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## THE GENUS *HYPOGLOSSUM* KÜTZING (DELESSERIACEAE, RHODOPHYTA) IN THE TROPICAL WESTERN ATLANTIC, INCLUDING *H. ANOMALUM* SP. NOV.<sup>1</sup>

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### ABSTRACT

Observations are made on the occurrence and distribution of the red algal genus *Hypoglossum* Kützinger (Delesseriaceae, Ceramiales) in the tropical western Atlantic. In addition to the type of the genus, *H. hypoglossoides* (Stackh.) Coll. & Herv., three other species are reported: *H. anomalum* sp. nov., *H. involvens* (Harv.) J. Ag., and *H. tenuifolium* (Harv.) J. Ag. A key is presented to distinguish these four species. The newly described species, *H. anomalum*, is like other species in the genus in that its branches arise endogenously from the primary axial row but it is unique in that the branches emerge from the parent blade at some point between the midline and the margin of the blade. The new species is reported from Puerto Rico and Florida.

**Key index words:** Delesseriaceae; *Hypoglossum*; ***Hypoglossum anomalum*** sp. nov.; Rhodophyta; tropical western Atlantic

In contemporary literature two species of *Hypoglossum* Kützinger are recognized to be present in the tropical and sub-tropical western Atlantic: *H. involvens* (Harv.) J. Ag. and *H. tenuifolium* (Harv.) J. Ag. (Taylor 1960, Chapman 1963, Croley and Dawes 1970, Earle 1972, Almodóvar and Ballantine 1983). For the latter species the variety *carolinianum* Williams is usually recognized (Searles and Schneider 1978, Kapraun 1980). In older literature, however, the European-based type of the genus, *H. hypoglossoides* (Stackh.) Coll. & Herv., had been reported to occur in the western Atlantic [Harvey 1853 (as *Delesseria hypoglossum*), Murray 1888, Collins and Hervey 1917]. Wiseman (1966) re-examined the original

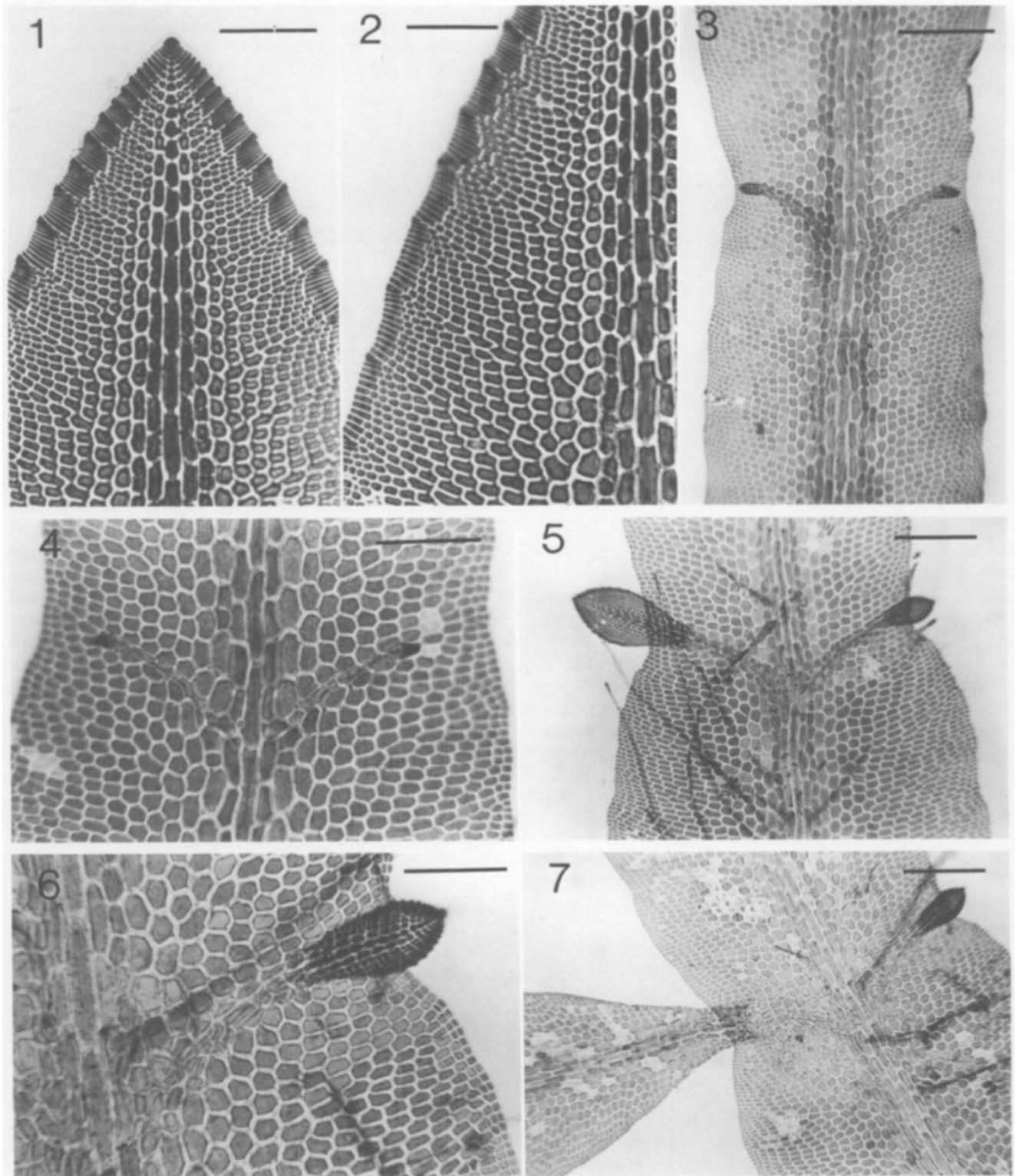
specimens from Charleston, South Carolina, on which Harvey (1853) had based his record of *Delesseria hypoglossum* from North America, and Wiseman confirmed that the plants were identifiable as the European species. Later Wiseman (1978) repeated his contention that the South Carolina plants were “closer” to *H. hypoglossoides* yet retained the name *H. tenuifolium* in his report. Recently Yarish et al. (1984) characterized *H. hypoglossoides* (as *H. woodwardii*) as belonging to the “warm temperate Mediterranean Atlantic” group of species, with a distribution restricted to the Mediterranean and eastern North Atlantic.

