

A reassessment of the *Hypoglossum* group (Delesseriaceae, Rhodophyta), with a critique of its genera*

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ABSTRACT: A reassessment of the *Hypoglossum* group (Delesseriaceae, Rhodophyta), with a critique of its genera. Eight genera are assigned to the *Hypoglossum* group: *Bartoniella* Kylin, *Branchioglossum* Kylin, *Chauviniella* Papenfuss, *Duckerella* Wynne, *Hypoglossum* Kützing, *Phytomophora* J. Agardh, *Pseudobranchioglossum* Bodard, and *Zellera* Martens. The circumscription of the group is emended to include forms with network-forming (*Zellera*) and spirally twisted (*Duckerella*) thalli. The definition of the group is also modified to include members (e.g. some species of *Hypoglossum*) in which tetrasporangia are produced by primary cells as in the *Caloglossa* group. Exogenous branching, a distinguishing feature of the closely related *Caloglossa* group, never occurs in the *Hypoglossum* group.

INTRODUCTION

In a survey of the taxonomy of the red algal family Delesseriaceae, Wynne (1983) assigned seven genera to the *Hypoglossum* group. This assemblage was characterized by the solid (non-reticulate) construction of its monopodial blades, restriction of its procarps to transverse pericentral cells, extension of all of its third-order cell rows to the blade margins, and production of its tetrasporangia in two or more layers. Criteria such as whether branching occurred from the midrib or from the blade margin and whether blades were essentially monostromatic or polystromatic throughout were employed to separate genera.

Several new species of *Hypoglossum* and *Branchioglossum* have been described in recent years, leading to a need for reassessment of the circumscriptions of some of the genera. In addition, recent collection of fertile *Zellera* have permitted a study of this poorly known genus, which some authors (e.g. Womersley, 1965; Itono, 1986) have suggested may be more properly placed in the *Hypoglossum* group than in the *Claudea* group, as advocated by Kylin (1956). A fresh look at the *Hypoglossum* group seems appropriate, and we have examined authentic material of each genus in an attempt to assess the essential taxonomic features.

* Dedicated to Dr. Dr. h. c. P. Kornmann on the occasion of his eightieth birthday.

MATERIALS AND METHODS

Plants were available either as herbarium mounts or wet-preserved specimens in 5 % formalin-seawater. For microscopic study small pieces of thallus were placed on slides and usually stained with a mixture of 1.0 % aniline blue with 30 % Karo Syrup acidified with HCl or similarly mounted but not stained. A Zeiss research microscope, equipped with a camera, was used for photomicrographs. Information on the collection data and herbaria in which the specimens are deposited (corresponding to all material depicted in the figures) is provided in the captions. Herbarium abbreviations follow Holmgren et al. (1981).

RESULTS

Hypoglossum Kützing

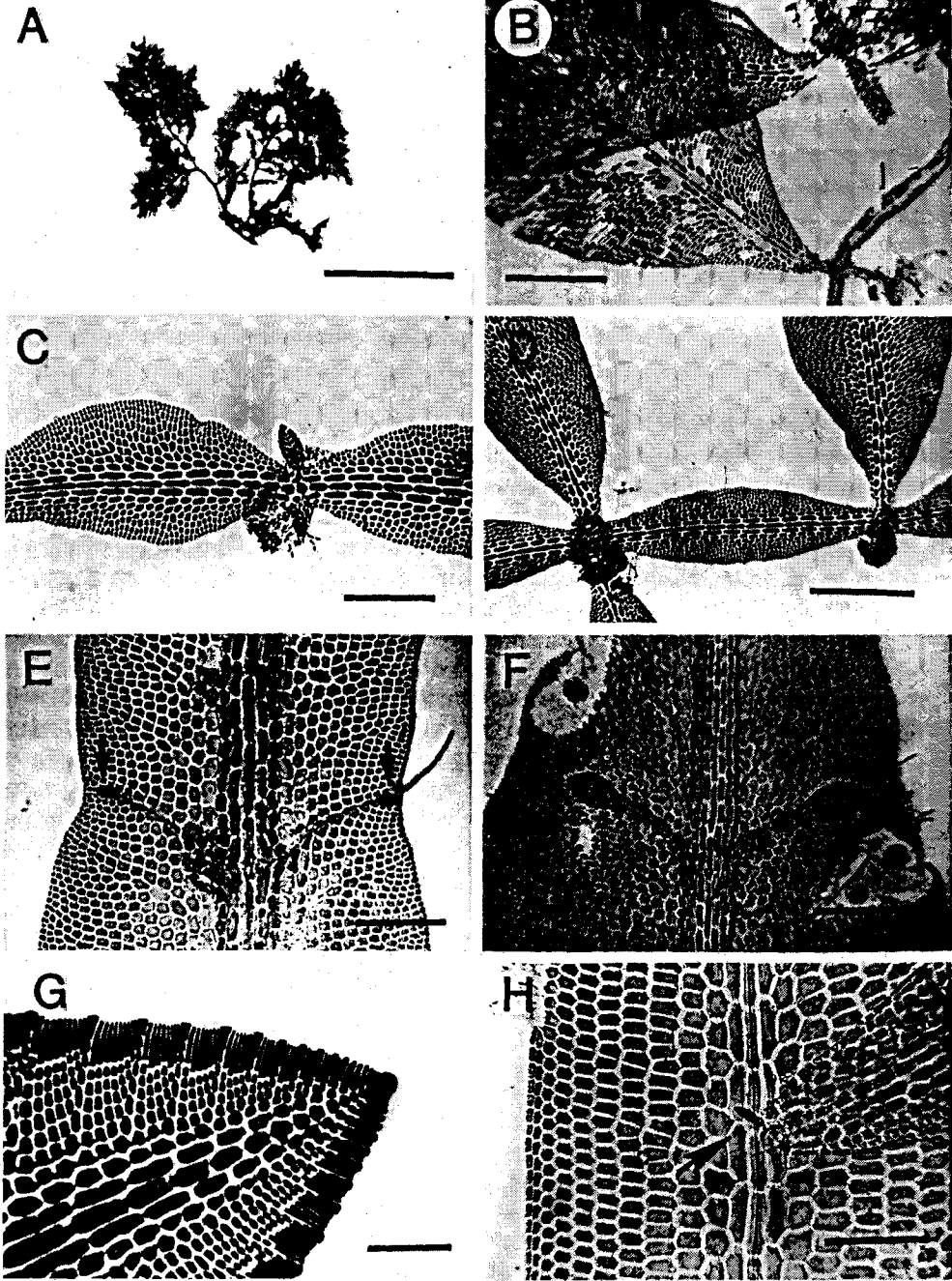
Encompassing about two dozen species, *Hypoglossum* is the largest genus of the *Hypoglossum* group. Kützing (1843) based the binomial *Hypoglossum woodwardii* on *Fucus hypoglossum* Woodward when erecting the genus, *H. woodwardii* becoming the lectotype. *Hypoglossum hypoglossoides* (Stackh.) Coll. & Herv. has been shown by Wynne (1984) to be the correct name for the lectotype. Generic traits include blades that are flat, lacking lateral veins, and monostromatic except for the midrib region. Branching, when present, is restricted to the midrib.

Species of *Hypoglossum* have been described from temperate and tropical seas in many parts of the world. Six species are reported from southern Australia (Womersley & Shepley, 1982), six from the tropical and subtropical western Atlantic (Wynne & Ballantine, 1986; Ballantine & Wynne, 1988; Wynne et al., in press), and six from Japan (Yoshida et al., 1985). Several reports of poorly known species have been published recently, such as those on *H. serratifolium* Okam. (Mikami, 1985), *H. minimum* Yamada and *H. nipponium* Okam. (Yoshida & Mikami, 1986), and *H. sagamianum* Yamada (Mikami, 1987). Examples of recently described species are *H. guineense* (Lawson & John, 1982) from tropical West Africa, *H. caloglossoides* (Wynne & Kraft, 1985) from the South Pacific, *H. anomalum* (Wynne & Ballantine, 1986) from the Caribbean, and *H. simulans* (Wynne et al., in press) from the Caribbean, northeastern Australia, and the South Pacific.

Fig. 1. *Hypoglossum* spp. A *H. dendroides*; B *H. rhizophorum*; C, D *H. caloglossoides*; E, F, G *H. anomalum*; H *H. simulans*. A Habit of typical herbarium specimen. B Unbranched blades arising from rhizome. C, D Formation of pairs of branches and holdfast at nodes of creeping axes. E Production of a pair of branch primordia (arrows). F Pair of young bladelets issuing from blade surface. G Blade apex. H Branch primordium (arrow) issuing from basal segment of parent blade.

