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SYSTEMATICS OF ANADYOMENE SPECIES (ANADYOMENACEAE, CHLOROPHYTA) IN THE TROPICAL WESTERN ATLANTIC¹

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ABSTRACT

Three new species of *Anadyomene* are described. *Anadyomene lacerata* has pinnately branched veins and a unique lacerated margin formed by elongated vein cells. *Anadyomene linkiana* consists of a perforate blade arising by polychotomous branching from a distinct stripe, and *A. howei* has an eperforate, delicate blade of polychotomously branched cells and a smooth margin of elongated vein cells. Distinguishing features of the five previously described species are clarified, and all eight taxa are illustrated. Observations in the field and from more than 400 herbarium specimens form the basis for a discussion of Indo-Pacific affinities, ecological adaptations, cell division, reproduction, and ordinal status.

A phylogenetic analysis based on 17 equally weighted characters produced a cladistic gradation, indicating that *Anadyomene* is a monophyletic genus. The most basal species (*A. saldanhae*, *A. linkiana*, *A. howei*, *A. menziesii*) show only polychotomous branching. In contrast, the distal group (*A. pavonina*, *A. stellata*, *A. rhizoidifera*, *A. lacerata*) have pinnate interstitial cells along the veins in addition to polychotomous branching at the vein apices.

Key index words: *Anadyomenaceae*; *Anadyomene*; *A. howei* sp. nov.; *A. lacerata* sp. nov.; *A. linkiana* sp. nov.; *Cladophorales*; *Cystodictyon*; tropical western Atlantic

Anadyomene Lamouroux 1812 (*Anadyomenaceae*, *Cladophorales*) is characterized by a unistratose blade or cluster of blades formed by the polychotomous branching of uniseriate veins, with the interstices, or spaces between the veins, completely or partially filled with cells that are smaller than those of the veins. All cells are laterally joined in one plane and form species-specific, fan-shaped patterns. Blades are attached to the substrate by rhizoids, which may intertwine to form a stipe. Rhizoids develop as downward extensions of the veins and are usually restricted to the basal or ventral prostrate portions of the blade.

Juvenile thalli generally develop from single zoospores that divide with the first upper cell developing into the initial veins and the lower cell forming the stipe/rhizoid system. The distal portion continues to divide and vein segments increase in size, whereupon laterals are initiated and also increase in size and number as the blade develops. Growth is both apical, at the distal margins, and intercalary, with the size and number of proximal cells increasing continuously.

Anadyomene is distinguished from the closely related genus *Microdictyon* by its blade, which forms a more or less continuous expanse, whereas the latter has a more open reticulate structure. The terminal filaments in the blade of *Microdictyon* are generally free, and the lateral filaments anastomose (mostly at their tips) below the ragged margin. In *Anadyo-*

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mene, by contrast, the rapid and complete joining of all apical segments results in an entire margin and a blade that is usually continuous, although in two species the blade is perforate. *Struvea* differs from *Anadyomene* by its mesh-like blade, nonseptate stalk, and central axis.

The first recorded specimen that can be assigned to *Anadyomene* was illustrated by Dillenius (1741) as *Lichenoides gelatinosum tenue reticulatum* (source C. Agardh 1822:400) from Isla de Providencia. The first binomial, *Ulva stellata*, was applied by Wulfen (in Jacquin 1786) to a species from the Adriatic. Lamouroux (1816) established the genus *Anadyomena* on the basis of a new species, *A. flabellata*, described from Corsica. If he was aware of Wulfen's publication, he did not recognize *Ulva stellata* (from the Adriatic) as the same alga as the one from Corsica. The original spelling, *Anadyomena*, was changed to *Anadyomene* by C. Agardh (1821:99), and the latter spelling has been conserved. In 1823, C. A. Agardh restored the proper epithet to *Anadyomene stellata*; however, subsequent workers (Kützinger 1849, Harvey 1858, Farlow 1876) continued to use *flabellata*. Bory de Saint-Vincent (1832:327) provided a clue to this nonacceptance in his statement that he did not understand why Agardh had substituted the epithet *stellata* for the more conventional name *flabellata*, as given by Lamouroux, for a plant not in the least like a star. Actually, the polychotomously branched veins radiating outward do suggest a multiple "starburst" pattern in *A. stellata*.

J. E. Gray (1866) divided *Anadyomene* into four genera. The name *Anadyomene* was retained for species with polychotomously branched veins and interstitial cells in a consistent parallel pattern (e.g. *A. stellata*). *Calomena* comprised plants with forked vein cells continued to the margins and the narrow interstitial spaces filled with very small, randomly arranged cells [e.g. *A. brownii* (J. E. Gray) J. Agardh]. *Grayemma* was distinguished by veins formed from several parallel series of cells rather than a single series (e.g. *A. menziesii*). *Cystodictyon* was distinguished by its perforate blades; it comprised only the type species, *Anadyomene leclancheri* Decaisne, from the Pacific, until J. Agardh added *C. pavoninum*, from Florida, in 1894. Heydrich (1894) rejected the genus, but he knew only the type species.

Wille (1910) considered *Cystodictyon* a section of *Anadyomene* and transferred *C. pavoninum* to that genus. However, although *A. leclancheri* has consistently been placed in *Anadyomene* by authors since Heydrich (Gilbert 1946, 1961, Velasquez et al. 1975, Silva et al. 1987), most except Wille have continued to segregate *C. pavoninum* (Kützinger 1849, Harvey 1858, Farlow 1876). Wille also reduced *Calomena* (misspelled *Calonema*) to a section of *Anadyomene*, into which he merged Gray's third genus, *Grayemma*. Because our cladistic analysis does not support the recognition of any segregate genera, we follow Wille

(1910) in treating *C. pavoninum* as a species of *Anadyomene*.

This study considers the tropical western Atlantic populations of *Anadyomene*. Treatment of this biogeographic assemblage from an evolutionary/monographic perspective separate from that of the Indo-Pacific is warranted, because the two regions have been isolated from each other for at least 3×10^6 years, and possibly as long as 20×10^6 years (Adey 1976). Approximately 400 specimens, including both historical and recently collected material, form the basis for the present investigation.

MATERIALS AND METHODS

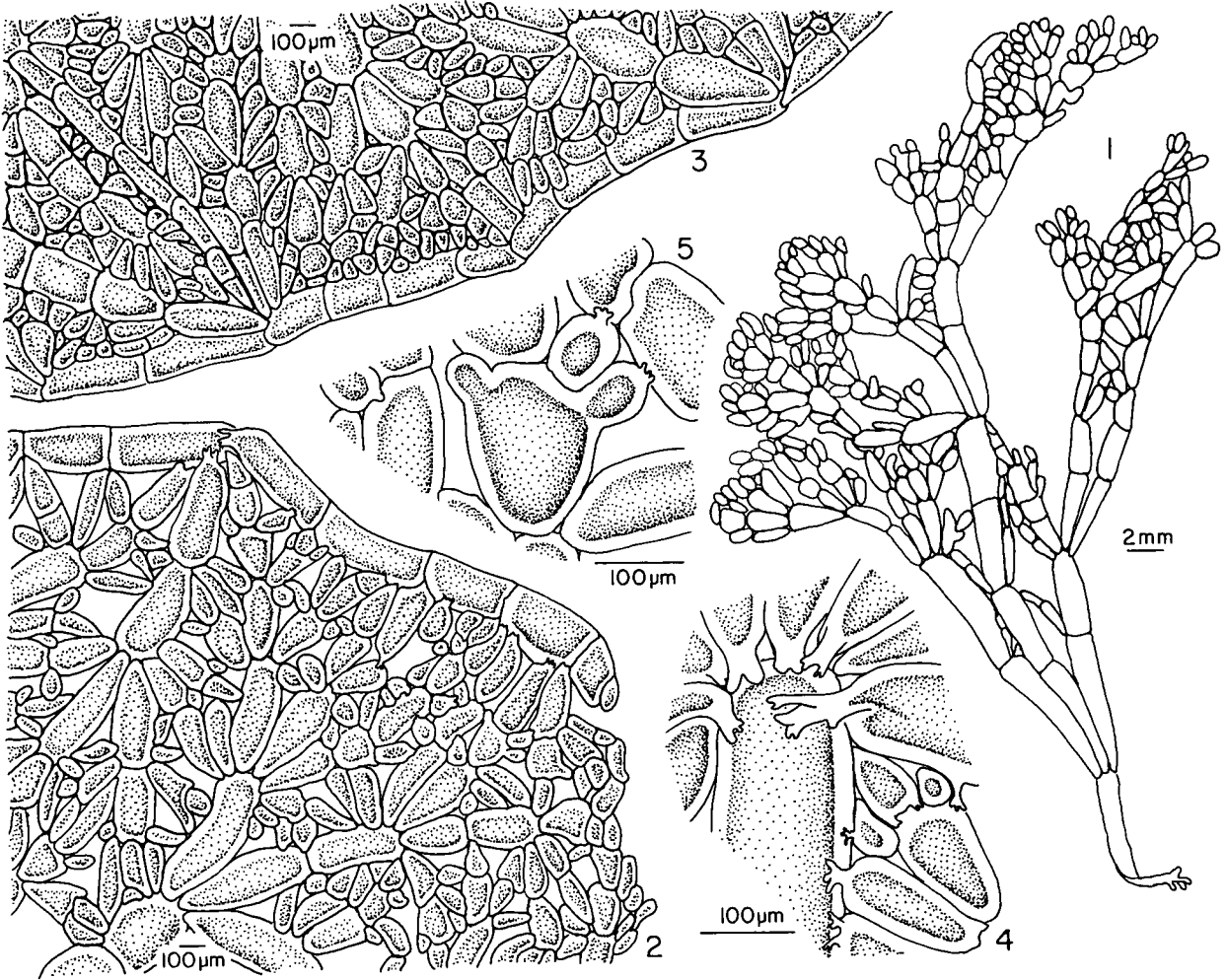
Dried herbarium specimens, wet preserved material, and, when available, living plants were examined macroscopically, and portions were prepared on microscope slides for anatomical study. Thallus segments were stained with 1% aniline blue and mounted using a 20% glucose syrup (Karo Syrup, Corn Products, Inc.) solution in distilled water containing a trace of phenol. In some cases, cell contents were cleared with a 5% solution of sodium hydroxide applied for 24 h. All anatomical drawings were made with a camera lucida on a Zeiss Universal Microscope to assure accuracy; internal measurements were made with a calibrated ocular micrometer.

The final data matrix, including eight species of *Anadyomene* and 17 characters, was analyzed phylogenetically using the PAUP 2.4 (Phylogenetic Analysis Using Parsimony; Swofford 1985) computer program. To avoid having to speculate on primitive versus derived states, we treated the characters independently and did not rank them within character groups. If a character state was missing or not applicable for a given species, a code of 9 was used. Wagner trees were produced using the options of global branch-swapping (GLOBAL), holding equally parsimonious trees in memory (MULPARS), and branch and bound (BANDB), which guarantees finding all minimum-length trees. A consistency index (CI), the range of a character state transition series divided by the number of times this character changes, was calculated for each character. A CI of 1.0 indicates perfect congruence, a CI of 0.33, that the character has changed from state 0 to state 1 (or vice versa) three times on the cladogram. Several other characters considered at various times in the analysis (e.g. vein width: length ratios, numbers of cells per vein) were ultimately rejected because they were too variable among the taxa to enhance the cladistic interpretation. Autapomorphic characters, unique to single species, were included even though they do not influence the topology.