Two other taxa have been described, both from Curaçao by Sluiter (1908). *Hypoglossum tenuifolium* f. *schoonhoveni* was distinguished by Sluiter by its large median tetrasporangial sorus; Taylor (1960) did not maintain it as a separate form. *Zellera boekei* Sluiter appears to be a *Hypoglossum* and was regarded by Taylor (1960) as a possible synonym of *H. involvens*. On the basis of Sluiter’s illustrations it seems more likely to be *H. tenuifolium*.

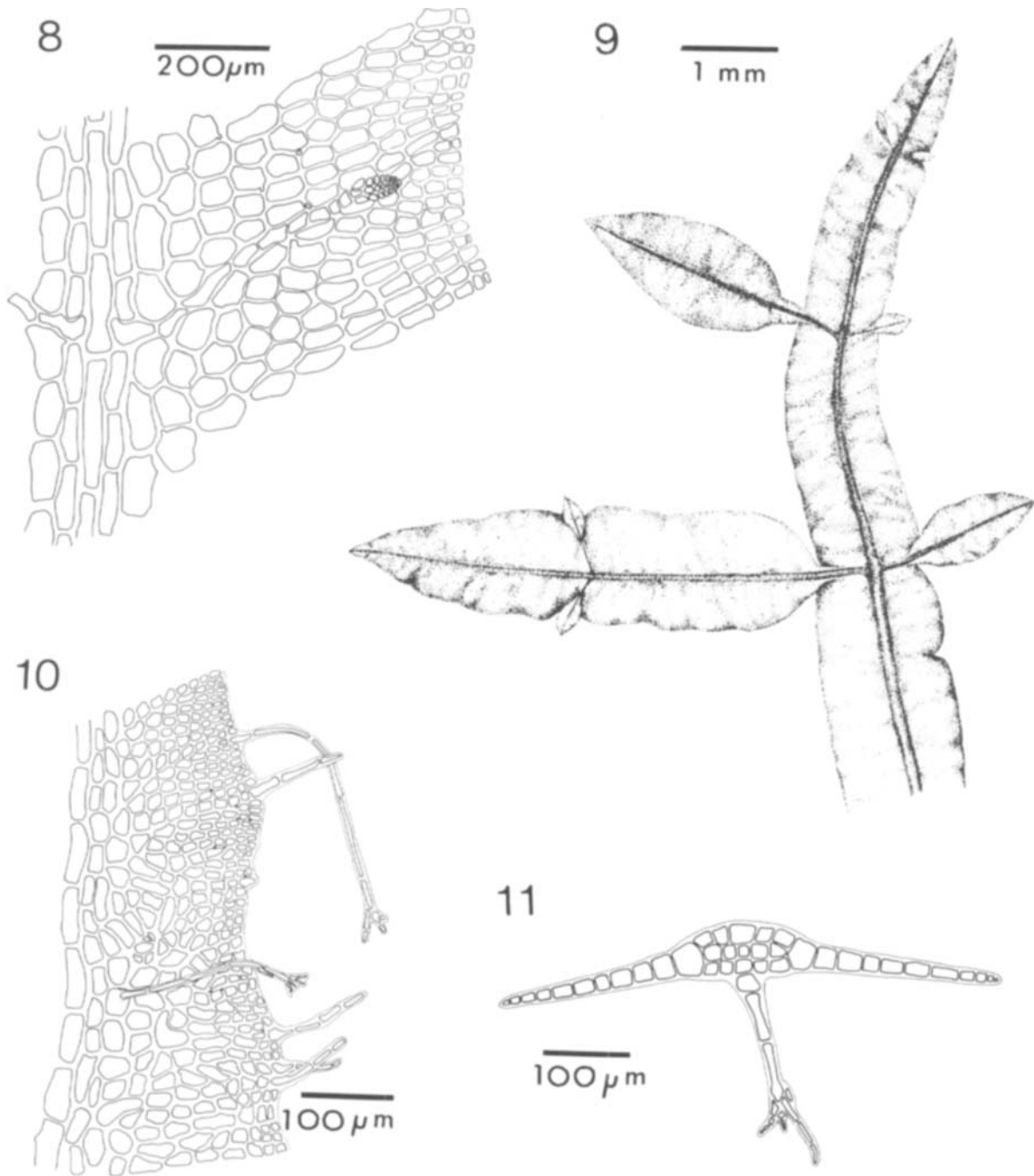
A fundamental characteristic of *Hypoglossum* and the other genera in the *Hypoglossum* Group is that the initials of all 3rd-order rows reach the margin of the blade (Nägeli 1845, Wynne 1983). In their study of southern Australian species of *Hypoglossum* Womersley and Shepley (1982) observed that in some species of the genus, including the type, each cell of the 2nd-order rows bears a 3rd-order row but that in other species not all cells of the 2nd-order rows bear 3rd-order rows. This same difference can be observed among collections of *Hypoglossum* from Puerto Rico. Based upon our study of recent collections, we have been able to discriminate four species of *Hypoglossum* in the tropical western Atlantic, including an undescribed species.