Scale bars: A = 3 cm; B, D, F, H = 200 μ m; C, E = 100 μ m; G = 25 μ m

Collection data: 1 A leg. R. Ricker & G. Kraft (MICH), 2. Dec 1980, Point Clune, Rottneest Is., W. A., Australia. 1 B leg. D. Ballantine 1750-b (MICH), 16. Jan 1985, 61 m, La Parguera, Puerto Rico. 1 C, D leg. G. Kraft 10442 & J. Huisman (MICH), 31. Jan 1982, 11 m, South Passage, Lord Howe Is., N. S. W., Australia. 1 E, G leg. D. Ballantine 1782 (MICH), 16. Jan 1985, 61 m, La Parguera, Puerto Rico. 1 F leg. J. Huisman & A. Withell (MELU), 23 Nov 1983, 18 m, East Blue Pools, Heron Is., Qld., Australia. 1 H leg. D. Ballantine (= Wynne 8328, MICH), 24. Feb 1987, 30 m, Malendure, Basse-Terre, Guadeloupe, French West Indies



Various characteristics are useful in separating species within *Hypoglossum*, one of the most important being differences in general habit. At one end of the spectrum is *H. dendroides* (Harv.) J. Ag. (Fig. 1 A), which has a much branched thallus attached by a well developed cartilaginous proximal portion, which seems to be perennial; at the other end of the spectrum are such species as *H. minimum* Yamada, which consists of a cluster of a few simple, minute blades attached by a discoid holdfast (Yoshida & Mikami, 1986). Thalli of *H. rhizophorum* consist of a narrow rhizome system giving rise to simple erect blades (Fig. 1 B) (Ballantine & Wynne, 1988). In *H. caloglossoides* there is a prostrate system of regularly constricted blades, with a holdfast and typically a pair of new axes produced at each constriction, or node (Figs 1 C, D) (Wynne & Kraft, 1985). Some deep-water species, such as *H. barbatum* Okam. and *H. simulans* (Wynne et al., in press), consist of loosely decumbent blades that form frequent secondary attachments by means of marginal rhizoids.

Many patterns of branching are seen throughout the genus. *H. revolutum* (Harv.) J. Ag. is distinctive in that its branching pattern is regularly ramisymphodial (Womersley & Shepley, 1982; Norris et al., 1984). All other species are monopodially organized. Branching is invariably endogenous, meaning that an axial cell cuts off a branch primordium which then grows out from the midrib of the parent blade. A unique variation is expressed by *H. anomalum*, in which a pair of branch primordia is cut off endogenously from a primary axial cell, but instead of arising directly from that point, each branch primordium develops as a filament in the plane of the parent blade (Fig. 1 E) which then emerges as a bladelet at some point between the midrib and the margin of the parent blade (Fig. 1 F). An interesting feature observed in *H. barbatum* and *H. simulans* is that one branch order often produces the next higher order from the basal segment (Fig. 1 H). Branching may be regularly alternate or opposite, or it may be variable in a given species. A strictly opposite pattern is true of *H. geminatum* Okam. (Yoshida & Mikami, 1986), *H. dendroides*, and *H. anomalum*. Womersley & Shepley (1982) observed that branches typically appeared in an abaxial position in the southern Australian species of *Hypoglossum*.

Two types of apical organization occur within the genus: (1) all cells of second-order rows bear third-order rows; or (2) not all cells of second-order rows bear third-order rows. The apex of *H. anomalum* (Fig. 1 G) conforms to the former pattern, whereas the apex of *H. simulans* (Fig. 2 A) conforms to the latter. Of the six species of *Hypoglossum* occurring in southern Australia, four have the first type of apical organization, whereas two have the second type (Womersley & Shepley, 1982). *H. tenuifolium* (Harv.) J. Ag. is also representative of the latter category (Wynne & Ballantine, 1986). Mikami (1987) recently claimed that in *H. sagamianum* some cells of second-order rows undergo intercalary divisions, which results in not all cells of these second-order rows bearing third-order rows. This is the first report of intercalary divisions occurring in *Hypoglossum*.

The blades of some species in the genus have entire margins, but others have characteristically denticulate margins. The marginal serrations are minute in *H. guineense* (Lawson & John, 1982) but prominent in *H. serratifolium* Okam. (Mikami, 1985). The marginal projections along the blades in *H. harveyanum* (J. Ag.) J. Ag. (Fig. 2 B) are derived from outgrowths of second-order cell rows, whereas those in *H. armatum* (J. Ag.) J. Ag. are from third- and fourth-order cell rows (Womersley & Shepley, 1982).

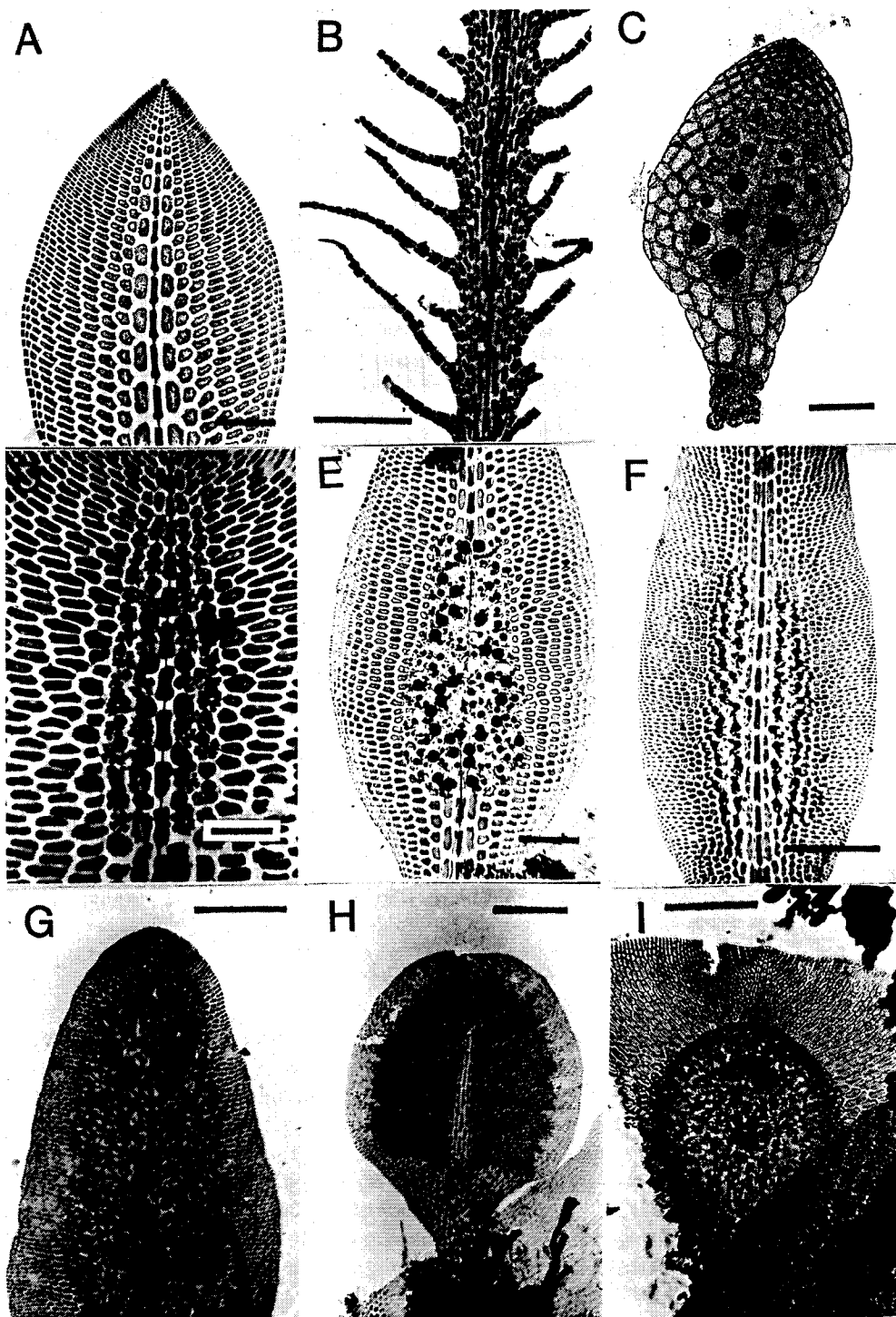
Investigators have been paying increasing attention to tetrasporangial features as a

means of differentiating species. Tetrasporangia are initially produced by the cortical cells and later by some primary cells in *H. hypoglossoides*, resulting in a sorus of two or more layers of tetrasporangia (Womersley & Shepley, 1982; Stegenga & Mol, 1983). In *H. revolutum*, sporangia are formed first from primary cells, including the lateral pericentral cells, and subsequently from cortical cells, resulting in several layers of sporangia of differing ages (Womersley & Shepley, 1982). In certain other species in the genus the tetrasporangia are produced only by the primary layer of cells, as in *H. protendens*, *H. minimum*, and *H. geminatum*. In *H. geminatum* only certain second-order cells of the primary layer cut off tetrasporangia (Yoshida & Mikami, 1986). Likewise, in *H. dendroides* tetrasporangia typically occur in a single layer (Fig. 2 C), being cut off from the lateral pericentral cells and adjacent lateral cells (occasionally by abaxial pericentral cells). The involvement of lateral pericentral cells in the production of tetrasporangia seems to be a specific trait. In *H. simulans* lateral pericentral cells participate in tetrasporangial production (Fig. 2D) followed eventually by other primary and cortical cells (Fig. 2E). In *H. nipponicum* Yamada (Notoya, 1986), *H. barbatum* (Fig. 2F), and *H. hypoglossoides* (Womersley & Shepley, 1982, as *H. woodwardii*), however, lateral pericentral cells do not participate in tetrasporangia production. In *H. anomalum* tetrasporangia are cut off by both lateral and transverse pericentral cells as well as cortical cells, producing a sorus lying directly over the midrib of the blade (Fig. 2G). In *H. sagamianum* tetrasporangia are produced on very small ultimate branches and are cut off from second-order cells, including the lateral pericentral cells. No third-order cell rows are present within the sorus (Mikami, 1987). Clearly, such observations on the precise sites of tetrasporangial production are of utility in separating species of *Hypoglossum*.