In phylogenetic systematics, the outgroup method is one of the best techniques for increasing objectivity in cladistic analysis. This method assesses character polarity by comparing characters in one or more outgroups, with taxa postulated to be most closely related to the study group (Wiley 1981). We selected *Microdictyon boergesenii* Setchell (Cladophorales, Anadyomenaceae) as the outgroup because of its close morphological and reproductive similarity to *Anadyomene*. Abbreviations of herbaria are taken from Holmgren et al. (1981).

KEY TO THE TROPICAL WESTERN ATLANTIC SPECIES OF ANADYOMENE

- | | |
|---|--------------------|
| 1. Blade perforate | 2 |
| 1. Blade eperforate | 3 |
| 2. Polychotomous branching only, interstitial cells random and oval in section, with a distinct stipe | <i>A. linkiana</i> |



FIGS. 1-5. *Anadyomene howei* sp. nov. FIG. 1. Habit of immature thallus showing disjunct nature of loose filaments. FIG. 2. Younger blade margin depicting characteristic vacant interstitial spaces. FIG. 3. Mature blade margin consisting of elongate vein cells with all interstitial spaces filled. FIG. 4. Cell tentacular attachments. FIG. 5. Budding of lateral cells.

2. Polychotomous branching accompanied by pinnate lateral branching, interstitial cells generally parallel and H-shaped in section, without a distinct stipe ... *A. pavonina*
3. Veins composed of several parallel uniseriate chains of cells ... *A. menziesii*
3. Veins composed of single uniseriate chains of cells ... 4
4. Interstitial cells random and oval in section ... 5
4. Interstitial cells generally parallel and H-shaped in section ... 6
5. Interstitial cells 105-150 μ m long, outer margin formed by elongated vein cells ... *A. howei*
5. Interstitial cells 37-60 μ m long, outer margin formed by small ellipsoidal cells ... *A. saldanhae*
6. Rhizoids covering lower surfaces of mature blade, veins usually dichotomously divided ... *A. rhizoidifera*
6. Rhizoids mainly in the basal regions of

- blades, veins mostly polychotomously, occasionally dichotomously, divided 7
7. Growing edge smooth or lobed, composed of small rounded or oval cells *A. stellata*
7. Growing edge irregularly lacerate, composed of elongated vein cells *A. lacerata*

SPECIES TREATMENTS

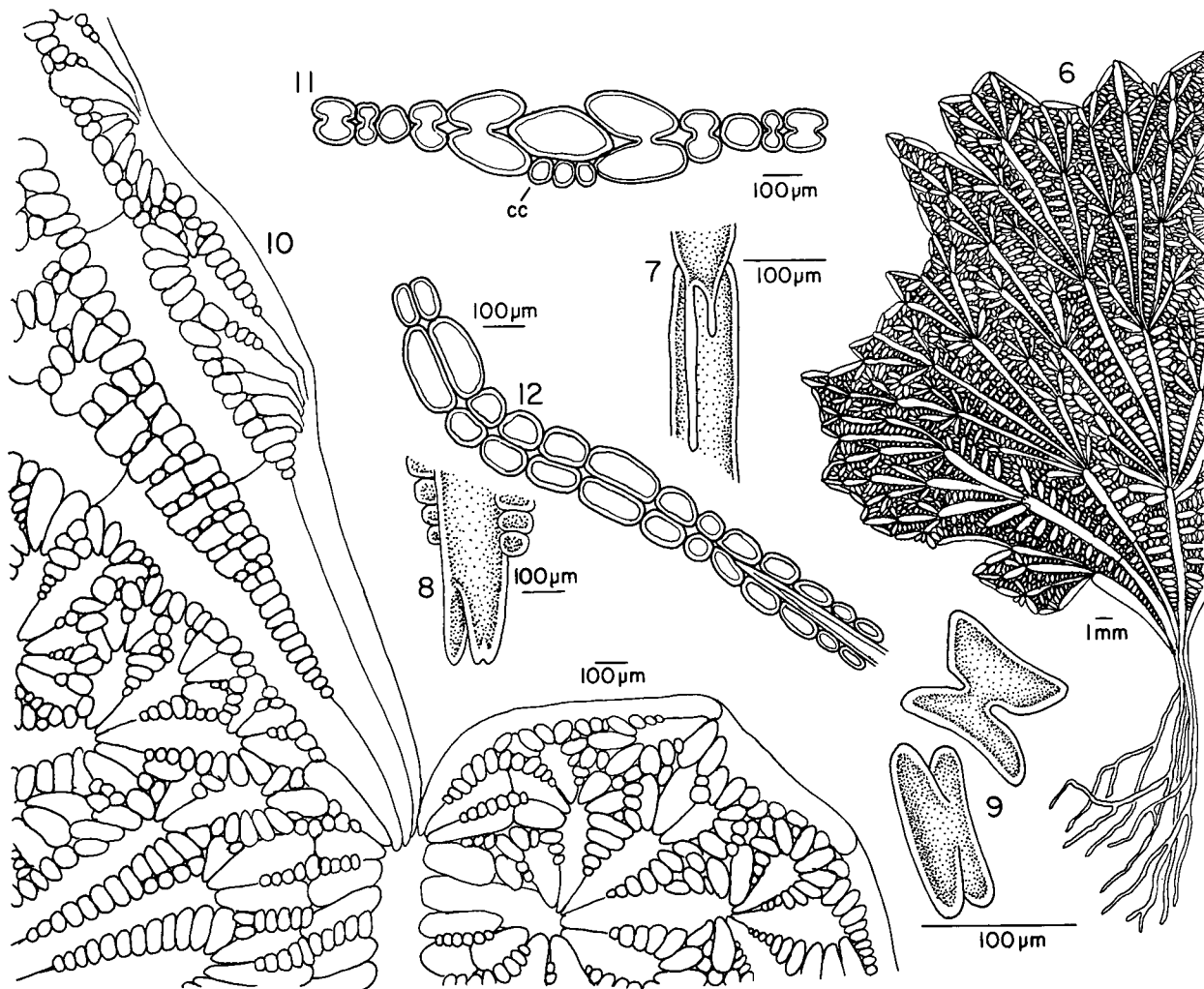
Anadyomene howei sp. nov.

(Figs. 1-5)

Thallus in diametro ad 5 cm prostratus pallide flavo-viridis veni filamenti elongati temeriter reticulati constatus; areae interstitialis cellulis oblongis impletis cellulis venatis basilaribus et cellulis interstitialibus a tentacula connexis; ramificationes omnino polychotomatae; margines distales a cellulis elongatis venatis constati.

Holotype: *Howe 5845* (NY), Bahamas, Great Ragged Island, in lagoon on sponge 0.3 m deep, 26 December 1907.

Etymology: Named in honor of Marshall Avery



FIGS. 6–12. *Anadyomene lacerata* sp. nov. FIG. 6. Habit of juvenile showing jagged margin. FIG. 7. Bifurcate vein attachment initiating corticating rhizoid. FIG. 8. Saddle-like connections to branching vein. FIG. 9. H-shaped interstitial cells. FIG. 10. Outer margin formed by vein cells. FIG. 11. Cross section of vein showing corticating rhizoids (cc). FIG. 12. Cross section along vein (off center) appearing as two thallus layers but actually bisecting the prongs of adjacent H-shaped cells.

Howe in recognition of his contributions to algal taxonomy.

Synonym: *Anadyomene stellata* f. *prototypa* Howe 1920:602 [type locality: Bahamas, Great Ragged Island].

Distribution: Bahamas.

Representative specimens examined: **BAHAMAS.** Great Ragged Island (Holotype): intertidal on *Rhizophora* roots in a turf of *Cladophoropsis membranacea*, 26 December 1907, *Howe 5842*; 5846 (NY). Caicos Islands: Malcolm Road, intertidal on shaded rock shelf, 19 December 1907, *Howe 5653* (NY).

Habit: Frond (stipe + blade) to 5 cm in diameter (plant width), prostrate, pale yellow-green. Blade thin, generally eperforate; immature blades (Figs. 1, 2) with small gaps where interstitial cells do not completely fill spaces between veins, mature blades (Fig. 3) with few gaps, margin smooth. Anchored by short rhizoids developing at base of veins when in contact with substratum.

Anatomy: Veins composed of a single uniseriate series of cells; cells elongated, length (0.38–0.70 mm) to width (0.22–0.30 mm) ratio approximately 2:1, 2–5 polychotomous branches at summit (locus) of each series. Veins radiating from distal end of parent vein to indeterminate distances throughout blade; centers of radiation not arranged in a particular pattern. Basal cells of veins attached by shallow, saddle-like bifurcations with tentacula at tips (Figs. 4, 5), other filament cells with blunt attachments. Interstitial spaces sparsely filled with relatively large (105–150 μm) ellipsoidal cells arranged in repeated polychotomous divisions, often with a scattering of open mesh areas; tentacula attaching interstitial cells to adjacent cells (Fig. 4). Margin smooth, composed of elongated vein cells (Figs. 2, 3), corticating rhizoids seldom present.

Remarks. This is the only eperforate Atlantic *Anadyomene* without a continuously expanding vein pattern spreading from the stipe (as the point source)

to the margins. The margin, composed of elongated vein cells, is unique for those species with solely polychotomous branching. The tentacula (to 40 μm long) that loosely hold the interstitial cells together are similar to those of *A. menziesii*; however, they are substantially longer (to 100 μm long) in the latter. The herbarium specimens examined indicate that the mature thallus is prostrate. The blade is fragile [Howe 5845 (NY)], often presenting a more open network than most species of *Anadyomene*. This species is similar to *Microdictyon boergesenii* [Howe 5653 (NY)] in that immature thalli often cluster to form a short loose turf [Howe 5842 (NY)]. *Anadyomene howei* shows not only apical growth but also the budding of lateral cells (Fig. 5), a feature not apparent in most other species of *Anadyomene*.

***Anadyomene lacerata* sp. nov.**

(Figs. 6–14)

Frondes foliosae ad 6 cm altae stipitatae pallide flavo-viridis base profunde cordatae veni filamenti elongati constatae ramificationibus polychotomatis; areae interstitialis ramis minoribus regulariter ordinatis impletas; venae basillares primariae in venis secundariis vel extensionibus ramorum deorsum 3–9 corticatae extensionibus deorsum rhizoideis formantibus; margines ut videtur laceratae cellulis elongatis venatis constatae.

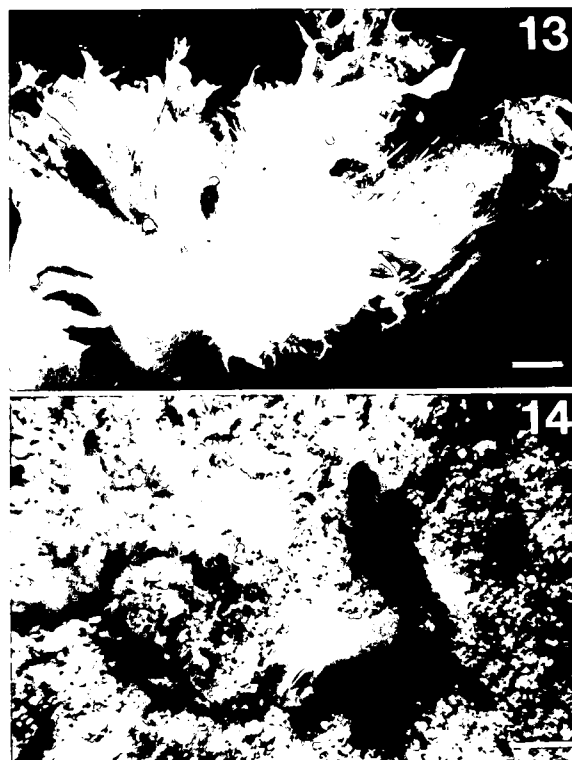
Holotype: D&M Littler 17020 (US 156540), Puer-to Rico, on the west side of Isla Monito, northwest of Isla de Mona (18°09.50' N, 67°59.96' W), growing 40 m deep, abundant and attached to pebbles on a large sand plain, 14 May 1989.