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FIGS. 1-7. *Hypoglossum anomalum* sp. nov. FIG. 1. Apex of blade. FIG. 2. Apical region, with initials of 2nd- and 3rd-order rows reaching blade margin. FIGS. 3 & 4. Opposite arrangement of blade primordia. FIG. 5. Location of emergence of blade between midline and blade margin. FIG. 6. Young blade emerging from parent blade. FIG. 7. Unequal development of a pair of blades. Scale bars: 40  $\mu$ m (Figs. 1, 2); 75  $\mu$ m (Figs. 4, 6); 150  $\mu$ m (Figs. 3, 5, 7).



FIGS. 8–11. *Hypoglossum anomalum* sp. nov. FIG. 8. Endogenous origin of blade from axial row but its emergence from parent blade at a point between midline and margin of parent blade. FIG. 9. Habit of alga. FIG. 10. Development of rhizoids from both margin and midregion of blade. FIG. 11. Cross-section of blade, with multicellular rhizoid.

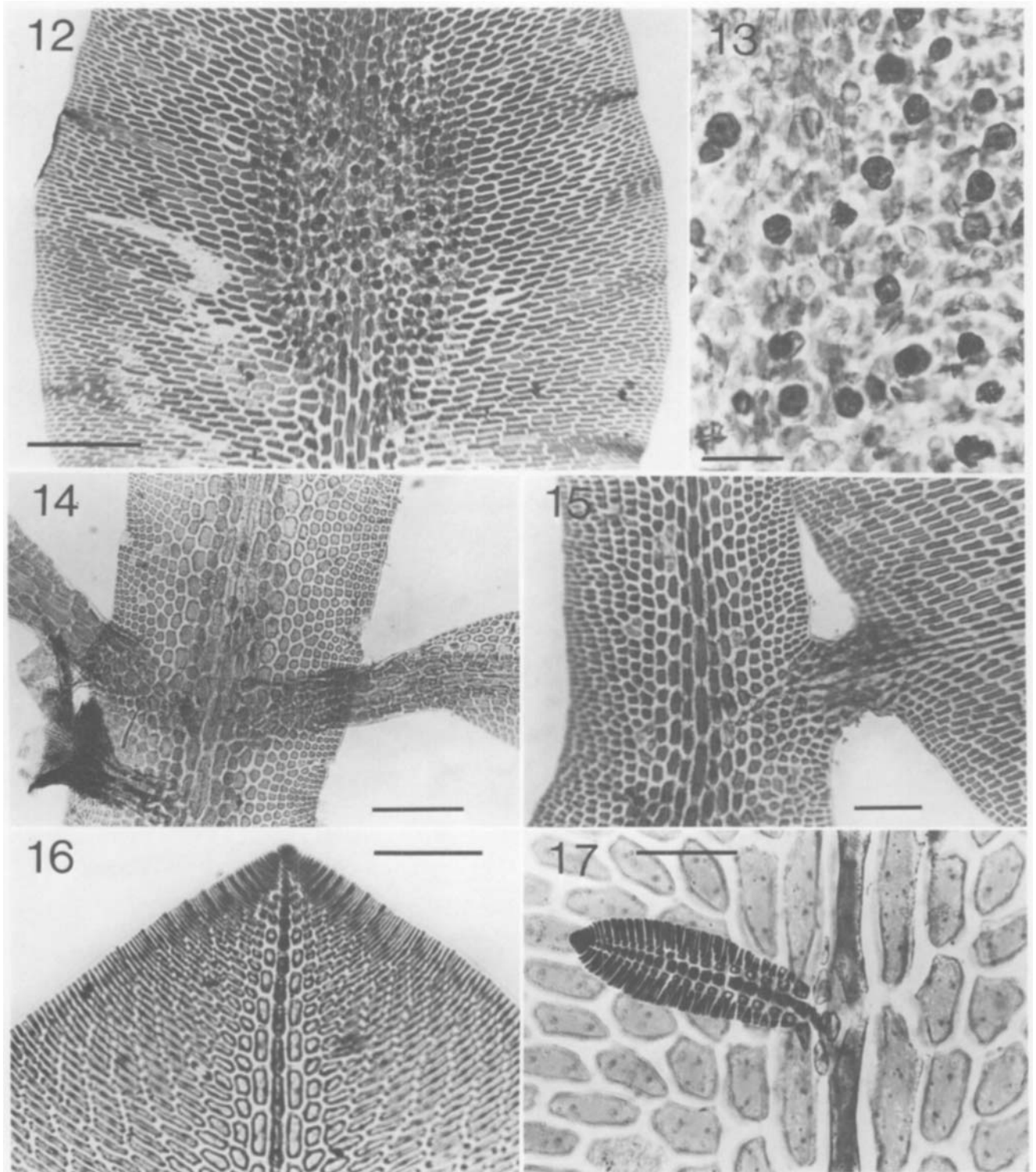
#### MATERIALS AND METHODS

SCUBA-collected or drift specimens were preserved in 5% formalin-seawater, and whole-mount slides were later prepared. Portions of thalli were placed on glass slides and stained with a mixture of 1% aniline blue/1 M HCl/Karo syrup/water (4:1:20:75). A standard Zeiss research microscope, equipped with a camera back and a drawing tube, was used for preparing the artwork. Voucher specimens have been deposited in the herbaria of the Department of Marine Sciences, University of Puerto Rico (MSM)

and of the University of Michigan (MICH). Herbarium abbreviations are according to Holmgren et al. (1981).

#### RESULTS AND DISCUSSION

It is possible to distinguish four species of *Hypoglossum* occurring in the tropical western Atlantic: *H. anomalum* sp. nov., *H. hypoglossoides* (Stackh.) Coll. & Herv., *H. involvens* (Harv.) J. Ag., and *H. tenuifolium*



FIGS. 12–17. FIGS. 12–15. *Hypoglossum anomalum* sp. nov. FIGS. 16 and 17. *Hypoglossum hypoglossoides*. FIG. 12. Tetrasporangial sorus. FIG. 13. Tetrasporangia. FIG. 14. Well developed pair of branches and rhizoid from midline. FIG. 15. Fusion of adjacent blades. FIG. 16. Apex of blade. FIG. 17. Endogenous origin of branch, with its immediate emergence. Scale bars: 40  $\mu\text{m}$  (Figs. 13, 16, 17); 150  $\mu\text{m}$  (Figs. 12, 14, 15).