Distribution patterns of the species are of interest. *H. hypoglossoides* is known from Atlantic Europe and the Mediterranean (Yarish et al., 1984; Gallardo et al., 1985), but also occurs in the western Atlantic (Wynne & Ballantine, 1986). *H. anomalum* was described from Puerto Rico and the Gulf of Mexico. In addition, this distinctive species has also been identified from Lord Howe and Heron Islands (eastern Australia), and the Seychelles in the Indian Ocean. The Heron Is. collections include male and female plants, which are depicted here for the first time. Male sori occur as a pair of broad regions on both surfaces of a bladelet, separated by a sterile midrib (Fig. 2H). Cystocarps are borne on the midline of a relatively broadened blade (Fig. 2I).

Branchioglossum Kylin

The genus *Branchioglossum* was described by Kylin (1924), with *B. woodii* (J. Ag.) Kyl. as type, a species originally known from Vancouver Island, Canada. Ramírez & Santelices (1981) attributed a bipolar distribution to *B. woodii*, indicating a northern hemisphere range from British Columbia to Baja California and a southern hemisphere range along the central coast of Chile. Mikami (1979) observed that the type of a Chilean alga known as *Erythroglossum bipinnatifidum* (Mont.) Kyl. is actually a *Branchioglossum*, and Wynne (1983) transferred that taxon to *Branchioglossum*. Wynne (1988b) has now presented evidence that *B. woodii*, *B. bipinnatifidum*, and *B. brattstroemii* Levring (1960) are taxonomic synonyms, *B. bipinnatifidum* being the correct name for the type of the genus. Wynne maintains *B. undulatum* Dawson (1962) as a distinct species, however, occurring from southern California to the Gulf of California.



Within the *Hypoglossum* group, *Branchioglossum* is distinguished by its flat monostromatic blades (except for the midrib region), lack of lateral veins, and marginal production of lateral branches. These marginal branches arise by the conversion of initials of second-order rows into primary initials, which become indeterminate in growth. This mode of branching is observed in *B. bipinnatifidum* (Fig. 3 E), as well as in most other species, [e.g. *B. prostratum* Schneider (1974); *B. minutum* Schneider (Schneider & Searles, 1975)]. In the recently described *B. pseudoprostratum*, however, Ballantine & Wynne (1987) observed that any marginal cell can become active as a branch initial (Fig. 3 G) whether or not it is the apex of a second-order row. Another variable feature within the genus is the apical organization. In most species, including the type and *B. nanum* Inagaki (Mikami, 1973), all cells of second-order rows bear third-order rows (Fig. 3 A), but in *B. pseudoprostratum* (Fig. 3 F) and *B. crispatum* (Harv.) Kyt., not all cells of second-order rows bear third-order rows. Another anomaly in *B. crispatum* is that it branches both from blade margins and midribs. In *B. bipinnatifidum*, the tetrasporangial sori cover both surfaces of the blade and lie in longitudinal bands running parallel to the midrib (Figs 3 C, D), whereas the sori in *B. pseudoprostratum* form discrete, circular regions lying over the midrib (Fig. 3 H). Spermatangial sori of *B. bipinnatifidum* (Fig. 3 B) and cystocarpic blades of *B. pseudoprostratum* (Fig. 3 I) are representative of these features throughout the genus.

At present about 10 species are recognized as belonging to *Branchioglossum*, occurring in the eastern and western Pacific, western Australia, and the subtropical/tropical western Atlantic.

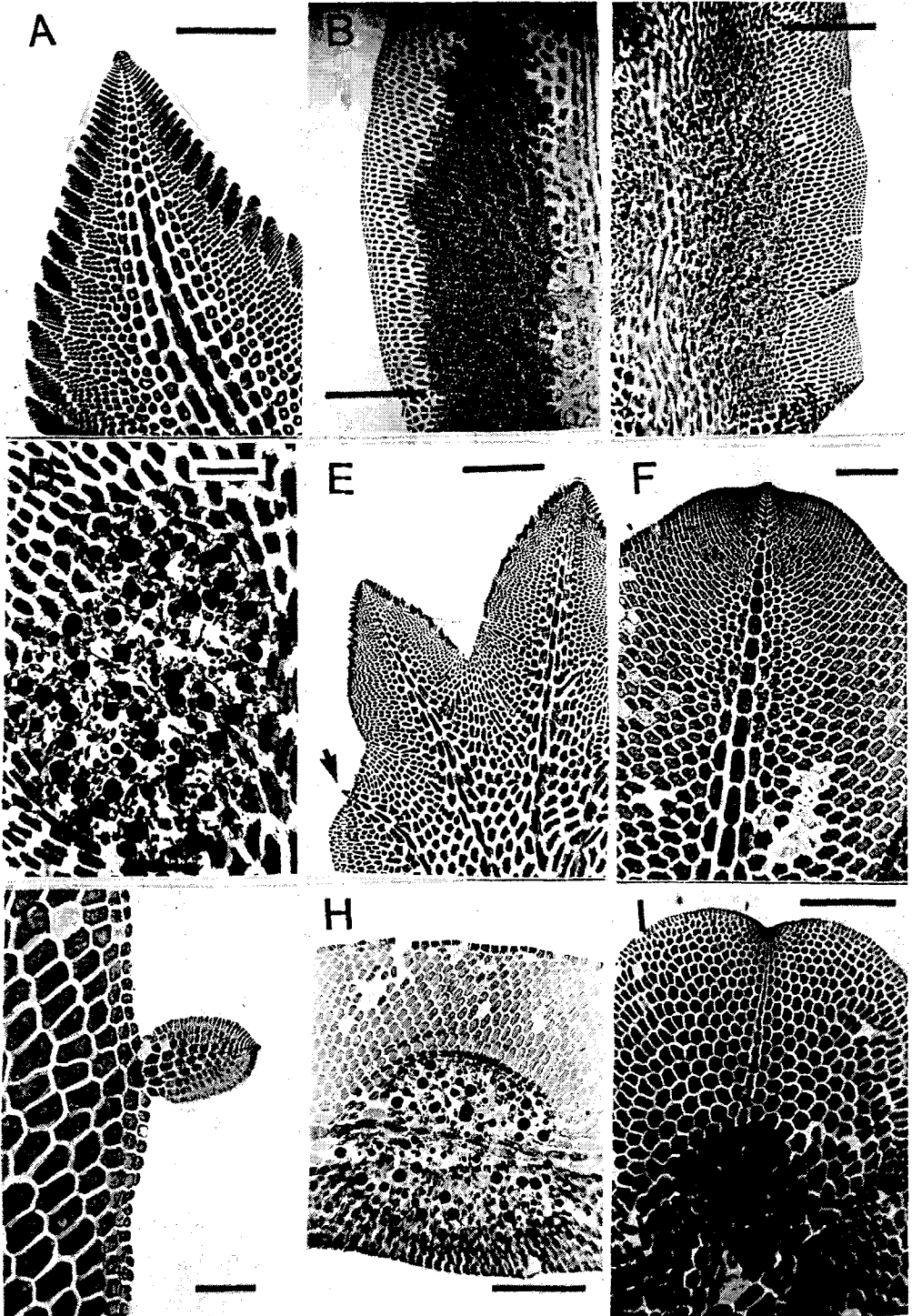
Pseudobranchioglossum Bodard

Bodard (1971) established this genus (and new species) based on *Pseudobranchioglossum senegalense*, an intertidal alga from the west coast of Africa. The syntype collections included cystocarpic and tetrasporic specimens. Bodard's account remains the only report of this alga, and I am grateful to him for loaning me his type collections.

The apical organization is such that all cells of second-order rows bear a third-order row (Fig. 4 B). This genus is like *Branchioglossum* in having blades with marginal branching (Fig. 4 A) that results from the conversion of initials of second-order rows into

Fig. 2. *Hypoglossum* spp. A, D, E *H. simulans*; B *H. harveyanum* "fimbriate form" C *H. dendroides*; F *H. barbatum*; G-I *H. anomalum*. A Blade apex. B Blade with denticulate margin. C Tetrasporangia formation in a single (primary) layer. D Early initiation of tetrasporangia from lateral pericentral cells. E Mature tetrasporangial sorus. F Mature tetrasporangial sorus. G Mature tetrasporangial sorus. H Spermatangial sorus. I Cystocarpic blade. Scale bars: A, D, E = 50 μ m; B = 1000 μ m; C, F-I = 200 μ m

Collection data: 2 A leg. A. Millar (MELU), 14. Nov 1982, Blue Pools, Heron Is., Qld., Australia. 2 B leg. I. G.S. (MICH), 10. Sept. 1977, Graham's Creek, Port Curtis, near Gladstone, Qld., Australia. 2 C leg. R. Ricker & G. Kraft (MICH), 2. Dec 1980, Point Clune, Rottneest Is., W. A., Australia. 2 D leg. G. Kraft 9064 (MELU), 1. March 1976, Ned's Beach, Lord Howe Is., N. S. W., Australia. 2 E leg. G. Kraft (MELU), 3. Oct 1976, Signal Point, Far Rocks, Lord Howe Is., N. S. W., Australia. 2 F leg. M. Kajimura (MICH), 7. July 1986, 40 m, Tsudo, Oki Is., Shimane Pref., Japan. 2 G leg. J. Huisman et al. (MELU), 11. Nov 1983, 12 m, Gorgonian Holes, Heron Is., Qld., Australia. 2 H leg. J. Huisman & A. Withell (MELU), 23 Nov 1983, 18 m, East Blue Pools, Heron Is., Qld., Australia. 2 I leg. J. Huisman et al. (MELU), 17. Nov 1983, Blue Pools, Heron Is., Qld., Australia