Etymology: This species is named from the unique, irregularly cleft, lacerate margin.

Distribution: Gulf of Mexico, Puerto Rico, U.S. Virgin Islands, Venezuela, Brazil.

Representative specimens examined: BRAZIL. Abrolhos: dredged, Hassler Expedition 1051 (MICH). Pernambuco: 20 m, U.S.F.C. Sta. Albatross, Sta. 2758, 16 December 1887, WRT 7317 (MICH). Pernambuco: 20 m, U.S.F.C. Sta. Albatross (27°54'32" N, 93°35'49" W), collected from the Johnson-Sea-Link submersible, 58 m, 2 October 1978, HBFH 5360; HBFH 5361. PUERTO RICO. Isla Monito: northwest of Isla de Mona (Holotype). Mayagüez: La Parguera off Media Luna Reef, dredged at 18.5 m on a sandy bottom, *Almodovar* 5641 (US). U.S. VIRGIN ISLANDS. St. Thomas: insular shelf south of Charlotte Amalie, dredged at 36 m, 11 August 1987, *Ballantine* 2973 (MICH). St. Jan [St. John]: 30 m, March 1906, *Borgesen* 1974 (NY). VENEZUELA: Archipelago de Los Hermanos: Isla Orchila, dredged at 30 m, 10 January 1966, *Díaz-Pisferrer* 21624 (NY).

Habit: Frond peltate to 6 cm above substratum (frond height) and 10 cm wide. Blade deeply cordate at base, pale yellow-green, foliose, eperforate (Fig. 6). Margin delicate, undulating and appearing lacerated (Fig. 13). Larger basal veins intermingling to form diminutive, but distinct, stipe. Anchored to pebbles or rubble by numerous thick-walled rhizoids that extend from stipe filaments.



FIGS. 13, 14. *Anadyomene lacerata*. FIG. 13. Underwater photograph showing lacerate outer margin. Scale bar = 1 cm. FIG. 14. Habit on a deep sand plain. Scale bar = 5 cm.

Anatomy: Veins composed of 1–3 elongate cells, mid-blade length (1.56–3.44 mm) to width (0.22–0.31 mm) ratio approximately 8:1; occasional exceptionally long veins composed of up to 7 shorter cells (perhaps representing marginal veins at an earlier stage of development), with 2–6 polychotomous branches at the summit of each set (locus). Veins originating at stipe, radiating peripherally, dividing and subdividing in a continuous series throughout blade, decreasing in size distally. Vein cells generally with blunt connections end-to-end, occasionally forked when initiating corticating rhizoids (Fig. 7). Base of veins forked and straddling apex of proximal cell (Fig. 8). Interstitial spaces filled with small cells perpendicular to main vein in a consistently parallel fashion, laterals that lack sufficient space to branch appearing as bars aligned in strictly parallel series; farther above, bars elongating and eventually branching polychotomously at loci. Interstitial cells generally dumbbell-shaped, or H-shaped in side view (Fig. 9), partially overlapping or straddling adjacent end cells. Elongated vein cells (Fig. 10) forming a lacerated margin (Fig. 13) with points or teeth of various sizes. From 3 to 9 corticating rhizoids (i.e. basal extensions of the polychotomous branches, Fig. 11) running adjacent and parallel to main veins proximally, descending to form the single stipe and developing the basal rhizoids.

Remarks. *Anadyomene lacerata* is generally restricted to a range of 15–60 m, where it occurs as scattered plants (one blade per holdfast) on sand plains

(Fig. 14). Plants appear peltate because of the single, short, perpendicular stalk and the horizontal position of the reniform blade above the substratum. The blade consists of only one layer; however, in cross section, the tips of the extremely H-shaped cells can be mistaken for separate layers (Figs. 11, 12). When the plants are dissected and cells are pulled apart, the single-layered structure is apparent.

The distinguishing characteristic of *Anadyomene lacerata* is the morphology of the outer margin. This is the only *Anadyomene* in the western tropical Atlantic with an eperforate blade that has pinnate lateral interstitial cells and a margin formed by a single row of elongated vein cells (Fig. 10). All other eperforate species with pinnate laterals, except *A. menziesii*, possess an outer margin formed by fairly small cells that are uniform in size and eventually develop into the standard structure of the blade. The relatively large *A. menziesii* often has a smooth, lobate outer margin of one to several parallel rows of vein cells. This type of margin occasionally is present in small thalli of *A. stellata* that occur in areas of high wave energy, presumably resulting in a stronger blade; however, such marginal veins are rare and only appear in small sections along the lobed edge. The lacerate margin is unique to *A. lacerata*, all other Atlantic species developing lobed, smooth, and/or ruffled margins.

***Anadyomene linkiana* sp. nov.**
(Figs. 15–21)

Membranae foliosae perforatae ad 3 cm altae stipitatae graminicolores veni filamenti elongati constatae, venis a stipitis et peripheraliter radiatis distaliter sensim minoribus, cellulis interstitialibus polychotomate ramosis minoribus ovalibus vel irregulariter formantibus temere dispositis, cellulis contiguus non superpositis; venae basales primariae in venis secundariis 3–6 ad filamentas inferiores parallelis contiguus corticatae, venis secundariis deorsum stipitem et rhizoideis formantibus.

Holotype: JSL 1484-16 (HBFH), Bahamas, San Salvador Island, Fernandez Bay (24°1.6' N, 74°32.5' W), collected from the Johnson-Sea-Link I submersible at 61 m deep, 13 October 1983.

Etymology: Named in honor of Edwin A. Link, the designer and builder of the Johnson-Sea-Link submersibles.

Distribution: Bahamas.

Representative specimens examined: BAHAMAS. San Salvador Island: Fernandez Bay [Holotype]; JSL 1484-16 (US 94850) [Isotype].

Habit: Plants foliose, 3 cm tall, 3 cm wide, grass-green. Blade highly perforate (Fig. 15) above a diminutive stipe, perforations delineated by vein cells to 3 mm in diameter, margin entire when mature. Anchored by extensions from stipe filaments that form numerous thick-walled rhizoids.

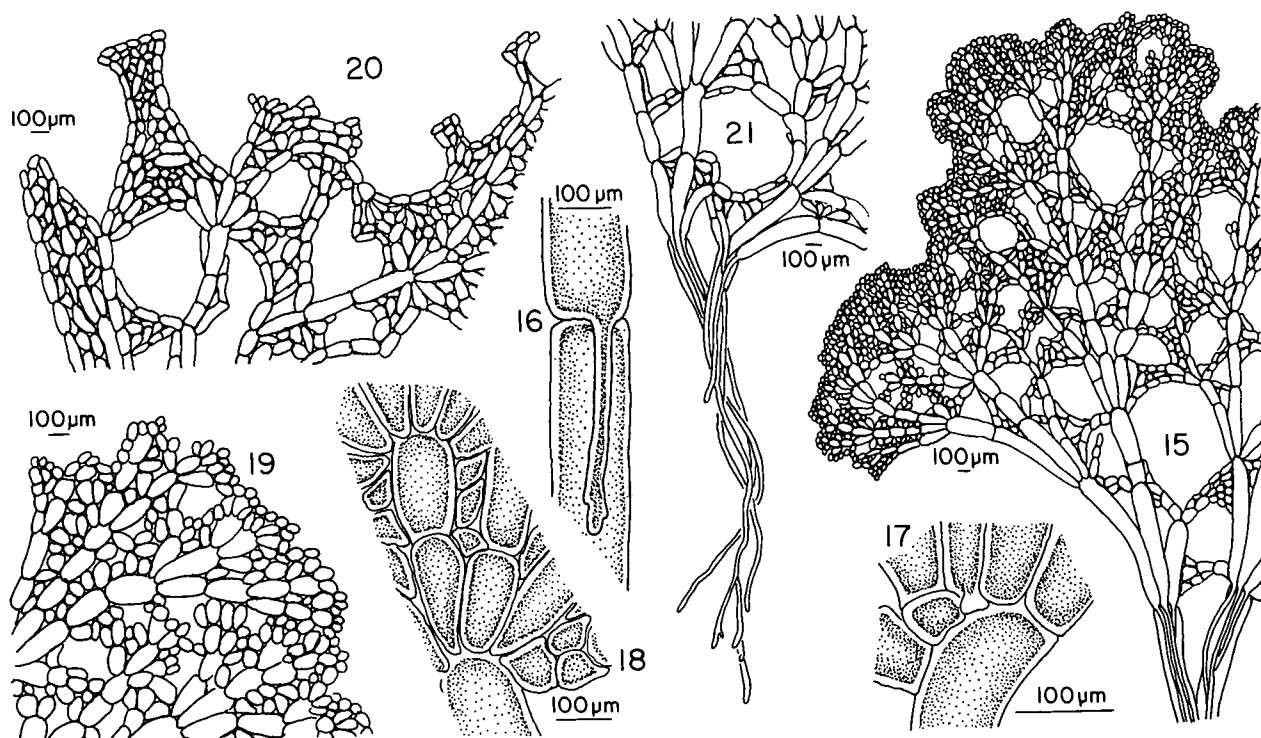
Anatomy: Veins uniseriate, cells cylindrical to ovate, decreasing in size distally (Fig. 15), mid-blade

cell length (0.45–0.60 mm) to width (0.15–0.22 mm) ratio 3:1 or less, basal cell of each vein largest (1.50–1.12 mm long, 0.25–0.34 mm wide) and contiguous with other basal cells, 3–6 polychotomous branches. Veins originating from stipe, radiating peripherally, dividing and subdividing in a continuous series throughout blade. Vein attachment blunt or with slight depression (saddle-like), corticating rhizoids forming proximally on one side of the blade (Fig. 16). Interstitial cells polychotomously branched, small, elliptical or irregularly shaped, arranged randomly; little or no overlap of adjacent cells throughout blade (Figs. 17, 18), interstitial cells attached by forked prongs wedged between adjacent cells. Immature outer margin (Fig. 19) composed of smaller oval cells, entire mature outer margin composed of vein cells (Fig. 20). From 3 to 9 corticating rhizoids proximal, running adjacent and parallel to veins, descending to form stipe (Fig. 20) and eventually thick-walled basal rhizoids.

Remarks. *Anadyomene linkiana* is similar to *Microdictyon calodictyon* (Montagne) Kützinger, which occurs in the Canary Islands, in its rhizoid, stipe, and vein structures; however, the interstitial cells of *M. calodictyon* do not cohere laterally, so that, compared with the distinct vein-encircled perforations of mature *A. linkiana*, many small spaces remain between the cells. Setchell (1929:518; Fig. 37) depicts a “denser” (i.e. with cells crowded tightly together) specimen of *M. calodictyon*, from material collected by Houagger in 1890, that appears almost identical to *A. linkiana*. Examination of the original material [Houagger 1890 (HF, UC)] reveals a distinct difference: The denser specimens of *M. calodictyon* have cells that are not connected laterally extending from the growing margins, whereas those at the margin of *A. linkiana* cohere laterally; in addition, mature *A. linkiana* is perforate with all openings bordered by veins. In apical growth these two species are again similar, as well as in budding off lateral cells from a parent cell, sensu Enomoto and Hirose (1970), a feature not easily observed in other species of *Anadyomene*.