(Harv.) J. Ag. The following key is used to delineate these taxa:

1. Branches occurring singly or in opposite pairs, arising and emerging from the midline of midrib of the parent blade ..... 2
1. Branches occurring in opposite pairs, emerging at points between the margin and midline (midrib) of the parent blade ..... *Hypoglossum anomalum*
  2. Apices of blades strongly incurved; localized patches of cells forming bullations that appear as a broad, conspicuous row or border just within the margins of the blade ..... *H. involvens*
  2. Apices of blades not strongly incurved; bullations along the blade margins not present ..... 3
3. A 3rd-order row produced from every cell of the 2nd-order rows; blades typically elongate, attenuate; sori broad, tetrasporangia arranged irregularly in the sorus ..... *Hypoglossum hypoglossoides*
3. A 3rd-order row not produced from every cell of the 2nd-order rows; blades typically broadly spatulate, blunt-tipped; tetrasporangia arranged regularly in narrow linear sori along the midline ..... *Hypoglossum tenuifolium*

### *Hypoglossum anomalum* sp. nov.

(Figs. 1–15)

*Alga e laminis repentibus, undulatis, usque ad 30 mm longis, et 1.0–1.8 mm latis constituta, monostromatica praeter costam, e stipitibus brevibus cylindricis corticatisque enascentibus; laminae ad substratum secundariae affixae per rhizoidea uniseriata ramosaque e latere abaxiali regionis costae, aut e cellulis pericentralibus aut e derivativis cellularum pericentralium regionis costae enascentia; rhizoidea e margine laminae quoque aliquando procreata; omnis cellula secundi ordinis series cellularum tertii ordinis ferens; ramificatio laminarum ad duos ordines, opposita saepe inaeque evoluta; primordia rorum e cellulis axialibus primariis endogene initiata, lamella, autem, e lamina parentis non emergente prius prope locum inter costam atque marginem laminae parentis; tetrasporangia in soris ovatis per regionem costae symmetrice procreata; sororum longitudo indefinita et latitudo 500  $\mu$ m; tetrasporangia usque ad 70  $\mu$ m diametro.*