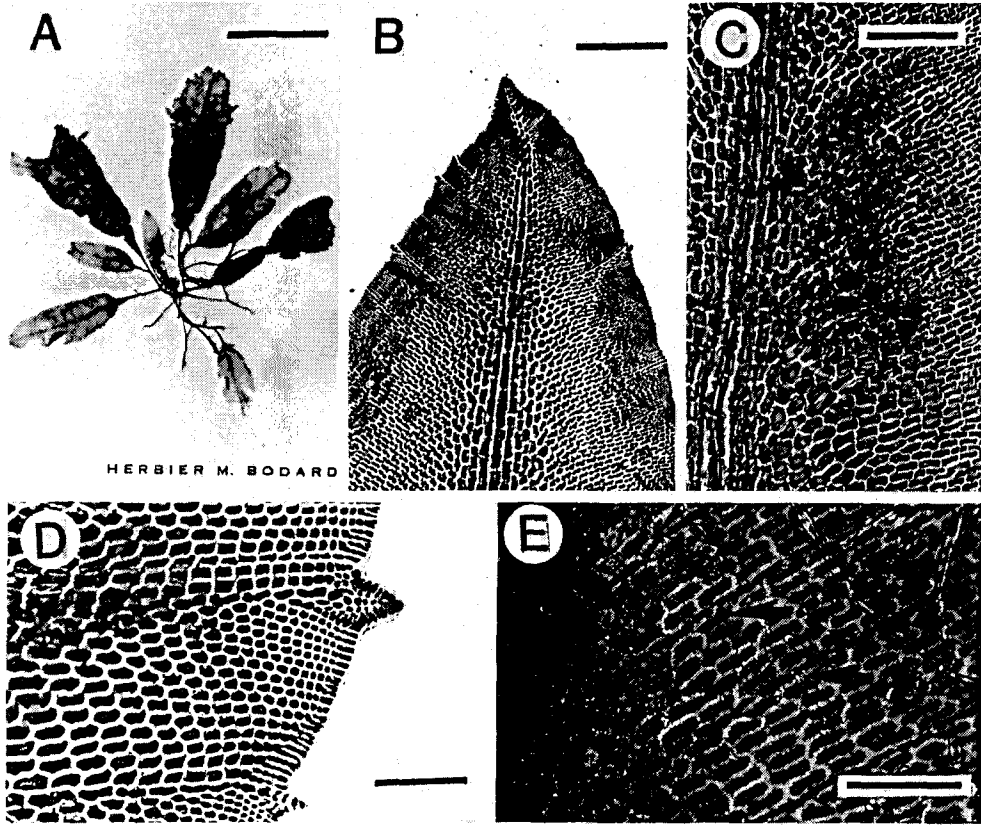


Fig. 4. *Pseudobranchioglossum senegalense*. A Isotype specimen. B Blade apex. C Early stage of tetrasporangial sorus. D Marginal branch from outgrowth of a second-order cell row. E Lateral nerves (arrows) formed by cortication of second-order cell rows. Scale bars: A = 2 cm; B–D = 100 μ m; E = 50 μ m

Collection data: leg. M. Bodard 2469 (Herb. M. Bodard, Univ. Lille), 27 Apr 1967. Senegal, Africa

Fig. 3. *Branchioglossum*. A–E *B. bipinnatifidum*; F–I *B. pseudoprostratum*. A Blade apex. B Spermatangial sorus. C Tetrasporangial sorus. D Detail of sorus showing initiation of tetrasporangia from cortical cells and cells of secondary cell rows. E One primordial (arrows) and one developing marginal branch. F Blade apex with early stage of tetrasporangial sorus. G Marginal branch. H Tetrasporangial sorus. I Cystocarpic blade. Scale bars: A, B, D, F, G = 50 μ m; C, H, I = 200 μ m; E = 100 μ m

Collection data: 3 A leg. R. Searles 72 = 68–14 (DUKE), 19. Nov 1972, Canal Puquitin, Chile. 3 B, C leg. R. Searles 72–22–3 (DUKE), 1. Nov 1972, Puerto Alert, Chile. 3 D, E leg. Wynne 3769 (MICH), 27. Dec 1972, Playa Hermosa, Puerto Penasco, Sonora, Mexico. 3 F, G leg. D. Ballantine 1794 (MICH), 14. Jan 1985, 50 m, La Parguera, Puerto Rico. 3 G, I leg. D. Ballantine 1755 (MICH), 16. Jan 1985, 61 m, La Parguera, Puerto Rico

indeterminate initials of lateral branches (Fig. 4 D). In *Pseudobranchioglossum*, as opposed to *Branchioglossum*, however, it is also possible for new blades to develop as proliferations from the midrib of old, denuded primary blades.

Blades have a well developed midrib which passes proximally into a thick stipe. Most of the blade is monostromatic, and in his key to genera of the Delesseriaceae Wynne (1983) erred in referring to this genus as having polystromatic blades. Bodard (1971) asserted that the distinctiveness of this genus lay in the presence of lateral nerves, which are unknown in *Branchioglossum*. An examination of the blades of *P. senegalense* showed that lateral nerves are expressed by second-order cell rows undergoing periclinal divisions, resulting in slightly thickened lines coursing out from the midrib (Fig. 4 E).

Bodard (1971) also described *Pseudobranchioglossum* as having cells of the second-order rows undergoing intercalary cell divisions. I have looked closely at the young blades of this species but have been unable to detect intercalary divisions of cells in the second order rows (Fig. 4 E), although the cortical cells that are cut off to form the lateral veins are of smaller size than the second-order rows cells and give the false appearance of having been derived by intercalary divisions.

Tetrasporangial sori (Fig. 4 C) are very similar to those of *Branchioglossum*. The main reasons for recognizing *Pseudobranchioglossum* as a distinct genus in the *Hypoglossum* group would seem to be the presence of lateral veins and the ability of eroded blades to branch secondarily from the midrib.

Duckerella Wynne

This monotypic genus was established for a species then known only from Madagascar, *Duckerella ferlusii* (Hariot) Wynne (Wynne, 1982). A distinctive trait of *Duckerella* is that the axes are sinistrally spiralled (Figs 5 A, B). Axes are repeatedly branched, and blade margins are denticulate (Fig. 5 C). Although Hariot (1902) described this species as a *Delesseria*, the initials of all third-order cell rows reach the blade margin, a trait at odds with genuine *Delesseria*. The apex of *Duckerella* agrees with Kylin's (1924) subcategory of the *Hypoglossum* type in which not all cells of second-order rows bear third-order rows (Fig. 5 D). Other features of this genus include monostromatic blades (except for a well developed midrib region), branching from the blade margins, and an absence of veins. Only tetrasporic plants are known. The tetrasporangial sori occupy the midrib region of the blade (Fig. 5 E) but are occasionally developed on small bladelets arising from a blade midrib.

In an examination of specimens of Delesseriaceae in the Berlin Botanical Museum (B), I came across an alga from Kenya labeled "*Membranoptera*". Upon closer inspection of this material, it was revealed that the two specimens are *Duckerella ferlusii*. Thus the distribution of this monotypic genus can be extended to the east coast of Africa. The collection data are: Osine, Lamu District, Kenya: 10. Sept. 1957, P. J. Greenway 9330 & S. P. Rawlins (in B, # 33888). The specimens are both epiphytic on undetermined plants, and reach 8 cm in height, which is considerably taller than the value of 2 cm previously known. Blades have midribs, regularly denticulate margins, and pseudodichotomous branching of the alga from Madagascar. Blades are characteristically helically coiled in the growing regions but become more planar in the older regions of the plant.