The diminutive *Anadyomene linkiana* differs from *A. pavonina*, the only other perforate Atlantic species, in its smaller and more numerous openings among randomly arranged interstitial cells, stipitate thallus, and nonoverlapping interstitial cells. *Anadyomene linkiana* has repetitive polychotomous branching, whereas *A. pavonina* develops pinnate branching along the veins, a pattern lacking in the former species.

Anadyomene linkiana is similar in cell arrangement to *A. saldanhae*, which also shows the random array of nonoverlapping interstitial cells; however, *A. linkiana* is perforate and has a distinct stipe (Fig. 21) as opposed to the scattered rhizoids of *A. saldanhae* (Figs. 39, 41). Also, the vein cells and branches of *A. linkiana* are distinctly larger toward the base of



FIGS. 15–21. *Anadyomene linkiana* sp. nov. FIG. 15. Habit. FIG. 16. Blunt attachment of vein initiating corticating rhizoids. FIG. 17. Blunt attachments of branching vein. FIG. 18. Interstitial spaces filled with polychotomously branched, elliptical or irregularly shaped cells, arranged randomly. FIG. 19. Immature outer margin. FIG. 20. Mature outer margin composed of vein cells. FIG. 21. Lower corticating rhizoids forming the stipe and rhizoids.

the blade and decrease markedly in length and width peripherally, compared with the gradual and almost unnoticeable decrease distally in *A. saldanhae*.

Anadyomene menziesii (J. E. Gray)
J. Agardh 1887:128
(Figs. 22–28)

Basionym: [*Anadyomene menziesii* Harvey 1858:50, nom. prov.] *Grayemma menziesii* Gray 1866:49–51 [type locality: Gulf of Mexico].

Distribution: Florida, Mexico, Bahamas.

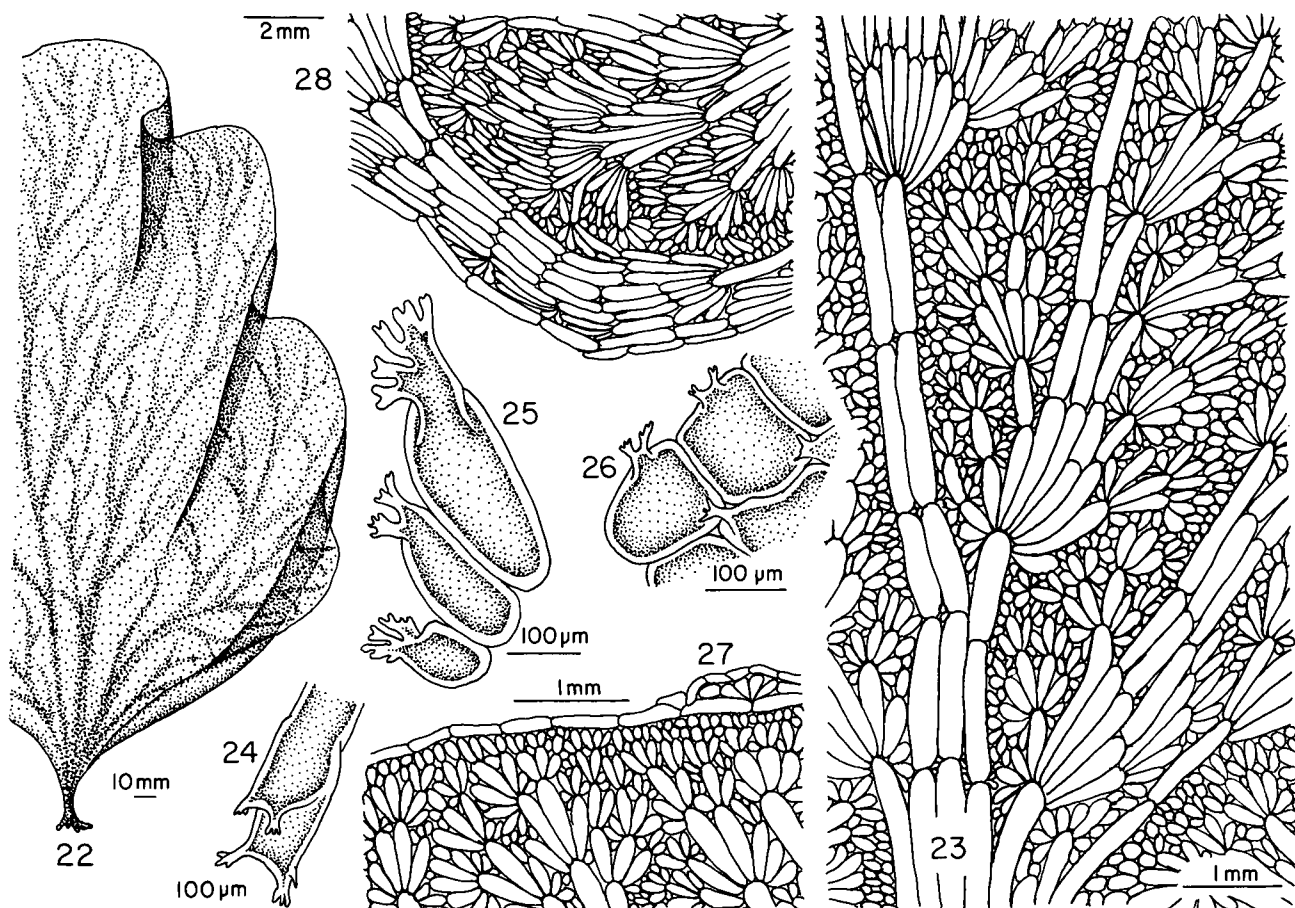
Representative specimens examined: FLORIDA. Southwest coast (25°27' N, 82°50' W), dredged, November 1980, HBFH 5780; HBFH 5789. MEXICO. Gulf of Mexico, 60 m, *Menzies 1802*, BM (Holotype). Quintana Roo: 15 km north of Puerto Morelos at Punta Nizuc, 81 m, entangled in fisherman's long lines, April 1983, *Ballantine 1266* (MICH). Campeche Bank: 80 m, 19 February 1960, *Rezak s.n.* (WRT 30317, MICH). BAHAMAS. 60 m, US 18418.

Habit: Plants large, to 45 cm tall, 26 cm wide, foliose, yellow-green. Blade eperforate, margin broadly lobed, base cuneate (Fig. 22). Larger basal corticating rhizoids intermingling to form short but distinct stipe. Anchored by extensions of stipe filaments that form numerous thick-walled rhizoids.

Anatomy: Unistratose blade developing from multiple uniseriate veins that are parallel and ad-

jacent to one another (Fig. 23), vein cell length (2.4–3.9 mm) to width (0.7–2.2 mm) ratio highly variable but approximately 1:7. Veins originating from stipe, radiating peripherally in a continuous series to blade margin, decreasing gradually in size distally. Immediately before branching, parallel veins splitting for a short distance, then each branching polychotomously (Fig. 23); veins developing parallel to one another to form the next section of veins, branches attaching to locus by saddle-shaped base, each side of the saddle having tentacula on forked or single tips (Fig. 24), other nonbasal vein cells developing blunt attachments. Interstitial areas filled by small, randomly arranged cells that divide polychotomously. Interstitial cells attached by tentacula (Figs. 25, 26), tentacula present on both surfaces. Smooth lobed margin consisting of 1–6 (up to 10) parallel rows of elongated vein cells (Figs. 27, 28).

Remarks. *Anadyomene menziesii* has been collected in great abundances only in the Gulf of Mexico, where it has been dredged at depths to 81 m. It can form large heads composed of multiple blades to 45 cm in diameter, possibly as large as 1 m (Humm 1956). The veins are formed from several chains of cells in parallel series (Fig. 23). In contrast, all other species of *Anadyomene* are much smaller than *A. menziesii* and have veins composed of single series of cells.



FIGS. 22–28. *Anadyomene menziesii* (J. E. Gray) J. Agardh. FIG. 22. Habit of young plant. FIG. 23. Veins growing parallel and adjacent to one another, random or polychotomous branching of interstitial cells. FIG. 24. Vein attachment with long tentacula. FIGS. 25, 26. Interstitial cell attachment with well-developed tentacula. FIGS. 27, 28. Outer margin formed by elongate vein cells.

The nomenclature of *Anadyomene menziesii* is confusing because Harvey (1858:50) initially states, "Should subsequent observations establish this plant as a species, it may be called *A. menziesii*." According to the International Code of Botanical Nomenclature (Article 34.1, Greuter et al. 1988), *A. menziesii* was a provisional name at that time and hence is invalid. The species was accepted by Gray (1866), who made it the type of a new genus, *Grayemma*. The first person to transfer *Grayemma menziesii* to *Anadyomene* was J. Agardh (1887).

Anadyomene pavonina (J. Agardh)
Wille 1910:114 ("*pavoniumum*")
(Figs. 29–34)

Basionym: *Cystodictyon pavoninum* J. Agardh 1894: 139 ("*pavoniumum*") [type locality: Florida]. The spelling "*pavoniumum*" is a misprint for "*pavoninum*," an adjective meaning peacock-eyed. The error was corrected in the index to the first fascicles of J. Agardh's *Analecta Algologica* (J. Agardh 1896).

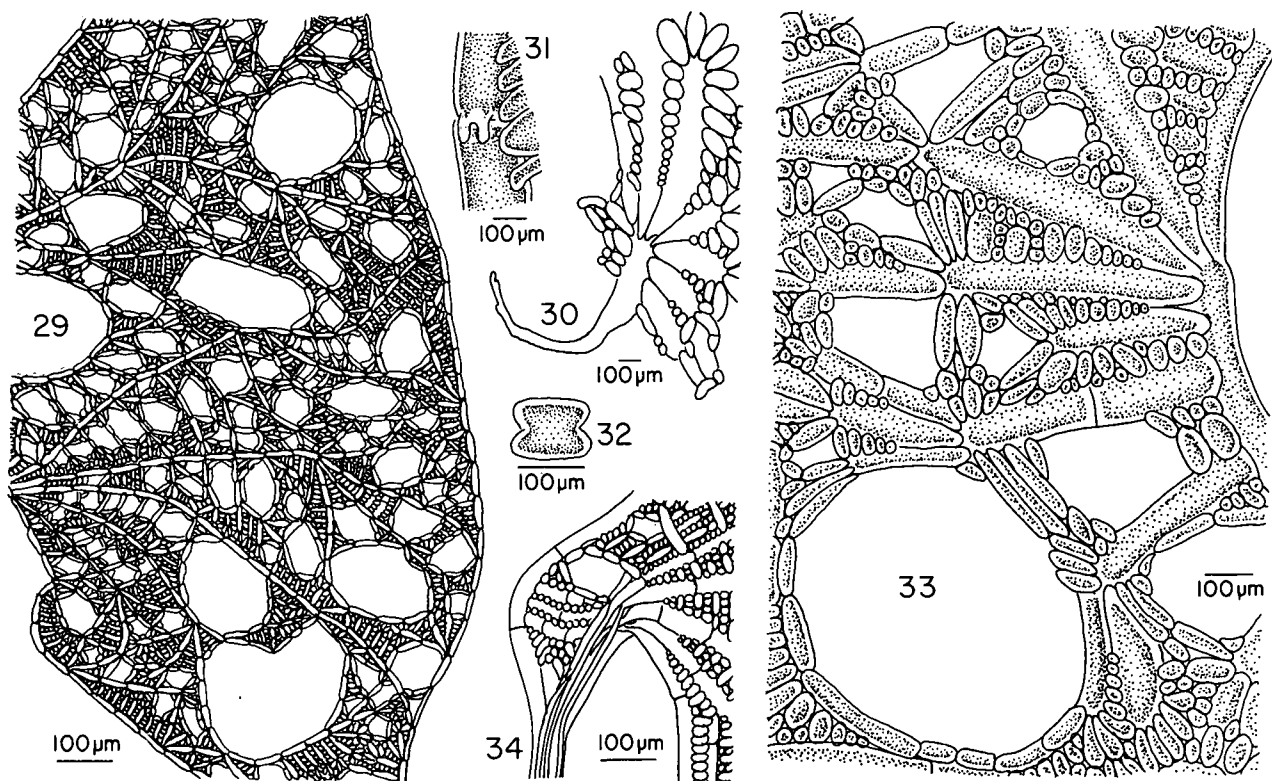
Distribution: Florida.