Alga consisting of repent, undulate blades, to 30 mm long and 1.0–1.8 mm wide, monostromatic except along the midrib, arising from short, cylindrical, corticated stipes; blades secondarily attached to substrate by uniseriate, branched rhizoids arising from abaxial side of the midrib region (Figs. 11 and 14), either from pericentral cells or their derivatives in the midrib region; rhizoids also occasionally produced from the blade margin (Fig. 10); all 2nd-order cells bearing 3rd-order cell rows (Figs. 1 and 2); branching of blades to two orders, opposite, often of unequal development; branch primordia initiated endogenously from primary axial cells but bladelet not emerging from parent blade until some point between midrib and margin of parent blade; tetrasporangia produced in ovate sori symmetrically along midrib region; length of sori indefinite and width 500  $\mu$ m (Fig. 12); tetrasporangia to 70  $\mu$ m in diameter (Fig. 13).

Holotype: *D. L. Ballantine 1782*, 16.i.1985, 61 m depth, edge of insular shelf, offshore from La Parguera, Puerto Rico. Deposited in MICH.

Isotypes deposited in DUKE, MSM, NCU, and US.

Additional collections: PUERTO RICO. Edge of insular shelf, offshore from La Parguera: *Ballantine 1719*, 16.i.1985 (58 m, on coral rubble); *Ballantine 1789* tetrasporic, 14.i.1985 (50 m); *Ballantine 1823*, 11.i.1985 (40 m); *Ballantine s. n.*, 4.xii.1985 (30 m). Edge of insular shelf, offshore from Salinas: *Ballantine 891d*, 5.i.1982 (30 m, on worm casings); *Ballantine 1174b*, tetrasporic, 17.i.1983 (27 m, on coral rubble). FLORIDA. Dry Tortugas, dredged off southwest channel (station 215): *Taylor 1024* 11.iv.1925 (36 m; MICH).

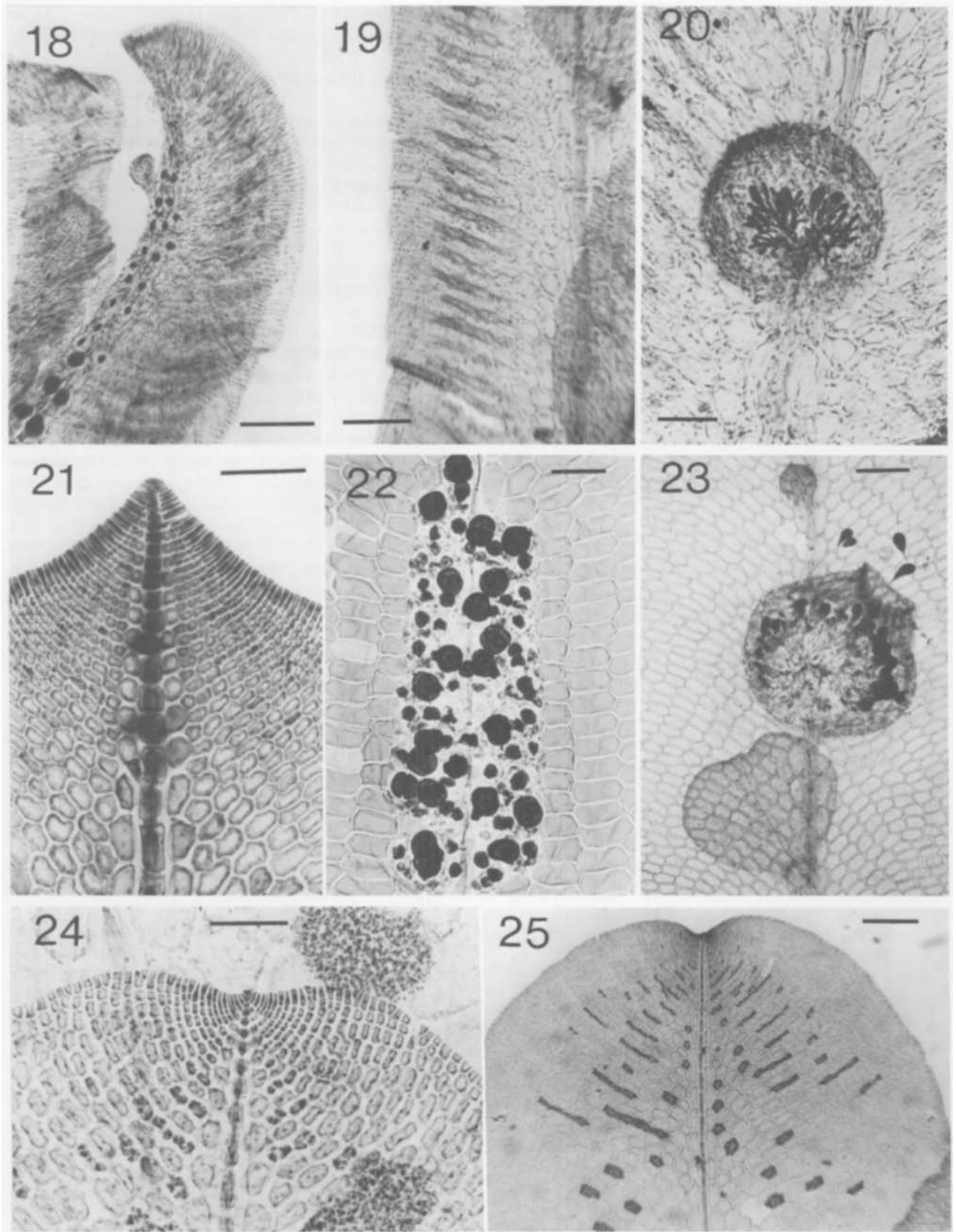
The most distinctive feature of *Hypoglossum anomalum*, and the reason for the specific epithet, is its unique manner of branching. The initial of a branch is cut off endogenously from a primary axial cell, as is typical for the genus (Fritsch 1945). However, instead of immediately emerging from the parent blade at that point, the initial undergoes divisions. This results in a filament that grows in the plane of the parent blade along a course parallel to that of a 2nd-order row of cells (Figs. 5, 8). Invariably two such branch primordia are cut off from the same axial cell, producing a pair of opposite bladelets (Figs. 3, 4, 9). At some point between the midline and the margin of the parent blade, each of the branch primordia emerges from the plane of the parent blade, typically on the same surface. The young blades are then evident as branches and proceed to broaden into blades similar to the parent blade (Fig. 6). The axial row which connects blades to the parent axis becomes corticated with age. Sometimes a branch emerges close to the midrib, more typical of *Hypoglossum*, but at other times a branch emerges closer to the blade margin, superficially resembling the branching in *Branchioglossum*.