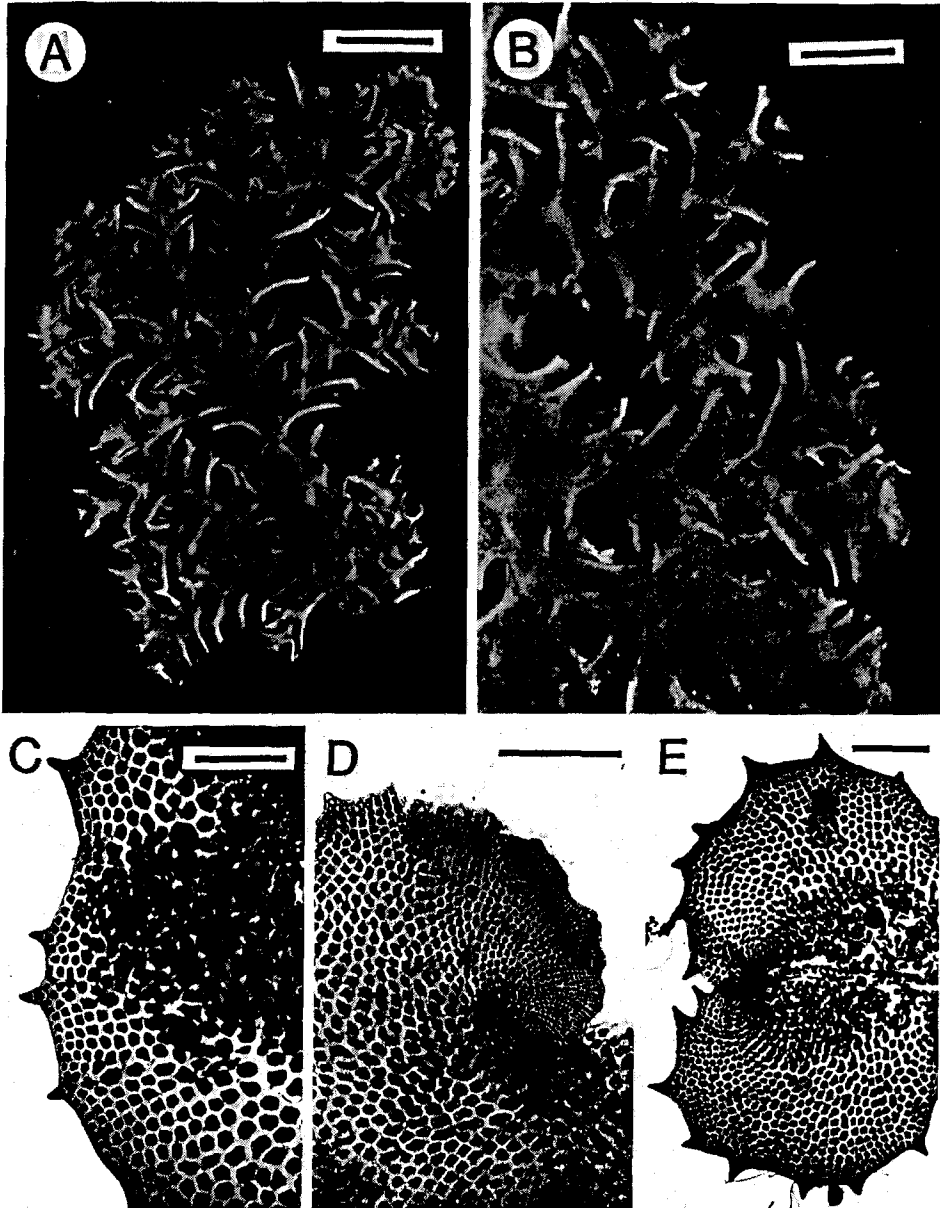


Fig. 5. *Duckereella ferlusii*. A, B Thallus consisting of marginally branched, spirally twisting blades. C Denticulate blade margins. D Blade apex. E Blade bearing median tetrasporangial sorus. Scale bars:

A = 1 mm; B = 500 μ m; C = 100 μ m; D, E = 200 μ m

Collection data: leg. S. Ducker (MICH), 11. Oct 1975, Plage Monseigneur, Fort Dauphin, Madagascar

Bartoniella Kylin

The genus *Bartoniella* was described by Kylin (1924) for a South African species, *B. crenata*. Kylin referred to *Phitymophora crenata* (J. Agardh, 1898), but that name was a nomen nudum. Under that binomial, however, the species was validly described by Mazza (1908). Thus, the correct citation of the type of the genus is *Bartoniella crenata* (J. Agardh ex Mazza) Kylin (Farr et al., 1979). Seagrief (1984) listed in taxonomic synonymy *Delesseria bartoniae* Schmitz, which is a nomen nudum that appeared in Delf & Michell (1921).

A second species, *B. prolifera* Kylin (1929), was later described from New Zealand. This species became the basis of the genus *Marionella*, established by Wagner (1954). A third species, *Bartoniella? equatoriana*, was described from the Galapagos by Dawson (1963) and assigned to the genus with a query. This species does not belong to the *Hypoglossum* group and has been transferred to a new genus in the *Membranoptera* group by Wynne (1988a).

Bartoniella is thus monotypic, *B. crenata* occurring along the east African coast, ranging as far north as Mambui, Kenya (Isaac, 1971), through Mozambique and southward to Port Alfred, Cape Province. The thallus consists of ribbon-like blades that branch from the margins; midribs are present but lateral nerves are absent (Fig. 6 E). Not all cells of second-order rows bear third-order rows (Fig. 6 A). Blades become polystromatic, but I have observed that in some thalli young blades are largely monostromatic, the polystromatic condition gradually appearing (Fig. 6 B).

Bartoniella has been characterized by Wagner (1954) and others as having its reproductive structures produced on final-order bladelets (Figs 6 D, F). New observations on many South African collections have shown that the tetrasporangial sori and cystocarps are not confined to only the final-order bladelets (Fig. 6 C). Some specimens collected near Durban, Natal Province, have a helically spiralling configuration, but those thalli occur side-by-side with non-spiralling thalli. Thus, no special significance has been given to them.

Chauviniella Papenfuss

Papenfuss (1956) erected this genus to include *C. coriifolia* (Harv.) Papenf. as the type, and a second species, *C. jadinii* (Børges.) Papenf. The type is known from southern and western Australia (Harvey, 1860, pl. CL), whereas *C. jadinii* is known only from Mauritius. These blades have an apical organization in which every cell of second-order rows bears third-order rows (Fig. 7 B). Blades of *Chauviniella* are flattened, ligulate, and branched from the midrib (Fig. 7 A). Blades become polystromatic, a midrib is evident, but lateral veins are lacking. Cross-sections of blades (Figs 7 C, D) reveal an organization typical for the subfamily Delesserioideae, in which a medulla composed of a random mixture of larger cells is surrounded by small rhizoidal cells. Such an organization is in contrast to that of subfamily Nitophylloideae, in which a cross-section reveals the cortical and medullary layers to be made up of regularly aligned cells (e.g. *Heterodoxia denticulata* J. Ag.; Fig. 7 F). Reproductive structures in *Chauviniella* are produced on small proliferations along the midrib. A cross-section of a mature cystocarp is shown in Figure 7 E. According to May (1965), tetrasporangial sori are produced on only one side of the

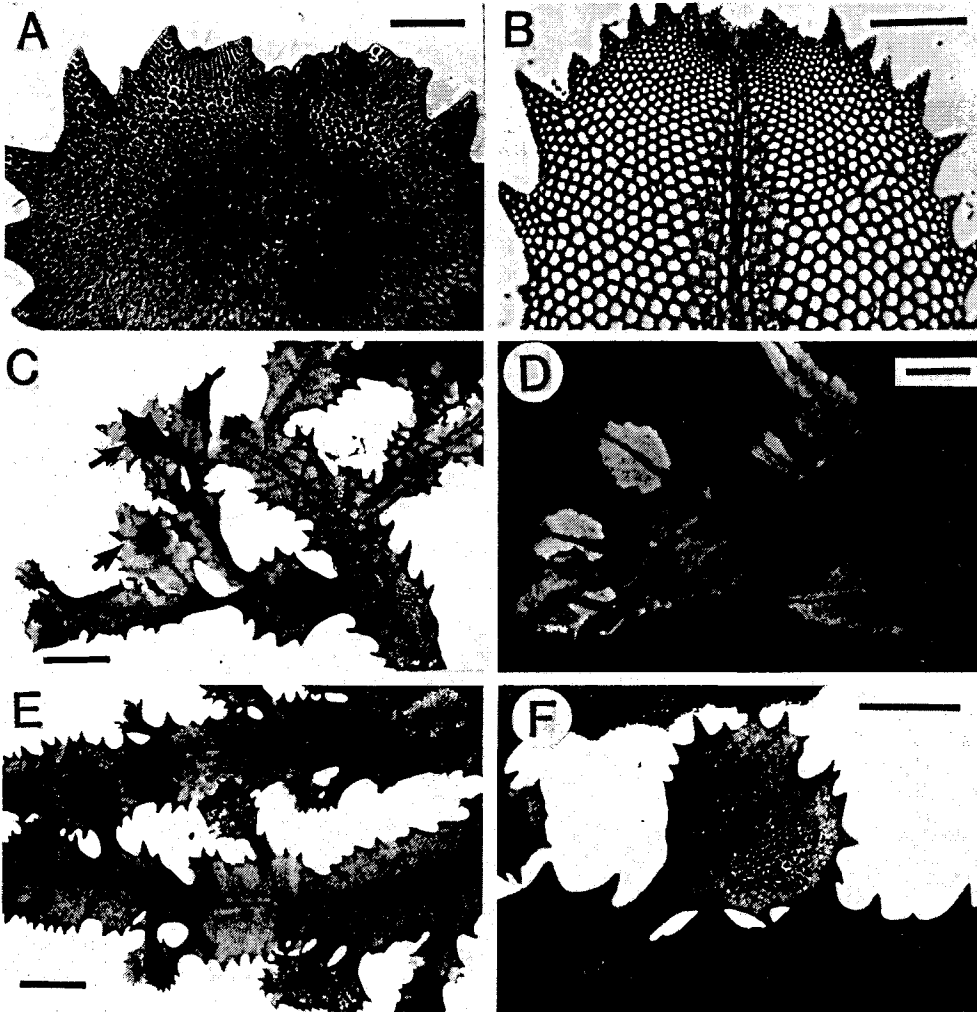


Fig. 6. *Bartoniella crenata*. A Blade apex. B Blade apex with onset of polystromatic condition along midrib. C Thallus with cystocarps. D Thallus (dark field) with spermatangial sori. E Tetrasporic thallus. F Marginal bladelet bearing a tetrasporangial sorus. Scale bars: A = 50 μm ; B = 200 μm ; C-E = 1000 μm ; F = 500 μm

Collection data: 6A, C, D leg. I. Harper (MICH & NAT-874 in NU), 29. Jan 1983, Rocky Bay, Park Rynie, Natal, South Africa. 6B leg. M. Wynne 7186 (MICH), 1 March 1983, Rocky Bay, Park Rynie, Natal, South Africa. 6E-F leg. M. Wynne 7027 (MICH), 14. Feb 1983, Mdloti Beach, Natal, South Africa

fertile proliferations. Our examination of a tetrasporophyte* of *C. coriifolia*, however, revealed the tetrasporangia to be produced on both surfaces of the fertile bladelet, the sori occupying the entire central region of the bladelets.