Representative specimens examined: FLORIDA. Dry Tortugas: Loggerhead Key, dredged 31 km off-

shore, 60 m deep, 18 October 1966, Earle 66282 (US). Jupiter Inlet: washed ashore, Phycoteca Boreali Americana 666 (US). Hourglass Cruise: Station C (27°37' N, 85°28' W), 6 November 1966, Dawes 4149 (US).

Habit: Prostrate blades perforate with well-delineated openings of various sizes (Fig. 29), margin entire, to 20 cm in diameter, dark grass-green. Attached by minute rhizoids at irregular points on margins (Fig. 30).

Anatomy: Veins composed of variable numbers of uniseriate cylindrical cells, mid-blade length (0.96–2.25 mm) to width (0.18–0.39 mm) ratio approximately 5:1, 4–5 polychotomous branches at locus. Veins radiating randomly from various loci within blade, creating no regular pattern (Fig. 29). Vein cells generally with blunt connections, bases of vein forked and straddling apices loci (Fig. 31). Interstitial spaces filled with small pinnately and pectinately arranged cells, dumbbell- or H-shaped (Fig. 32), partly overlapping or straddling adjacent end cells; occasionally linked by small tentacula, more often blunt. Not all interstitial spaces filled with cells; conspicuous perforations predominating. Outer mar-



FIGS. 29–34. *Anadyomene pavonina* (J. Agardh) Wille. FIG. 29. Habit of generally prostrate membrane. FIG. 30. Typical rhizoid extending from margin. FIG. 31. Forked attachment of vein. FIG. 32. Interstitial cell. FIG. 33. Membrane showing pinnate arrangement along internal veins as well as along veins that encircle perforations. FIG. 34. The only example of corticating rhizoids observed within this species.

gins and hole peripheries bordered by elongated vein cells (Fig. 33). Corticating typically absent with only one exception observed (Fig. 34).

Remarks. This is the only perforate Atlantic *Anadyomene* with a vein/interstitial cell pattern that does not expand continuously from stipe to margin. The margin of *A. pavonina* closely resembles that of *A. lacerata* in that elongated vein cells form the periphery in both. However, *A. pavonina* has a smooth margin and abundant perforations, compared with the lacerated margin and lack of perforations in *A. lacerata*. *Anadyomene pavonina* possesses a flat, sessile blade with numerous large perforations in contrast to the peltate, deeply cordate blade of *A. lacerata* or the stipitate, extremely perforate small blade of *A. linkiana*.

Anadyomene rhizoidifera Joly et Pereira 1973:70,
figs. 1–7 [type locality: Brazil]
(Figs. 35–38)

Distribution: Brazil.

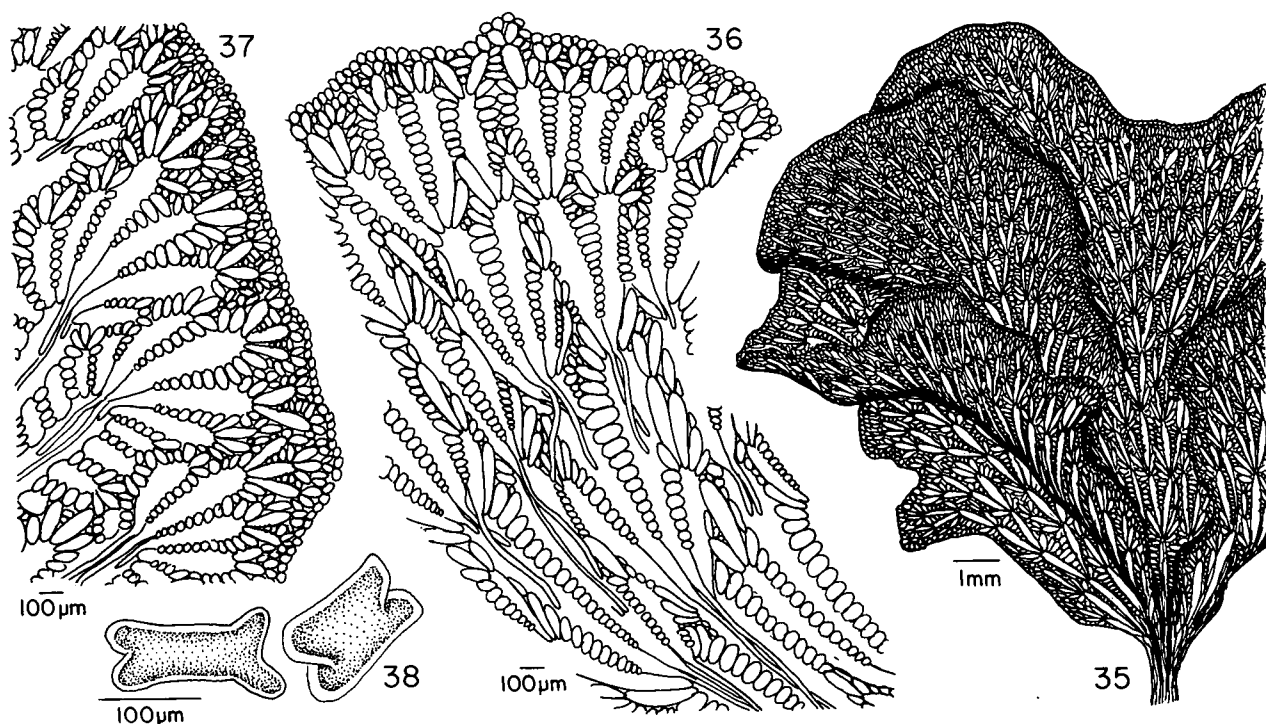
Representative specimens examined: BRAZIL. Pernambuco: Cabo, Praia do Gaibu, 25 July 1968, *Pereira* s.n. (SPF 2637) [Isotype]. Bahia: 25 May 1915, *Rose* 19609b (NY, US).

Habit: Plants erect, to 2.8 cm tall, 4 cm wide, dark green, forming small tufts (Fig. 35). Blades appearing torn or raggedly fan-shaped with no natural per-

forations, peripheral margins entire, lobed or undulate. Anchored by thick-walled rhizoids that entangle to form a short stipe.

Anatomy: Veins usually composed of 1 ovate cell (occasionally 2) with a mid-blade length (1.28–2.25 mm) to width (0.12–0.25 mm) ratio approximately 8:1 in mature blades (Fig. 36). Vein branching dichotomous (branches occasionally 1 or 3; Fig. 36); each branch giving rise to another series of 2, the process repeating. Base of each vein forked, with one side soon elongating to form corticating rhizoids (Fig. 36). Veins originating at stipe in immature thalli and along basal areas in older thalli, radiating peripherally, dividing and subdividing dichotomously in continual series throughout blade, decreasing in size distally. Interstitial spaces filled with smaller, pinnately arranged cells appearing as lateral or transverse bars tightly parallel to one another. Both ends of interstitial cells partly overlapping or straddling vein cells (Fig. 38). Margins consisting of small spherical cells (Figs. 36, 37). From 3 to 9 corticating rhizoids running adjacent and parallel to mature veins or hanging suspended (pendant). Rhizoids originating from proximal ends of vein branches at mature loci, covering entire lower surfaces (except youngest margins), giving rough texture to blades.

Remarks. The major character that distinguishes



FIGS. 35–38. *Anadyomene rhizoidifera* Joly et Pereira. FIG. 35. Habit. FIG. 36. Margin of small spherical or oval cells, and the forked veins with proximal development of rhizoids or corticating rhizoids and pinnate interstitial cells. FIG. 37. Veins can have as many as 3–4 branches, a variation hypothetically due to an increased rate of growth or favorable environmental conditions. FIG. 38. H-shaped interstitial cells.

Anadyomene rhizoidifera, the abundant rhizoids on the entire underside of the blade, may be questionable because *A. stellata* also tends toward this character, presumably under environmental control. It appears that in all Atlantic species of *Anadyomene*, the older basal portions of vein branches have the potential to elongate and subsequently form rhizoids. Usually, only the major veins at the base of *A. stellata* form such extensions, which then continue parallel and adhere to the next lower vein, giving rise to small, inconspicuous stipes in young plants or producing multiple points of attachment at the bases of older blades. However, these extensions can occur in any region of the thallus in *A. stellata* and are often pendant, as in *A. rhizoidifera* (Joly and Pereira 1973).

The reported character of single-celled veins in *Anadyomene rhizoidifera* is seen in the isotype (SPF 2637); however, other material examined from Brazil [Rose 19609b (NY, US)] shows that the veins can occasionally be composed of two cells. The highly variable *A. stellata* also can have veins formed from one, two, or many cells. Therefore, we conclude that the characters diagnostic of *A. rhizoidifera* have the potential to occur in *A. stellata*, but appear to be relatively consistent in *A. rhizoidifera* and sporadic in *A. stellata*. All specimens of *A. rhizoidifera* examined are considerably smaller than typical *A. stellata* and more turf-like. We lack sufficient data to do

other than treat the two species as separate, but further study could prove that they are variations of the same entity.

Joly and Pereira (1973) report that *Anadyomene rhizoidifera* can be 5–7 cell layers thick. From the few specimens available, we observe only a single layer (excluding rhizoids). Theoretically, if a section were cut along veins, where several of the deeply incised H-shaped cells abut and overlap the bifurcations of the lateral filaments (i.e. in the zone where most of the tips overlap), then the appearance of up to 5 cell layers could result [Figs. 11, 12; see also Børgesen (1925:26)]. Joly and Pereira (1973) additionally comment on the presence of internal rhizoids within veins, but we have not been able to verify this character in the limited material available.