Although the branch primordia of each pair have a comparable sequence of growth to the time of their emergence from the parent blade, there often is a subsequent unequal development, one of the members of the pair growing more rapidly than the other (Fig. 7). There are about 25 species of *Hypoglossum* now recognized (Wynne and Kraft 1985), and we know of no other species of *Hypoglossum* that has been described as having this unusual pattern of branch initiation. We have also observed the lateral fusion of adjacent blades (Fig. 15).

*Hypoglossum hypoglossoides* (Stackhouse)  
Collins & Hervey  
(Figs. 16, 17)

Syn.: *Delesseria hypoglossum* (Woodw.) Lamour.  
*Hypoglossum woodwardii* Kütz. (see Wynne 1984).  
*H. tenuifolium* var. *carolinianum* Williams

Recent collections. PUERTO RICO. Edge of insular shelf, offshore from La Parguera, growing on



*Verongia: Ballantine 15*, 18.xii.1978 (18 m); 1.6 km seaward of Margarita Reef, La Parguera: *Ballantine 2102*, 30.vi.1985, female (24 m, epiphytic on *Udotea*). 1.5 km seaward of Media Luna Reef, La Parguera: *Ballantine 1843*, 24.i.1985 (17 m). BELIZE. Long Cay, growing on *Verongia: Ballantine 379*, 27.vi.1979 (29 m).

*Hypoglossum hypoglossoides* has been confused with *H. tenuifolium* in the past. They differ in that in *H. hypoglossoides* all cells of the 2nd-order rows bear 3rd-order cell rows, as has been depicted in this species by Kylin (1923 and 1924, as *H. woodwardii*). This pattern is demonstrated in Figure 16. Other features serve to separate these two species. Vegetatively, the midline in young blades of *H. hypoglossoides* is uncorticated, but it becomes corticated with numerous closely spaced cells in older blades. The midline of blades in *H. tenuifolium* tends to remain uncorticated, although basal portions of thalli do become corticated. Reproductively, tetrasporangial sori in *H. hypoglossoides* form broad continuous or interrupted arrangements on either side of the midrib (Kylin 1924), whereas those in *H. tenuifolium* form scattered patches from individual cells on the blade. Branches arise endogenously from primary axial cells and emerge from the midline (Fig. 17), which is similar to the mode of branching in *H. tenuifolium* and *H. involvens* but dissimilar to that of *H. anomalum*.

*Hypoglossum involvens* (Harvey) J. Agardh  
(Figs. 18–20)

Recent collections: FLORIDA. Florida Keys, Key Largo: *Hommersand* (in NCU, MICH), 4.iv.1965. Upper Maticumbe Key: *Hine 668-134* (in USF 15281), cystocarpic & tetrasporic, 12.vi.1968, epiphytic on *Thalassia*. Knight Key: *Kapraun & Wynne 4424* (in MICH), tetrasporic, 31.xii.1975.