* Point Peron, Western Australia: leg. G. Kraft # 7250 & R. Ricker, 6. Aug. 1979 (MELU, A 36863).

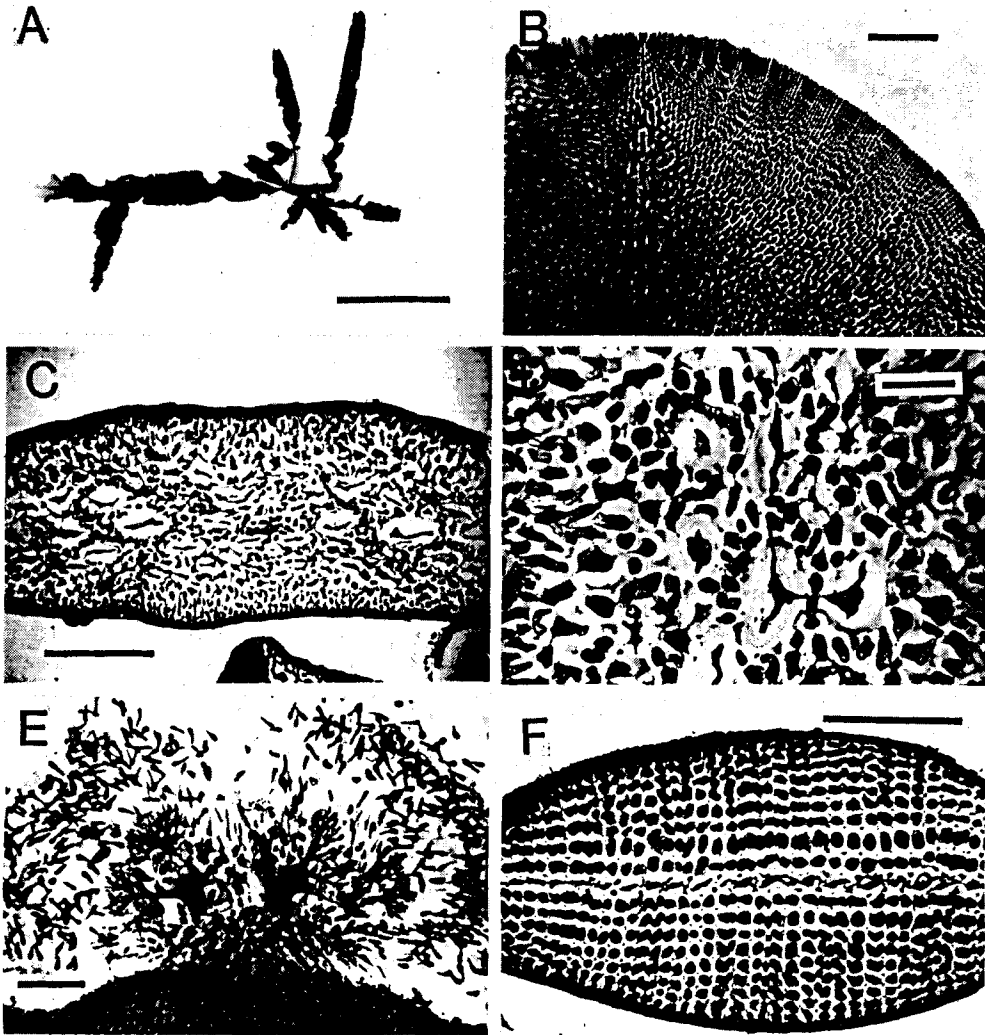


Fig. 7. A–E *Chauviniella coriifolia*; F *Heterodoxia denticulata*. A Habit of typical herbarium specimen. B Blade apex. C Cross-section of median portion of blade. D Detail of blade interior showing unorganized arrangement of medullary cells. E Cross-section of cystocarp. F Cross-section of blade showing the ordered organization of the medulla typical of the Nitophylloideae. Scale bars:

A = 5 cm; B, E = 50 μ m; C, F = 1000 μ m; D = 250 μ m

Collection data: 7 A leg. G. Kraft 4314 (MELU), 5. Apr 1972, Seal Bank, Kangaroo Is., S. A., Australia. 7 B leg. R. Scagel PR-LXIII-93 (UC & MICH), 29. Aug. 1962, Point Peron, W. A., Australia. 7 C–E leg. G. Kraft (MELU), 9. Aug 1979, 7 Mile Beach, near Dongara, W. A., Australia. 7 F leg. G. Kraft (MELU), 9. Aug 1979, 7 Mile Beach, near Dongara, W. A., Australia

Phitymophora J. Agardh

This genus includes two species, the correct name for the type being *Phitymophora amansioides* (Sonder) Womersley. When Womersley (1965) transferred Sonder's *Delesseria amansioides* to this genus, he did not cite the correct Sonder (1853) reference. This species, occurring in southern Australia, was formerly known as *P. imbricata* (Aresch.) J. Agardh. A second species, *P. linearis* (Laing) Kyl. from New Zealand, has been studied in some detail by Wagner (1954). The suite of traits that delineate this genus from other genera in the *Hypoglossum* group are the following: blades are polystromatic and branch from the midrib; branches are closely overlapping; and not all cells of second-order rows bear third-order rows.

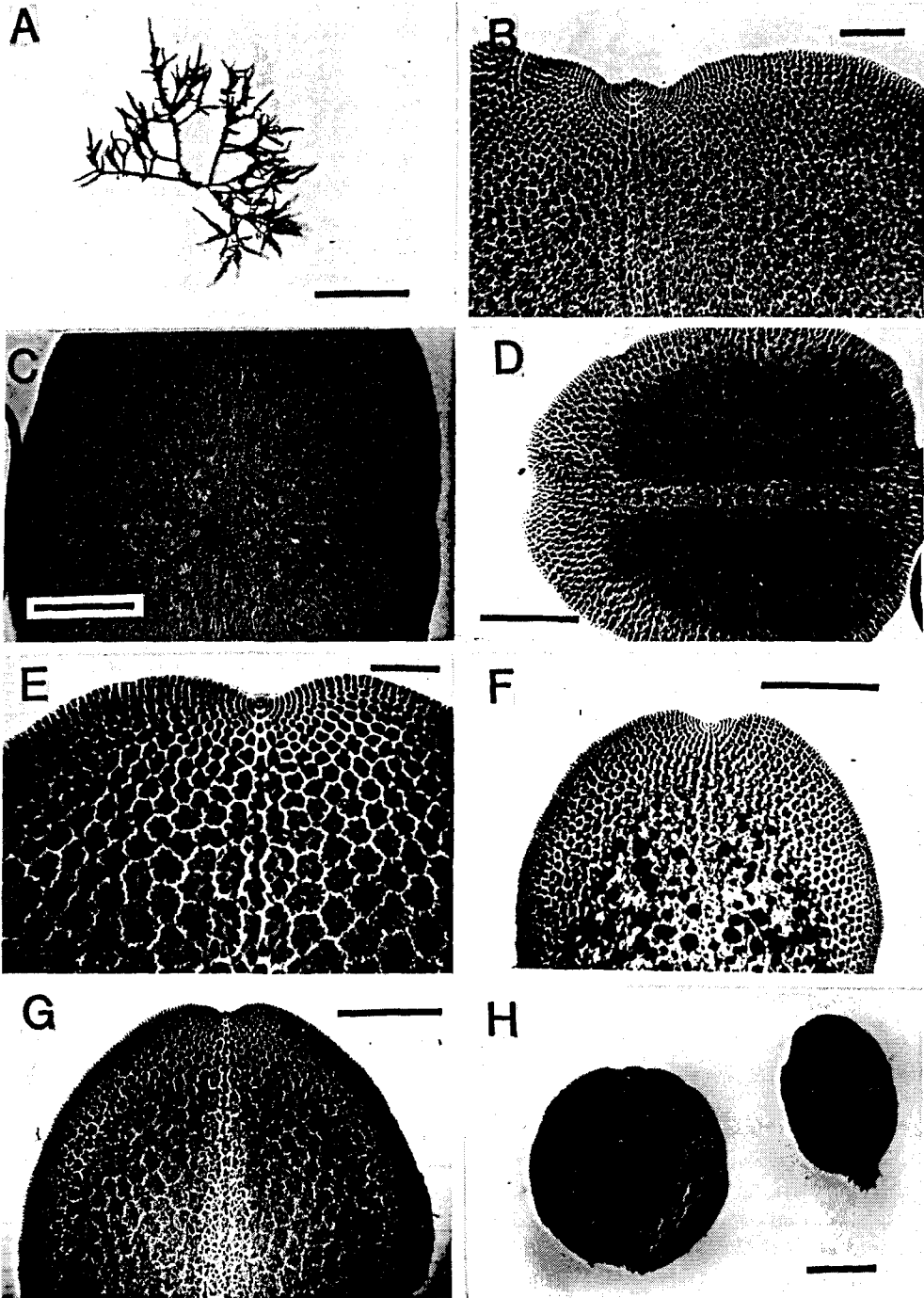
The habit of *P. amansioides* has been depicted by Harvey (1862, pl. CCXL, as *Chauvinia imbricata*) and is seen in Figure 8 A. Thalli have up to five orders of branches, whereas thalli of *P. linearis* have only two or three orders of branching and are of smaller stature (Laing, 1897; Kylin, 1929; Wagner, 1954). The apical organization of the blades in both species is comparable in that not all cells of second-order rows bear third-order rows (Figs 8 B, E). Reproductive structures are borne on proliferations of the final order. Spermatangial (Figs 8 D, G) and tetrasporangial sori (Figs 8 C, F) can cover most of the surface area of these bladelets, save for sterile margins and the midline region. On female thalli the cystocarps are produced usually singly on the midline of the final order of branching (Fig. 8 H).