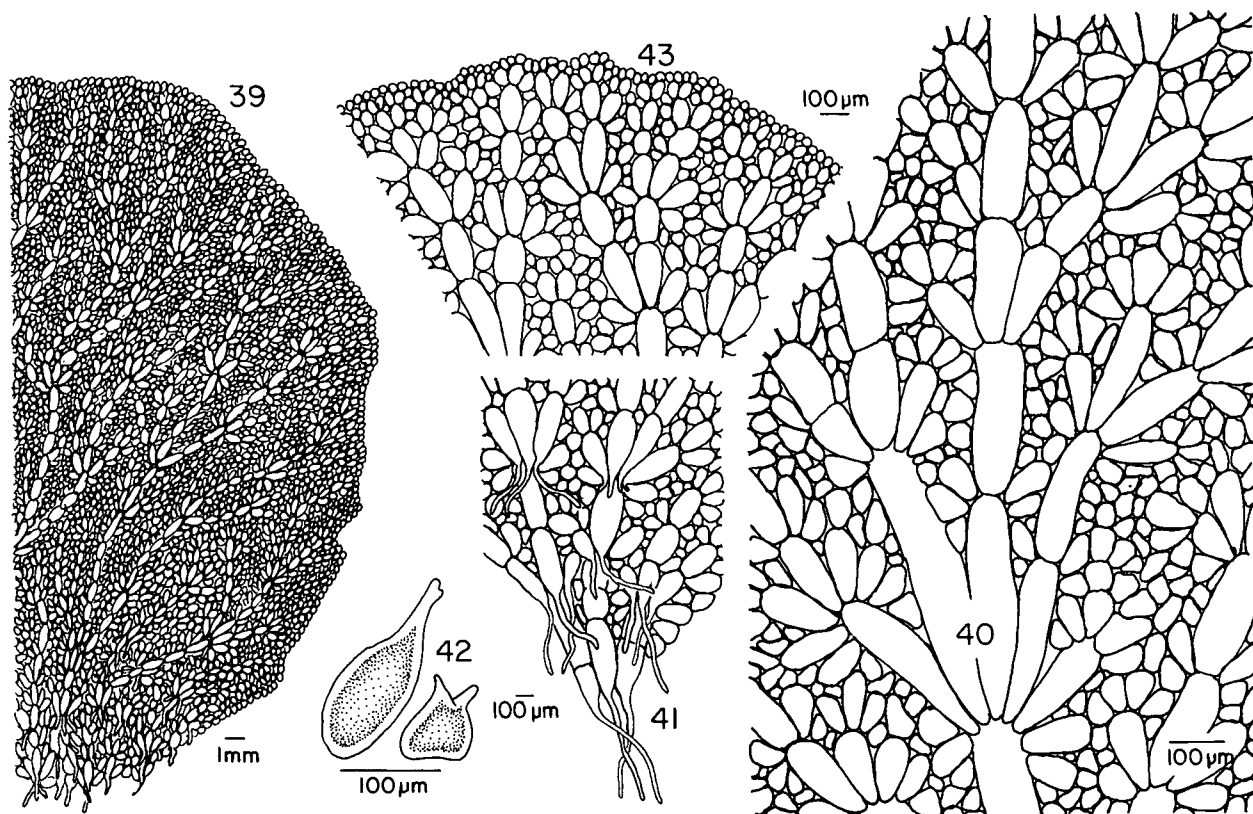
Anadyomene saldanhae

Joly et Oliveira Filho 1969:30

[type locality: Banco Dogareza, off the coast of Victoria, Espírito Santo State, Brazil] (Figs. 39–43)

Distribution: Bermuda, Bahamas, Florida, Cuba, Dominican Republic, Puerto Rico, Belize, Brazil.

Representative specimens examined: BERMUDA. Wallace Bay: southeast end of Hamilton Island, abundant in shallow water, 28 April 1953, Bernatowicz 53-277 (US). CUBA. Pinar del Rio Province:



FIGS. 39–43. *Anadyomene saldanhae* Joly et Oliveira. FIG. 39. Habit. FIG. 40. Polychotomous branching pattern with little or no overlap among cells, interstitial cell arrangement polychotomous or random. FIG. 41. Base of blade with noncortivating rhizoids. FIG. 42. Interstitial cells showing foot-like tentacula typically wedged between adjacent cells. FIG. 43. Margin composed of small spherical or oval cells.

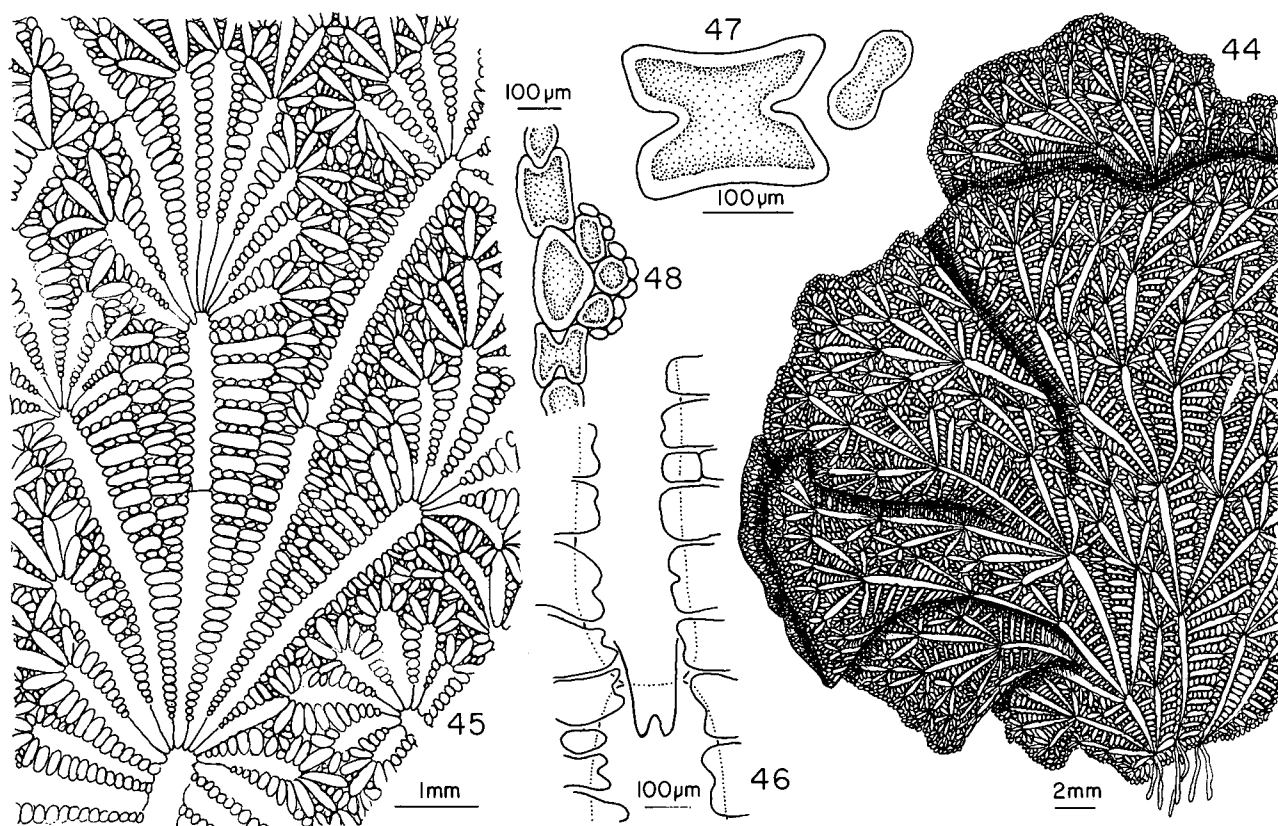
Ensenada del Cajon off Cabo de San Antonio, attached to other algae, 22 May 1914, Tomas Barrera Expedition 275k (US). FLORIDA. Looe Key: off Big Pine Key, Monroe County, 1–5 m deep, 19 June 1984, *D&M Littler 15412* (US). PUERTO RICO. Mayagüez: PRINUL Mission 2 site for “La Chalupa” undersea laboratory, 10 km west of Punta Ostiones, 30 m deep with sponges, 26 December 1972, *Dahl 1242* (US 50211). BELIZE. Tobacco Range: intertidal on mangrove roots, 9 June 1989, *D&M Littler 19227* (US).

Habit: Plants erect to 9 cm tall or prostrate in low light habitats, foliose, grass green. Blades rigid, eperforate, fan-shaped or irregularly fan-shaped, margin entire (Fig. 39). Attached by rhizoids growing from portions of vein cells at base of blade, generally no well-defined stipe.

Anatomy: Veins uniseriate, cylindrical to swollen, composed of an indefinite number (3 to >12) of elongate cells. Mid-blade length (0.65–0.88 mm) to width (0.25–0.35 mm) ratio 4:1 or less, largest cell of each vein segment located proximally (1.00–1.38 mm long, 0.25–0.35 mm wide) and contiguous with other basal cells (Fig. 40); 4–6 polychotomous branches at apex of segment. Veins originating from basal areas, radiating peripherally, dividing and subdividing in a continuous series throughout blade,

decreasing in size distally. Vein attachment always blunt, formation of rhizoids only on one side of vein loci (Fig. 41), each set either dorsal or ventral, not mixed. Interstitial spaces filled with polychotomously branched, small (37–60 µm diameter), elliptical or irregularly shaped cells, randomly arranged. Little or no overlap of adjacent cells; interstitial attachment throughout blade by pointed, mitten-shaped or forked prongs (Fig. 42), usually wedged between adjacent cells. Outer margin of small spherical cells (Fig. 43). Cortivating rhizoids absent, rhizoids extending from basal portions of lower veins, commonly suspended free or adhering to substratum.

Remarks. The most distinctive characters of *Anadyomene saldanhae* are the absence of overlapping cells within the eperforate blade, the random arrangement of interstitial cells following repeated polychotomous divisions, and the outer margin composed of small spherical cells. The polychotomous branching is sometimes obscured in older blades. *Anadyomene saldanhae* occurs from the intertidal, where it is frequently found with *A. stellata* on mangrove roots, to 79 m deep [JSL 1482-37 (US)], growing decumbent on stones and pebbles. Plants are generally darker green and less undulating or frilly than *A. stellata* and have a more leathery texture.



FIGS. 44–48. *Anadyomene stellata* (Wulfen in Jacquin) C. Agardh. FIG. 44. Habit. FIG. 45. Cell arrangement showing pinnate and pectinate (comb-like) branching patterns of interstitial cells. FIG. 46. Occasional forked connection of vein cell. FIG. 47. H-shaped interstitial cells. FIG. 48. Cross section showing 1:3:9 configuration of corticating rhizoids adjacent and parallel to the rib.

The cell arrangement and structure of *Anadyomene saldanhae* most resembles that of *A. howei*. Both species show only polychotomous branching of both veins and interstitial cells. *Anadyomene saldanhae* has small (37–60 µm diameter), irregularly shaped interstitial cells with wedge-shaped connections or poorly developed tentacula, whereas *A. howei* has considerably larger (105–150 µm diameter) and more ellipsoid interstitial cells, producing small but well-developed adventitious tentacula that provide a firm attachment to adjacent cells. The nature of the outer margin is the most useful character in distinguishing the two species. *Anadyomene saldanhae* has small, spherical marginal cells (Fig. 43); *A. howei* has large, linear vein cells delineating its outer margins (Figs. 2, 3).

Anadyomene ("Anadyomena") *stellata* (Wulfen)
C. Agardh 1822:400
(Figs. 44–56)

Basionym: *Ulva stellata* Wulfen in Jacquin 1786: 351 [type locality: Adriatic (BM)].