*Hypoglossum involvens* was described by Harvey (1853) from Key West, Florida. Harvey referred to two morphological features that clearly distinguish it from the other species of the genus in the western Atlantic, namely, the strongly involute blade apices (Fig. 18) and a conspicuous border of bullations along the blade margins (Figs. 19, 20). The former characteristic is more easily observed in fresh or wet-preserved specimens than in pressed material. The latter characteristic persists even in wet-preserved or herbarium specimens that have been soaked up. Harvey's (1853) plate XXII-A, figure 3, aptly depicts the distinctive appearance of the interrupted zone of elongate cells running inside the margins of the

blades. The blade is not flat in this region, but groups of cells have collectively formed broad pockets, or concavities, and these bullations occur in two long series creating the borders noted in Harvey's original description.

The blades of *Hypoglossum involvens* are extremely delicate and filmy, much as in *H. tenuifolium*, and they are much branched and fastigiate also as in that species. The blades tend to be very narrow, usually less than 1 mm wide, and the apices of the blades are attenuated rather than blunt as in *H. tenuifolium*. Tetrasporangia are confined to a narrow sorus running indefinitely along the midline of the blades (Fig. 18). Mature tetrasporangia measure 50–70  $\mu\text{m}$  diam.

This species appears to be rather rare, and according to A. Hine's notes on the specimen in USM, it is an "ephemeral spring plant, occurring only in April and May, sometimes into June." The specimen from Knight Key (*Wynne 4424*), however, was collected in late December; it does not have the bullations but otherwise agrees with *H. involvens*.

The record of occurrence of this species in Puerto Rico by Almodóvar and Ballantine (1983) was based on the single collection by V. Rosado (*Almodóvar 5958*, in MSM & MICH), but it conforms to *H. hypoglossoides* rather than *H. involvens*. For the present, then, *H. involvens* is removed from the flora of Puerto Rico and is known only from Florida.

*Hypoglossum tenuifolium* (Harv.) J. Ag.  
(Fig. 21–25)

Recent collections: PUERTO RICO. 1.5 km seaward of Media Luna Reef: *Ballantine s. n.*, 29.viii.1973 (17 m); *Ballantine s. n.*, 19.ii.1974 (17 m); *Ballantine 1676*, tetrasporic, 7.xii.1984 (17 m). Edge of insular shelf, off Margarita Reef: *Ballantine 67*, female & tetrasporic, 6.iv.1978 (30 m); *Ballantine 1518*, male, 12.ii.1984 (27 m, on *Verongia*). 1.6 km seaward of Margarita Reef: *Ballantine 1652*, female, 10.xi.1984 (27 m); *Ballantine 2020*, 7.iii.1985 (27 m); *Ballantine 2101*, male, 30.vii.1985 (27 m; epiphytic on *Udotea*).

This species was described by Harvey (1853) as *Delesseria tenuifolia* from Key West, Florida, and was later transferred to *Hypoglossum* by J. Agardh (1898). Harvey stated that the blades were exceedingly thin (hence, the specific epithet) and semi-transparent and that the blades were more delicate than those in the type of the genus. Harvey described the tetrasporangial sori as being very small and placed on either side of the midrib, very close to the tips of

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FIGS. 18–25. FIGS. 18–20. *Hypoglossum involvens*. FIGS. 21–25. *Hypoglossum tenuifolium*. FIG. 18. Blade with incurved apex and bearing tetrasporangia with bullations evident. FIG. 19. Portion of a blade with row of marginal bullations. FIG. 20. Cystocarpic blade. FIG. 21. Female blade bearing procarps. FIG. 22. Tetrasporangial sorus. FIG. 23. Cystocarp on midline of blade. FIG. 24. Blade bearing young spermatangial sori. FIG. 25. Older male blade, with spermatangial sori coalescing into bands. Scale bars: 40  $\mu\text{m}$  (Figs. 21, 24); 75  $\mu\text{m}$  (Figs. 20, 22); 200  $\mu\text{m}$  (Figs. 23, 25).

young blades. He also distinguished this species from *H. hypoglossoides* by the midrib having an articulate appearance and consisting of a triple row of cells, with large polygonal cells lying along the midline. In the basal parts of the thalli the axes are denuded, and the midrib does become thickened, to about 2 or 3 mm in diameter.

Various authors (Børgesen 1919, Taylor 1942, 1960) have described this alga as forming bushy, much branched, fastigiate clumps, the blades closely overlapping, like pages in a book. The color has been said to be "light pink to greenish, or nearly colorless" (Taylor 1960).