On a specimen of *P. amansioides* collected by Ms. Fiona Scott at Ile Amsterdam (37°55' S, 77°40' E) in the southern Indian Ocean, we have observed clusters of a very small (0.5–1.0 mm across), apparently parasitic alga (Fig. 9 A). Male, female, and tetrasporic plants occur on the host, and an extensive system of rhizoids is apparent issuing from the base of the epiphyte and coursing into the host tissue. Apical organization of the individual blades (Fig. 9 B) is identical to that of the host. It appears that this minute parasitic alga represents an undescribed genus of adelphoparasite in the Delesseriaceae, there being no known parasitic member of the *Hypoglossum* group (Wynne & Scott, in press).

Zellera Martens

Zellera tawallina was described by Martens (1866) from the Moluccas, in present-day Indonesia, and the genus remains monotypic. The form of the thallus has generally been described as an incomplete (Martens, 1866; Kylin, 1956) or unconnected network (Weber-van Bosse, 1923). Womersley (1965) referred to unpublished studies by E. A. Mitchell which showed that the thallus was an incomplete network with only occasional unions between branch tips and the lower faces of older blades. *Zellera* was first classified by Kylin (1956) with this other network-forming delesseriaceous genera *Claudea* and *Vanvoorstia*, but Papenfuss (1962) cautioned that its true affinities would remain uncertain until wet-preserved material had been studied. Womersley & Shepley (1959) suggested that the cell lineages of the blades of *Zellera* were similar to both the *Caloglossa* and the *Hypoglossum* groups, since all tertiary initials reach the thallus margin. Later, Womersley (1965) indicated that *Zellera* seemed related to the *Hypoglossum* group on the basis of apical organization and procarp arrangement.

Itono (1986) presented excellent figures of sterile specimens of *Zellera*, demonstra-



ting that the apical organization includes a number of third-order cell rows, the initials of which all reach the blade margin. He also noted that some of the cell rows continued further development, which resulted in an irregularly denticulate blade margin. Itono concluded that *Zellera* is more closely related to the *Hypoglossum* group than the *Claudea* group, in which he considers *Claudea* to be the sole member.

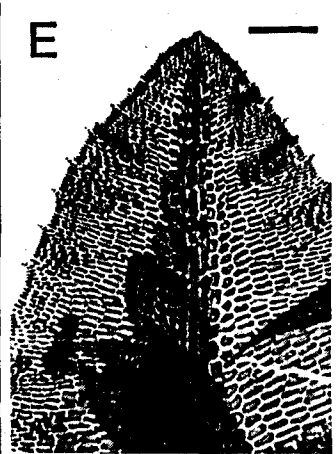
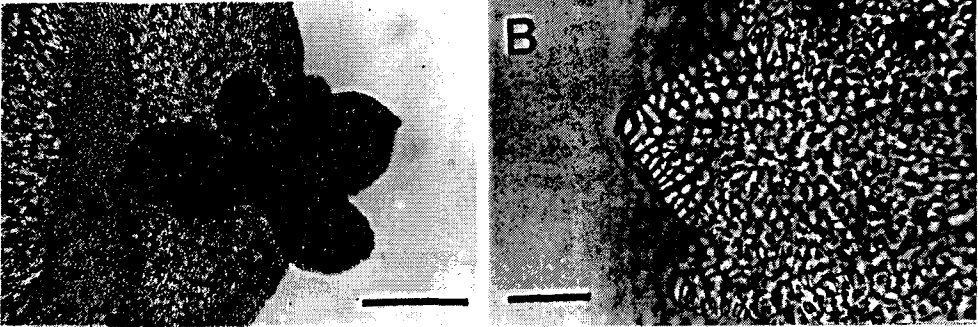
The present material from Indonesia (obtained by the Indonesian-Dutch Snellius II Expedition) reveals a high degree of union between three different orders of branches. As described by previous workers, the branching is unilateral along the midrib and abaxial in origin. The largest plants (Fig. 9 C) have five orders of blades, which is equivalent to saying that a primary axis may bear up to four orders of branches. The more proximal second-order branches fuse with the adaxial surfaces of adjacent first-order branches, but the distal second-order branches are free. Most third-order branches fuse with the adaxial surfaces of adjacent second-order branches (Fig. 9 D), but some distal third-order blades remain free. Some fourth-order branches are also produced, and most of these branches become fused on contact with the adaxial surfaces of adjacent third-order branches. It is the apical cell of a branch that becomes enlarged and initiates contact with the midrib of an adjacent branch. Additional cells close to the apex of the branch making contact also contribute to the formation of the fusion. All of these unions result in quadrangular meshes with right-angled sides.

The present observations confirm Itono's (1986) account of apical organization in *Zellera*. Most second-order row cells bear third-order rows (Figs 9 E, 10 A), and the margins of mature blades are highly denticulate. Lateral pericentral cells are cut off before transverse pericentral cells. Typically, the transverse pericentral cells are not present until the 8th or 9th segment from an apical cell. The apex of a blade initiating contact with an adjacent blade becomes modified because of the enlargement of the apical cell (Fig. 10 B), and cells of second-order rows may or may not bear third-order rows. All orders of blades have evident midribs, and lateral veins are absent. Midribs are more well developed in lower orders of the blades, and the proximal portion of the plant consists of a heavily corticated, succulent stipe (Fig. 9 C).

Tetrasporangial sori are borne only on free fourth-order blades and are thick in the central region of the blade (Figs 9 F, 10 C). Sori measure about 460–530 μm in width and about 1000–1100 μm in length. Cross-sections of sori (Fig. 10 D) reveal the tetrasporangia to be cut off from cortical cells rather than primary cells of the blade. At first the tetrasporangia lie in two planes, but as various cortical cells cut off more sporangia, the sorus contains numerous sporangia in various stages of maturation and lying in several planes. Mature tetrasporangia are 50–60 (–68) μm in diameter. On the male plant observed, spermatangial sori formed discrete patches randomly spread on the alae of blades of the final two orders.

Fig. 8. *Phytymophora*. A–D *P. amansioides*; E–H *P. linearis*. A Habit of typical herbarium specimen. B Blade apex. C Tetrasporangial bladelet. D Spermatangial bladelet. E Blade apex. F Tetrasporangial bladelet. G Spermatangial bladelet. H Cystocarpic bladelet. Scale bars: A = 4 cm; B = 50 μm ; C, D = 200 μm ; E = 250 μm ; F, G = 1000 μm ; H = 500 μm

Collection data: 8 A leg. S. Ducker (MELU-A3177), 17. Feb 1966, Point Lonsdale, Vic., Australia. 8 B, C leg. M. Wynne 5587 (MICH), 23. March 1981, Point Lonsdale, Vic., Australia. 8 E–H leg. M. Wynne 5895 (MICH), 10. Feb 1981, Shag Point, Otago, South Island, New Zealand



In addition to Indonesia, *Zellera* has also been reported from New Guinea (Schmidt, 1928) and southern Japan (Itono, 1986). A specimen collected from Kelana, New Guinea, and deposited in the British Museum, bears the label "*Delesseria karnbachii* Grunow n. sp.", an apparent nomen nudum. It is *Zellera tawallina*. It appears that there has been some confusion in separating *Zellera* from species of *Claudea*. Cordero's (1977, plate XXVI, Fig. B) "*Claudea multifida*" appears to be *Zellera*, as does Tseng's (1983, plate 71, Fig. 4) "*Claudea batanensis*", since in both illustrations the series of blades appear to be unilaterally arranged on the abaxial surfaces. Several collections of Philippine algae identified as *Claudea multifida* deposited in MICH proved to actually be *Zellera tawallina*. Thus, the distribution of *Zellera tawallina* should also include China and the Philippines.

In genuine *Claudea*, branches are arranged on the adaxial surfaces of successive segments along the midrib of blades (Papenfuss, 1937; Tanaka, 1967; Norris, 1987). In *Zellera*, the branches are abaxial and produced less regularly along the midrib (Fig. 9 E). Cystocarps of *Claudea* are conspicuously stalked (Harvey, 1858; Papenfuss, 1937), whereas they are sessile in *Zellera* (Martens, 1866). *Zellera* is like *Claudea* in that the nets have four-sided interstices.

