discoid holdfast	simple or subsimple	1	smooth	absent	in irregular chevrons on both sides of midline
H. tenuifolium	erect, bushy to 10 cm tall	alternate, to several orders	2	smooth	only near base	in irregular chevrons on both sides of midline
H. tortile	erect, to 3 cm tall	alternate	?	smooth, strongly undulate (tortuous)	absent	?
H. wynnei	erect to decumbent, to 23 mm long	alternate (or simple)	1	smooth (marginal rhizoids)	absent	?

Tab. 1 (contd.). Comparison of species of *Hypoglossum*.

	Tetrasporangial sori	*Formation of sporangia by lateral pericentral cells*	*Tetrasporangial sori: layers*	*Distribution*	*Distinctive features*	*References*
H. androlamellare	paired, one or more pairs per blade	no	many	Tanzania	male sori in regular chevrons	this paper
H. annae	on small ultimate blades, stichidia-like	yes (incl. transverse pericentrals)	primary only (apparently)	Indonesia, Philippines	reproductive structures restricted to small final-order blades	this paper
H. anomalum	round, continuous over midrib	yes	many	widespread in tropics	unique mode of branching	Wynne & Ballantine (1986)
H. armatum	ovate, occupying much of young blades	yes	many	western and southern Australia	margin with irregularly developed spines	Womersley & Shepley (1982)
H. attenuatum	small, angular	yes	many	Pacific Costa Rica and Mexico, Colombia, Galapagos (Indian Ocean ?)	combination of habit and reproductive features	Gardner (1927), Taylor (1945), Dawson (1962)
H. barbatum	central, over midrib	yes	many	Japan, Hawaii, eastern Australia, Bermuda	combination of habit and reproductive traits	Okamura (1901), Abbott (1999)
H. caloglossoides	discrete, median	yes	many	eastern Australia, Hawaii, Florida	regularly constricted prostrate axes; simple, erect (fertile) blades at nodes	Wynne & Kraft (1985)
H. dendroides	limited, on small ultimate blades	yes (incl. transverse pericentrals)	primary	western and southern Australia	ultimate blades narrow; restricted no. of 3rd-order cell rows	Womersley & Shepley (1982)
H. geminatum	paired, distal end of ultimate blades	yes	primary	Japan	3rd-order cell rows lacking within sporangial sori	Yoshida & Mikami (1986)
H. guineense	?	?	?	tropical western Africa	cystocarps on special stalked reduced bladelet	Lawson & John (1982)
H. harveyanum	median, on ultimate and penultimate blades	yes	many	eastern and southern Australia	cystocarp with extended neck	Womersley & Shepley (1982)
H. heterocystideum	rounded to elongate, on both sides of midline	yes (and occasional transverse pericentrals)	many	eastern, southern, and western Australia	marginal cells near apex may fuse to form rhizoids for attachment	Womersley & Shepley (1982)
H. hypoglossoides	fairly continuous elongate patches on both sides of wide midrib	no	many	Atlantic Europe, Azores, Mediterranean, Caribbean to Brazil	paired sporangial sori separated by broad sterile midrib region	Maggs & Hommersand (1993)
H. involvens	narrow, running indefinitely along midline	apparently yes	?	Florida	marginal bullations along blade margins; fastigiate habit	Harvey (1853), Wynne & Ballantine (1986)

Tab. 1 (contd.). Comparison of species of *Hypoglossum*.

	Tetrasporangial sori	*Formation of sporangia by lateral pericentral cells*	*Tetrasporangial sori: layers*	*Distribution*	*Distinctive features*	*References*
H. minimum	small, discrete, ovate	yes	primary	southern Japan, Hawaii	habit of simple blades	Yoshida & Mikami (1993)
H. nipponicum	narrow, elongate, paired along midline	no	many	central Japan	combination of habit and reproductive traits	Yamada (1930), Notoya (1986), Wynne *et al.* (1989, as *H. barbatum*)
H. parvulum	oblong, ovate	apparently yes	not stated	Juan Fernandez Islands (Chile)	sporangial sori confined to proximal part of blade	Levring (1941)
H. protendens	ovate to elongate, covering midrib and up to half of marginal width	yes (incl. transverse pericentrals)	primary	western and southern Australia	some marginal cells forming 2-3-celled outgrowths	Womersley & Shepley (1982)
H. retusum	?	?	?	Pacific Mexico	apical notch, marginal rhizoids	Dawson (1962)
H. revolutum	broad, median	yes	many	Australia	branching sympodial; blades revolute	Womersley & Shepley (1982)
H. rhizophorum	longitudinal, extending indefinitely	yes	many	Caribbean, Hawaii, South Pacific	narrow rhizome	Ballantine & Wynne (1988)
H. sagamianum	narrow, confined to small ultimate blades	yes	primary	Japan	intercalary cell divisions in 2nd-order rows	Mikami (1987)
H. serratifolium	narrow, median, on small ultimate and penultimate blades	yes	many	Japan	strongly serrate blade margins; small median sori	Mikami (1985)
H. simulans	narrowly elongate along midline	yes	many	widespread in tropics	wings cells near midrib longitudinally oriented	Wynne *et al.* (1989), this paper
H. subsimplex	longitudinal, extending indefinitely	yes	primary	Caribbean, Florida	simple or subsimple blades; sporangial sorus	Wynne (1994)
H. tenuifolium	longitudinal, extending indefinitely	yes	many	Caribbean, Florida	obtuse/emarginate blade apex; greenish color *in vivo*	Børgesen (1919)
H. tortile	?	?	?	Japan	densely spiralling habit	Noda (1970)
H. wynnei	small, obovate	yes	many	Hawaii	combination of habit and reproductive traits	Abbott (1996, 1999)