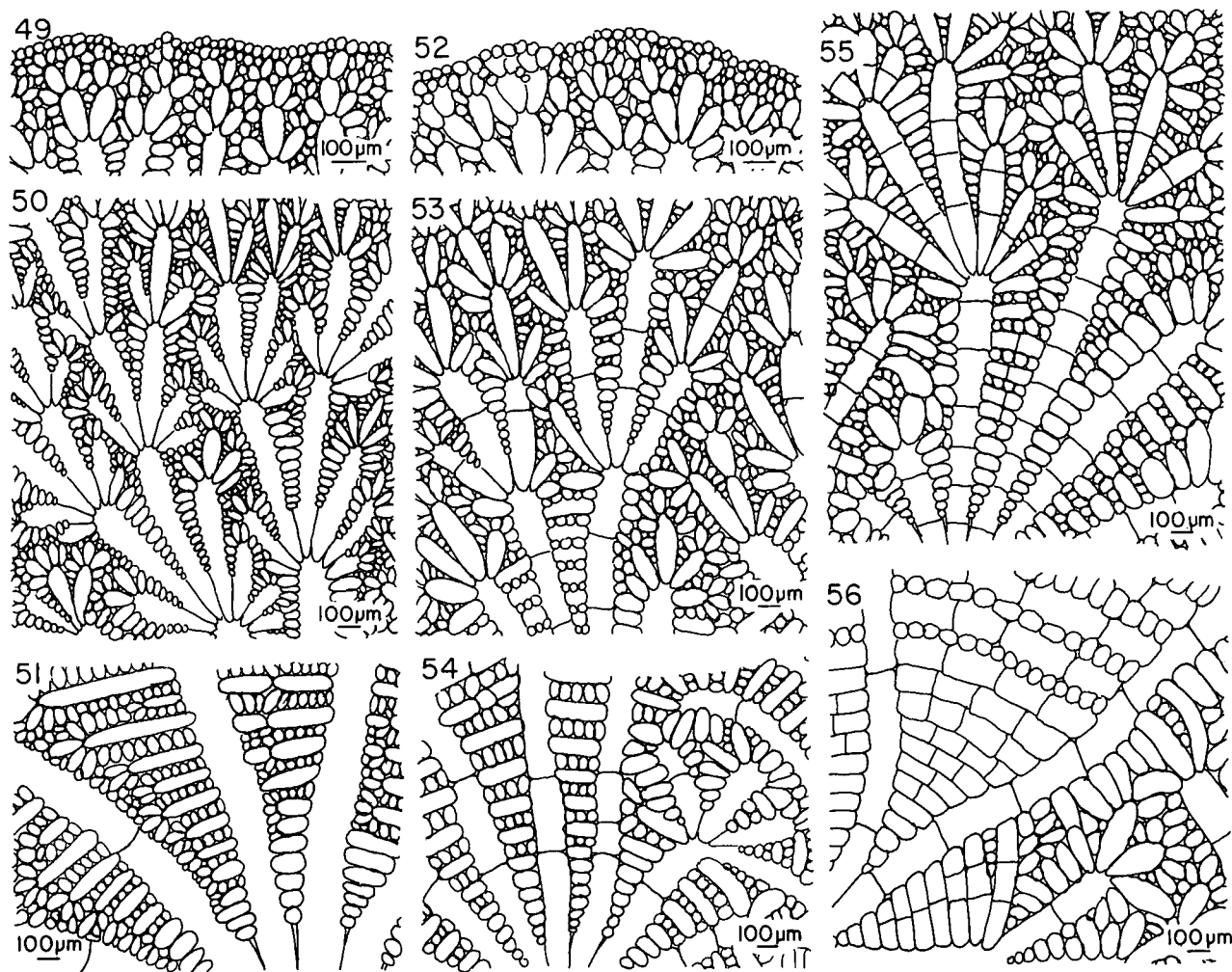
Synonyms: *Anadyomene* ("Anadyomena") *flabellata* Lamouroux 1812:187 [type locality: "in Corsicae mare"], first figured in Lamouroux 1816:366, pl. XIV, fig. 3 [type locality changed to "Dans la Mousse de Corse des pharmaciens"]. *Anadyomene cutleriae*

Gray 1866:48, pl. 44 [type locality: Bermuda]. *Anadyomene stellata* var. *floridana* Gray 1866 [type locality: Key West, Florida]. *Anadyomene stellata* var. *luxurians* De Toni 1889:369 [type locality not specified].

Distribution: Bermuda, Bahamas, Florida, Mexico, Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Guadeloupe, Dominica, Martinique, Barbuda, Barbados, Belize, Panama, Mediterranean.

Representative specimens examined: **BAHAMAS**. Bimini: north channel of Bailey Town Lagoon, on shell of *Atrina*, 25 July 1958, Moul 10400 (US 5242). **BARBADOS**. Bath: October 1906, Henderson 1906 (NY). **DOMINICA**. St. Andrew's Parish: Calibishie, drift, 25 February 1967, Taylor & Rhyne 67-580 (US 47582). **HAITI**. Sud: Jeremie, La Pointe, 6 May 1941, Bartlett 17875 (US). **JAMAICA**. Port Antonio: tufts along shore of east harbor, 17 February 1893, Phycotheca Boreali Americana 169 (US). **MARTINIQUE**. St. Anne: Pointe Dunkerque, growing on calcium carbonate substrate, 7 m deep, 18 July 1986, D&M Littler 11676 (US).

Habit: Plants erect, to 8 cm tall, often forming densely packed, ruffled clumps and turfs in intertidal habitats or single upright sheets in protected subtidal areas; light yellow-green. Blade rigid, eperforate, young thalli fan-shaped with entire margins, mature thalli margins lobed or undulate (Fig. 44).



FIGS. 49–56. *Anadyomene stellata* (Wulfen in Jacquin) C. Agardh. FIGS. 49–51. “*Stellata*” configuration, generally an 8:1 vein cell length to width ratio. FIG. 49. Margin. FIG. 50. Mid-blade. FIG. 51. Base of blade. FIGS. 52–54. “*Floridana*” arrangement, 4:1 ratio. FIG. 52. Margin. FIG. 53. Mid-blade. FIG. 54. Base of blade. FIGS. 55, 56. “*Luxurians*” morph, 2:1 ratio. FIG. 55. Mid-blade. FIG. 56. Base of blade.

Anchored by rhizoids loosely entangling to form short stipes in immature individuals, attaching over a broad area in mature thalli.

Anatomy: Veins uniseriate, cells cylindrical to clavate; vein of young blades composed of 1–3 cells (Figs. 45, 49–51), mid-blade vein cell length (1.88–3.00 mm) to width (0.25–0.38 mm) ratio approximately 8:1; veins of older, more ruffled blades composed of 3–7 cells (Figs. 52–54), mid-blade length (0.66–1.75 mm) to width (0.28–0.38 mm) ratio approximately 4:1 or less; very old thalli often containing more than 7 cells per vein, with a 2:1 length to width ratio (Figs. 55, 56). Veins branching polychotomously (2–6 branches) at segment apices, with lateral interstitial cells pinnate and pectinate. Veins radiating peripherally from origin at stipe, dividing and subdividing in continuous series throughout blade while decreasing in size distally. Vein cells generally with blunt end connections, occasionally forked when initiating corticating rhizoids (Fig. 46).

Bases of vein segments bifurcate and straddling apices of proximal segment. Interstitial spaces filled with small, pinnate cells that appear as lateral or transverse bars tightly parallel to one another at bases of veins. Interstitial cells H-shaped (Fig. 47) with each end having blunt forks straddling adjacent rhizoids (rarely with tentacula), outer margins consisting of small spherical cells (Figs. 49, 52). From 3 to 9 corticating rhizoids (Fig. 48) adjacent and parallel to veins proximally.

Remarks. *Anadyomene stellata* is generally a shallow-water plant, frequently found growing in dense clusters reminiscent of loose heads of lettuce, or forming a foliose, ruffled turf just below mean lower low water. Smaller thalli or clumps of thalli have been found to a depth of 91.5 m [JSL 1486-19 (US)]. Vein branches are highly variable in *A. stellata*. Those composed of 1–3 successive cells, with a length to width ratio of approximately 8:1 (Figs. 49–51), have been ascribed to the “*stellata*” morph; those com-

prising 3–7 cells (Figs. 52–54), to var. *floridana* (Gray 1866); and those commonly composed of 12 short cells, with a length to width ratio of about 2:1, to var. *luxurians* (De Toni 1889; Figs. 55, 56). From close examination of both living and herbarium material, we speculate that this variation reflects either the age of the thallus or, to a lesser extent, environmental conditions. From 1 to 3 cells per vein section (i.e. between loci) typify young, fast-growing blades; 3–7 cells indicate an intermediate stage; and more than 7 cells tend to occur in old blades, with the apical portions often torn and in poor condition. Occasional specimens [e.g. *Killip 41105* (US 68494)] possess all three patterns on the same thallus, showing that formal taxonomic recognition of these morphs is not warranted. Mediterranean material appears identical to western Atlantic specimens. Therefore, *A. stellata* stands as a single, but highly variable, species.

The cell arrangement and structure of *Anadyomene stellata* most resembles that of *A. lacerata*. Both species have large, elongated veins that branch polychotomously at the apices, with the interstitial cells developing in parallel rows between the veins. Another similarity is that both possess corticating rhizoids that generally (but not always) adhere to the major veins in the lower portions of the blades. However, markedly different marginal morphologies distinguish the two species, the former having small oval cells and the latter having long vein cells bordering the margin. We conclude that this major structural difference is not related to depth, in view of the fact that numerous specimens of *A. stellata* from collections deeper than 40 m (the maximum recorded depth of *A. lacerata*) retain their characteristic morphology.

DISCUSSION

Indo-Pacific comparisons. *Anadyomene lacerata* is unique in comparison with all known Indo-Pacific eperforate species because of the same distinctive character that differentiates it from other Atlantic species, i.e. elongated vein cells forming a lacerate margin. The regularly parallel arrangement of interstitial cells common to many Atlantic species (*A. stellata*, *A. rhizoidifera*, *A. lacerata*, *A. pavonina*) appears to be absent in Pacific species. Additionally, the blades of several Indo-Pacific species [*A. plicata* C. Agardh, *A. brownii* (Gray) J. Agardh, *A. eseptata* Gilbert, and *A. wrightii* Harvey ex Gray] are corticated by overlapping interstitial cells. Such cortication, produced by overgrowth of independent interstitial cells, results in a multistratose blade, a feature absent in all known Atlantic species. *Anadyomene linkiana* differs from *A. leclancheri* Decaisne and *A. clathratum* (Martens) Heydrich, the perforate Indo-Pacific species, in its small size, distinct stipe, and lack of overlapping cells and the absence of well-developed tentacula. *Anadyomene howei* is distinct from all Indo-Pacific species because of the nonover-

lap of cells in the totally polychotomous branching pattern, the reduced tentacular structure, and the random pattern of veins.

Ecological adaptations. Species of *Anadyomene* possess a thin, sheet-like form and, according to the functional/form model (Littler and Littler 1980), might be expected to maximize photosynthetic tissue at the expense of structural mechanisms to deter predation by herbivores. However, the differentiated sheet-like thallus is not simple, and it is our belief that the so-called veins are not specialized for translocation, as the term implies, but function as strengthening ribs (termed costae by Joly and Pereira 1973). In the dozens of torn thalli that we observed microscopically, it was clear that the veins decreased the proliferation of damage, much in the manner of rip-stop fabrics used in camping textiles.

In examining over 400 herbarium specimens, and many in the field, we observed few if any signs of herbivory (e.g. bite marks). One strategy for avoiding predation is to grow in habitats where herbivores are scarce (i.e. refugia escapes sensu Littler and Littler 1988). *Anadyomene lacerata*, *A. menziesii*, and *A. pavonina* all grow on deep sand plains, where there are few herbivorous fishes and sea urchins because of lack of protective shelter from carnivorous predators. Algae characteristic of sand plains often show a pronounced lack of resistance to herbivory (Hay 1981). The vertical-wall habitat of San Salvador Island, Bahamas, where *Anadyomene linkiana* was collected in 1983, has high populations of carnivorous fishes (Sphyraenidae, Carangidae, Scombridae) with little or no spatial heterogeneity and, as a result, supports few herbivores. Although we have examined relatively few specimens of *A. rhizoidifera*, we believe that this species may avoid predation by growing as small tufts in the shallow intertidal zone, where fish have difficulty gaining access.