Another feature which separates *Hypoglossum tenuifolium* from the three other species of the genus occurring in the tropical western Atlantic is that not all cells of the 2nd-order rows produce 3rd-order rows (Figs. 21 and 24). (See also Børgesen 1919, fig. 341b.) Thus, one does not see the crowding effect of secondary and tertiary initials along the margins near blades' apices that is characteristic of those species in which 3rd-order rows are produced from every cell of the 2nd-order rows. The apices of blades are usually blunt (Fig. 24) but may be attenuate if rapidly growing (Fig. 21). A further useful trait in recognizing *H. tenuifolium* is the orderly appearance of the tetrasporangia in the narrow sori at least in the early stages. The tetrasporangia are less orderly arranged in older sori. Tetrasporangia are arranged symmetrically along and directly over the midline (Fig. 22), as also shown by Børgesen (1919, fig. 341b). The spermatangial sori in *H. tenuifolium* are produced initially from scattered individual cells (Fig. 24). In older blades, spermatangial sori typically coalesce into larger bands running diagonally out from the midline (Fig. 25). The urn-shaped cystocarps occur on the midline (Fig. 23), and their appearance conforms to Børgesen's (1910, 1919) accounts.

From the various illustrations provided in their papers, it is evident that *H. tenuifolium* is present in the Virgin Islands (Børgesen 1919), North Carolina (Schneider 1975), Cuba (Kusel 1972), Colombia (Schnetter and Bula Meyer 1977), and Brazil (Cordeiro-Marino and Guimaraes 1981). However, the single figure given by de Rios (1972) for her record of *H. tenuifolium* in Venezuela would appear to represent *H. hypoglossoides*.

Williams (1949, 1951) likened his newly described *Hypoglossum tenuifolium* var. *carolinianum* to the European type of the genus (i.e. *H. hypoglossoides*). The variety was described from shallow water and stated to have a height of only 1 cm. It is clear from both Williams' (1949) figures and those of Kapraun (1980) for this variety that this taxon, var. *carolinianum*, is in agreement with *H. hypoglossoides* in regard to organization of the apex, appearance of the tetrasporangial sori, and other features. Likewise, Oliveira's (1969) record and figures for this variety from Brazil also appear to be this same entity. We see no reason

to maintain it as a distinct variety but would merge it within *H. hypoglossoides*.

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## INCORPORATION OF TRITIATED THYMIDINE BY EUCARYOTIC MICROALGAE<sup>1</sup>

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### ABSTRACT

The uptake and incorporation of tritiated thymidine (<sup>3</sup>H-TdR) by axenic laboratory cultures of marine diatoms and dinoflagellates was measured. <sup>3</sup>H-TdR was incorporated into nucleic acids by all four algae examined during a two to six hour period prior to cytokinesis and not during other times of the cell cycle. Between 90–95% of the <sup>3</sup>H label incorporated into (cold trichloroacetic acid insoluble) nucleic acids was recovered from DNA. Incorporation of <sup>3</sup>H-TdR appears to accurately indicate the timing of DNA synthesis. The incorporation of <sup>3</sup>H-TdR by eucaryotic algae during long term (24 h) incubations does not generally preclude using <sup>3</sup>H-TdR uptake to estimate bacterial production and growth during short term incubations.

Key index words: algae; cell division; DNA; diatoms; dinoflagellate; nucleic acids; RNA; thymidine; tritium

Nucleic acids from all microorganisms are assembled from the same five nucleotide bases; however, only three of the five component nucleotides are common to both RNA and DNA. All nucleic acid contains adenine, guanine and cytosine with thymine being unique to DNA, and uracil being unique to RNA. The specificity of the thymine to DNA makes it an ideal tracer of DNA metabolism. Radiolabelled thymine is not readily incorporated into DNA (Crawford 1958, Cleaver 1967, Munch-Petersen 1970) and has not been extensively studied.

However, the incorporation of the radiolabelled nucleoside [<sup>3</sup>H] thymidine (thymine deoxyribose: TdR) into DNA has a long history of use in cell biology (Gelfant 1966, Cleaver 1967, Van't Hoff 1968, Metzler 1977, Dirksen et al. 1978). The ability of higher plants, animals and bacteria to take up and incorporate <sup>3</sup>H-TdR into nuclear DNA has been well documented (Firket and Verly 1958, Cleaver 1967, Davidson 1968). However, TdR uptake and metabolism has not been extensively studied in microalgae (Sagen 1965, Galleron and Durrand 1979, Lloyd and Cantor 1979).

For most eucaryotic algae the cell division cycle is composed of four discrete, sequential intervals (Chisholm 1981, Puisseux-Dao 1981). Typically two temporal gaps (G-1 and G-2 stages) separate periods of DNA synthesis (S-stage) from cell division (D-stage, karyokinesis and cytokinesis). New DNA is formed by semi-conservative replication. Thus when <sup>3</sup>H-TdR is supplied exogenously, it could be taken up and phosphorylated to thymidine monophosphate (dTMP) by the salvage pathway enzyme thymidine kinase. Further phosphorylation by thymidylate kinase to deoxythymidine 5-triphosphate (dTTP) precedes incorporation into DNA. <sup>3</sup>H-thymidine would thus be incorporated into replicating DNA only during the S-interval of the cell cycle (Davidson 1968, Natchtwey and Cameron 1968). Several recent laboratory studies have reported insignificant incorporation of <sup>3</sup>H-TdR by marine cyanobacteria and eucaryotic algae (Cuhel and Waterbury 1984, Pollard and Moriarty 1984, Bern

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