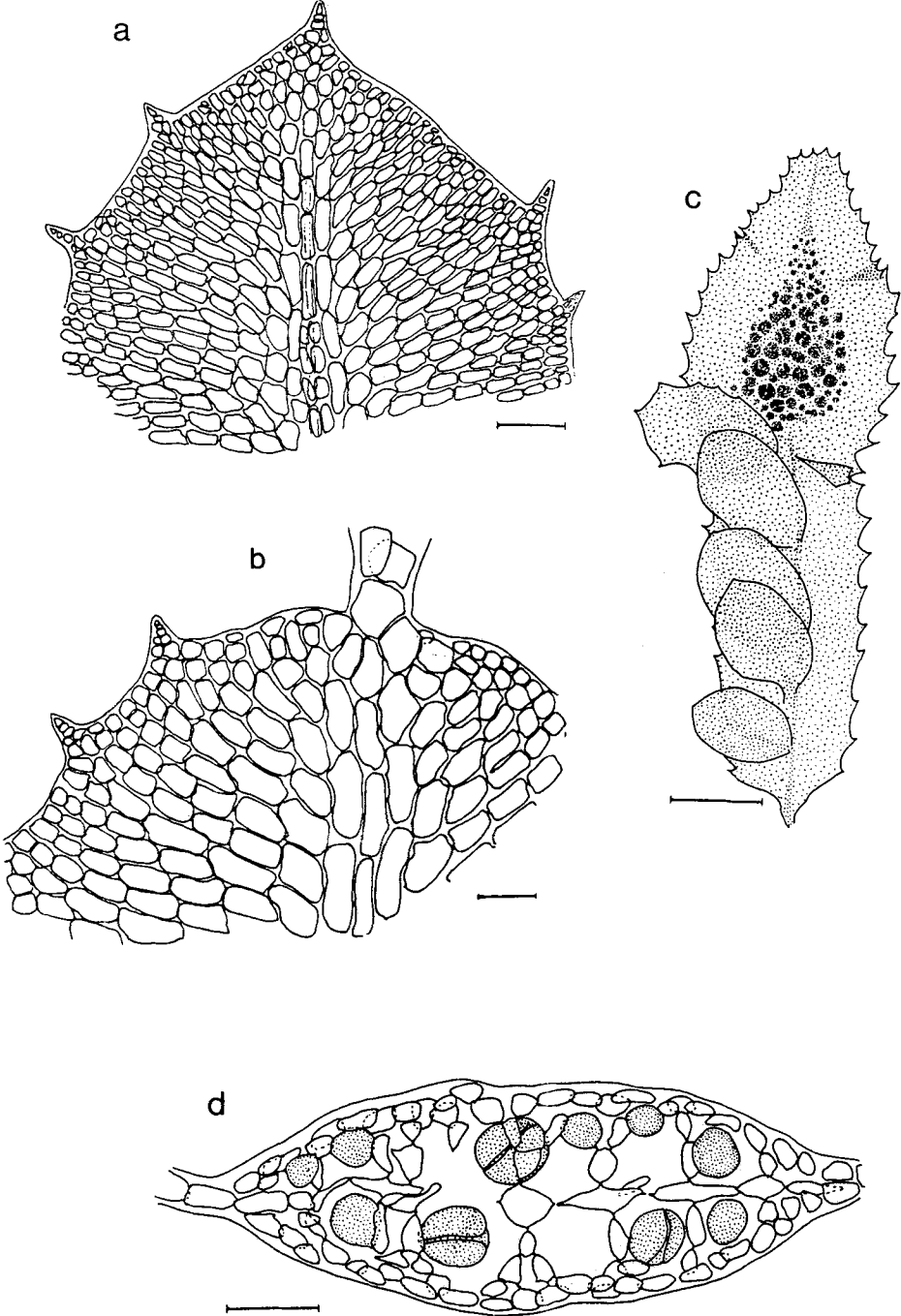
DISCUSSION

In Kylin's (1924) original description of the *Hypoglossum* group, he specified that members had blades lacking lateral nerves and intercalary cell divisions. In *Pseudobranchioglossum* of Bodard (1971), a genus which is otherwise very similar in most respects to *Branchioglossum*, lateral nerves are expressed because cells of second-order rows cut off corticating cells. Mikami's (1987) observation that intercalary divisions do occur in second-order cells of *Hypoglossum sagamianum* necessitates a further modification of Kylin's (1924) definition. The assignment of *Duckerella* to the *Hypoglossum* group added a species with spirally twisted blades. Thus, these exceptions necessitate some modification of the definition of the *Hypoglossum* group.

Zellera had been affiliated with *Claudea* (in the *Claudea* group) primarily because both genera have network-forming thalli. The apical organization of *Zellera tawallina* is more similar to that of most members of the *Hypoglossum* group, whereas the cell lineages demonstrated in the apex of *Claudea* are more like those in genera of the *Sarcomenia* group. The more natural assignment of *Zellera* appears to be with the *Hypoglossum* group. This re-assignment also results in a modification of the description of the *Hypoglossum* group to include network-forming members. Present observations on specimens of *Zellera tawallina* from Indonesia have shown that there is a high degree of

Fig. 9. A, B Parasite on *Phytomophora*; C–F *Zellera tawallina*. A Tetrasporic plant. B Female plant. C Habit of typical herbarium specimen. D Union of third-order branches with second-order branches. E Blade apex. F Tetrasporangial blades. Scale bars: A, F = 200 μ m; B = 25 μ m; C = 5 cm; D = 300 μ m; E = 50 μ m

Collection data: 9A, B leg. F. Scott 218-A (MICH), 2. Apr 1987, Ile Amsterdam (Fr.). 9C leg. Indonesian-Dutch Snellius II Expedition (L-11319 A), 27. Sept 1984, Stat. 4.150; NE Taka Bone Rate (Tijger Isl.), Taka Garlarang atoll, Indonesia, 06° 28' S, 121° 18' E. 9E leg. Smithsonian Oceanogr. Sorting Ctr. (MICH), 23. June 1978, Apo Isl., Dauin, Negros Oriental, Philippines. 9D, F leg. Indonesian-Dutch Snellius II Expedition (L-11463 D), 6. Oct 1984, Stat. 4.152; SW Salajar, NW coast of Pulau Guang, Indonesia, 0.6° 21' S, 120° 27' E.



fusion: of second- with first-order branches, of third- with second-order branches, and of fourth- with third-order branches. Thus, the usual characterization of *Zellera* as having thalli with "incomplete networks" seems unwarranted.

Kylin's (1956) main differentiation between the *Hypoglossum* group and the *Caloglossa* group was that in the former tetrasporangial initials arose from the cortical cells, forming two or more layers of tetrasporangia, whereas in the latter tetrasporangial initials arose from the central, or primary cells, forming a single layer of tetrasporangia. We now recognize that although some species of *Hypoglossum*, including the type, conform to Kylin's account, other species have tetrasporangia borne on primary cells. Tetrasporangia in *H. sagamianum*, *H. protendens*, *H. minimum*, and *H. geminatum* are produced entirely or almost entirely by primary cells, which is a trait shared with the *Caloglossa* group. Although this feature can no longer serve as an effective means of separating these groups, Papenfuss (1961) demonstrated that the *Caloglossa* group (*Caloglossa* and *Taenioma*) is the only one in the Delesseriaceae showing exogenous branching (i.e. branch primordia are cut off by an axial cell prior to the formation of pericentral cells). The *Caloglossa* group thus should be maintained as a distinct group.

As a result of the preceding review and considerations, an emended definition of the *Hypoglossum* group is proposed: thalli bladelike, either flattened or spirally twisted, entire or network-forming; growth uniaxial, intercalary divisions lacking in primary axial rows but at times present in second-order rows; tertiary cell-row initials always reaching blade margin; procarps restricted to primary axial row; tetrasporangia either largely restricted to primary cells or cortical cells of blades.

In conclusion, a key to the genera of the *Hypoglossum* group is provided:

- 1 Thallus in the form of a network. *Zellera*
- 1 Thallus not in the form of a network. 2
 - 2 Blades (except midrib region and stipe) essentially monostromatic 3
 - 2 Blades essentially polystromatic throughout. 6
- 3 Thallus blade-like, flattened, not spirally twisted. 4
- 3 Thallus spirally twisted, at least distally *Duckerella*
 - 4 Branching typically from the midrib *Hypoglossum*
 - 4 Branching typically from the blade margin (rarely from midrib of eroded blade). 5
- 5 Lateral nerves absent; branching restricted to blade margin. *Branchioglossum*
- 5 Lateral nerves present; branching both from blade margin and from midrib of eroded blades *Pseudobranchioglossum*
 - 6 Branching from blade margin. *Bartoniella*
 - 6 Branching from midrib 7
- 7 All cells of second-order rows bearing third-order rows; branches not frequent nor imbricate *Chauviniella*
- 7 Not all cells of second-order rows bearing third-order rows; branches closely set, imbricate. *Phitymophora*

Fig. 10. *Zellera tawallina*. A Apex of free blade. B Apex of attached blade. C Blade bearing distal tetrasporangial sorus. D Cross-section of sorus. Scale bars: A = 50 µm; B, D = 50 µm; C = 500 µm. Collection data: 10 A–D leg. Indonesian-Dutch Snellius II Expedition (L-11463 D), 6. Oct 1984, Stat. 4.152; SW Salajar, NW coast of Pulau Guang, Indonesia, 0.6° 21' S, 120° 27' E.

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