Anadyomene stellata is exceptional in that it is frequently found in many habitats exposed to high herbivory. Targett (1979) developed a chemosensory behavioral assay (i.e. gastropod tentacle withdrawal) and several other bioassays (fish mortality, fish erythrocyte hemolysis, inhibition of bacterial growth, and tissue culture) to determine the presence of biologically active substances that could potentially discourage predators. Of the 19 species of subtropical and tropical marine macroalgae tested by Targett and Mitsui (1979), only *Anadyomene stellata* responded positively in all five tests, and it consistently ranked as the most toxic alga. These authors hypothesized that the biologically active substance may be of proteinaceous origin. The presence of this toxin may deter herbivory and enable *A. stellata* to colonize a broader spectrum of habitats than other species of *Anadyomene*.

We noted that *Anadyomene saldanhiae* was most often found growing close to, and was often attached to, the basal areas of *A. stellata*. It is logical to postulate that this pairing could represent a plant–plant

defense association (sensu Hay 1986, Littler et al. 1986), with the larger, chemically defended *A. stellata* serving as a refuge for the presumably more palatable *A. saldanhae*. Such an interaction would be counter to the process of competitive exclusion in that the predominant species hypothetically would have a net positive, rather than negative, effect on the abundance of a secondary species utilizing the same general resources (e.g. light, space, and nutrients).

This interpretation is strengthened by the findings of Lewis (1987), who quantified the crustacean epifauna associated with a seagrass and five macroalgae in the northeastern Gulf of Mexico. He found that *A. stellata* harbored far more individual crustaceans than any of the five other predominant species examined. It is our belief that such crustaceans use external food sources (i.e. sources other than the "host" macroalga) but utilize *A. stellata* as a haven because of its micro-scale 3-dimensionality and its chemical toxicity to predators. This is an anti-theft analog to the animal-plant defense associations reported by Littler et al. (1987), in which areas near the bases of the purple sea fan, *Gorgonia ventalina* Linnaeus, and the fire coral, *Millepora al-cicornis* Lamarck, act as refuges from fish herbivory for many palatable species of macroalgae. Hypothetically, *A. stellata* facilitates a similar defense association, but with the plant-animal roles reversed.

Reproduction. The life history of *Anadyomene* is basically identical to that shown by Cladophoraceae and Ulvaceae, namely, an alternation of diploid sporophytes with morphologically similar, dioecious, haploid gametophytes, entailing quadriflagellate zoospores and biflagellate gametes (Iyengar and Ramanathan 1940, Enomoto and Hirose 1970, Mayhoub 1975). Our observations of swarmer formation in *A. saldanhae* and *A. stellata* are the first reported for western Atlantic species. Swarmers form either in veins or in interstitial cells in localized areas of any region of the thallus except the base and are released from each cell through a single conical opening identical to that illustrated for *Microdictyon* (Børgesen 1925:36, fig. 8, Iyengar and Ramanathan 1941:158, figs. 1, 2). Approximately 10% of the thallus is involved in swarmer formation. Enomoto and Hirose (1970:273, fig. 1) depict ellipsoid mother cells for *Anadyomene wrightii*; however, we noted no changes in shape from the normal vegetative cells of the thallus during swarmer formation and release.

Cell division and ordinal status. The ordinal status of *Anadyomene* is controversial. Many authors include it in the Siphonocladales (e.g. Bold and Wynne 1978). Some place it in the Cladophorales (e.g. van den Hoek 1984, Wynne 1986), and still others merge both orders (see O'Kelly and Floyd 1984). The debate centers on the method of septum formation and branching, which had not been well documented for *Anadyomene*. Segregative cell division, attributed to the Siphonocladales, is defined as the cleav-

TABLE 1. List of characters used in cladistic analysis matrix (Table 2). CI = consistency index.

1. Interstitial cells absent (0); interstitial cells present (1) [Autapomorphy].
2. Blade eperforate (0); blade perforate (1) [CI = 0.5].
3. Interstitial cells not attached by poorly developed tentacula prongs wedged between cells (0); interstitial cells attached by poorly developed tentacula wedged between cells (1) [CI = 1.0].
4. Interstitial cells attached by other than H-shaped cells (0); interstitial cells generally attached by H-shaped cells (1) [CI = 1.0].
5. Interstitial cells not attached by well-developed tentacula (0); attachment by well-developed tentacula (1) [CI = 1.0].
6. Corticating rhizoids absent in lower portion of blade (0); corticating rhizoids consistently present in lower portion of blade (1) [CI = 0.33].
7. In mature plants, rhizoids arising randomly where veins make contact with substratum (0); rhizoids grouped together to form a small but distinct stipe (1) [CI = 0.33].
8. Veins composed of single chains of cells (0); veins composed of several chains of cells in parallel series (1) [Autapomorphy].
9. Margin formed solely by elongated vein cells (0); margin formed by small spherical cells (1) [CI = 0.5].
10. Margin smooth, lobed, and/or ruffled (0); margin toothed and ragged (1) [Autapomorphy].
11. Vein pattern random (0); vein forming at base of blade and radiating in a repetitive pattern (1) [CI = 0.33].
12. Interstitial cells developing only polychotomously from the vein (0); interstitial cells arranged pinnately from the sides of the veins (1) [CI = 1.0].
13. Rhizoids restricted to basal portions of the thallus or areas in contact with substratum (0); rhizoids always covering all the dorsal surfaces of the mature blades (1) [Autapomorphy].
14. Base of vein a blunt or shallow depression (saddle) with tentacula seldom present (0); other than blunt (1) [CI = 1.0].
15. Base of vein filament other than a blunt, forked saddle (0); base a blunt, extremely deep, forked saddle (1) [CI = 1.0].
16. Base of vein filament without tentacula (0); base with tentacula at the tips of the forked saddle (1) [CI = 1.0].
17. Veins branching polychotomously with generally 4-6 divisions (0); veins branching dichotomously with occasionally 1-3 divisions (1) [Autapomorphy].

age of the protoplast within the parent cell into two or more bodies that then develop walls and expand, eventually disrupting the parent cell. Centripetal septum formation, as found in the Cladophorales, originates during branch formation as a budding from the parent cell. A side branch is initiated by a papilliform protuberance, which includes protoplasm and chloroplasts that accumulate in it as it enlarges and gradually expands into a normal-sized cell, with the new cell wall forming at the base. In this budding process, as well as in the commonly found intercalary divisions of filaments, septum formation appears to occur from the outside wall inward [illustrated by Enomoto and Hirose (1970:276, fig. 4, 1971:91, fig. 2) for *A. wrightii* and *Microdictyon okamurai* Setchell, respectively]. All species of *Anadyomene* that we examined possess centripetal septum formation (e.g. Fig. 5), which clearly relates them to the Cladophorales.

TABLE 2. Matrix of characters from which the cladogram (Fig. 57) was derived (missing = 9). BOE, *Microdictyon boergesenii* (outgroup); HOW, *Anadyomene howei*; LAC, *A. lacerata*; LIN, *A. linkiana*; MEN, *A. menziesii*; PAV, *Anadyomene pavonina*; RHI, *A. rhizoidifera*; SAL, *A. saldanhae*; STE, *A. stellata*. Character numbers as in Table 1. * = autapomorphic character.

Taxa	Characters																
	1*	2	3	4	5	6	7	8*	9	10*	11	12	13*	14	15	16	17*
BOE	0	9	9	9	9	0	0	0	0	0	0	9	0	0	0	0	0
HOW	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
LAC	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	0	0
LIN	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0
MEN	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	0
PAV	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0
RHI	1	0	0	1	0	1	0	0	1	0	1	1	1	1	1	0	1
SAL	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0
STE	1	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0	0

Another feature linking *Anadyomene* to the Cladophorales is the corticating rhizoids. Five of the eight species of Caribbean *Anadyomene* commonly have corticating rhizoids on the proximal veins. A similar feature is present in two species of Cladophoraceae, *Cladophora prolifera* (Roth) Kützinger and *C. conferta* Crouan and Crouan (van den Hoek 1982), in which rhizoids arise from the bases of the older laterals and lower ends of older cells. The rhizoids of *Anadyomene* and these two *Cladophora* spp. do not become separated from the protoplast of the parent cell by a wall as in *Apjohnia laetevirens* Harvey or *Struvea ramosa* Dickie (Papenfuss and Chihara 1975).

Using cytoplasmic rRNA sequence analysis, Zechman et al. (1989) have begun to examine the phylogenetic relationships of the controversial multinucleate orders of Chlorophyta. Their preliminary results cladistically depict *Anadyomene*, *Cladophora*, *Chaetomorpha*, and *Cladophoropsis* as forming a single, closely knit group, thus supporting the interpretation that the Siphonocladales and Cladophorales are closely related; however, they offer no judgment as to whether the relationship is sufficiently close to combine the two orders.

Phylogenetic analysis. As pointed out earlier, the genus *Anadyomene* has been divided into segregate genera and subgenera (Gray 1866, Wille 1910, and others); however, our phylogenetic analysis of the tropical western Atlantic species suggests that this is not justified. The PAUP program (Swofford 1985), utilizing the 17 characters given in Table 1 and the matrix in Table 2, generated five equally parsimonious trees, all similar with only inconsequential variations in order of placement. Each consists of a definite gradation showing mostly uniform branching from a single main axis, with no particular group dominating (represented by the first tree, Fig. 57). *Anadyomene saldanhae* and *A. linkiana* appear at the bases of all trees either as sister taxa (depicted in Fig. 57) or independently, both species having cells joined by poorly developed tentacula wedged between cells (character #3). The next group appearing in all five trees combines *A. menziesii* and *A. howei*, with their well-developed tentacula both on inter-

stitial cells (character #5) and on veins (character #16). These first four species (Menziesii group) are separated from the other four relatively derived species (Stellata group) by three characters. The most important of these is the pinnately arranged cells along the lateral edges of the veins (character #12). The two other characters that separate *A. pavonina*, *A. stellata*, *A. rhizoidifera*, and *A. lacerata* are the deeply H-shaped interstitial cells (character #4) and the closely allied, deeply forked connections of the basal cells on each vein branch (character #15).

Anadyomene pavonina is distinguished from other members of the Stellata group by the infrequent appearance, or absence, of corticating rhizoids (character #6), which are prevalent in *A. stellata*, *A. rhizoidifera*, and *A. lacerata*. *Anadyomene pavonina* is also distinguished from these three derived species by its perforate blade (character #2) and its random arrangement of veins (character #11). *Anadyomene stellata* and *A. rhizoidifera* group closely in all five trees and are separated from the main branch by the presence of outer margins formed by small oval cells (character #9). The consistent formation of rhizoids covering all dorsal surfaces of the mature blade (character #13) and the normally dichotomous branching of the veins (character #17) in *Anadyomene rhizoidifera* dissociate it from *A. stellata*. The uppermost species, *A. lacerata*, possesses a distinct stipe on the peltate mature thallus (character #7) and also is unique in having a lacerate outer margin (character #10).

In view of the phylogenetic analysis, the division of *Anadyomene* into four distinct genera (sensu Gray 1866) is untenable. Gray's *Calomena*, characterized as having dichotomously branched veins throughout the frond, would only apply in the tropical western Atlantic to *A. rhizoidifera*, a species close to *A. stellata*. *Grayemma*, a genus based on the presence of several parallel series of cells (character #8) forming the veins, would not only be closely related cladistically to *A. howei* but also tightly aligned with *A. saldanhae*, which appears on a separate branch of the cladogram (Fig. 57). Certain specimens of *A. saldanhae*, especially from Harrington Sound, Bermuda [*Ber-*

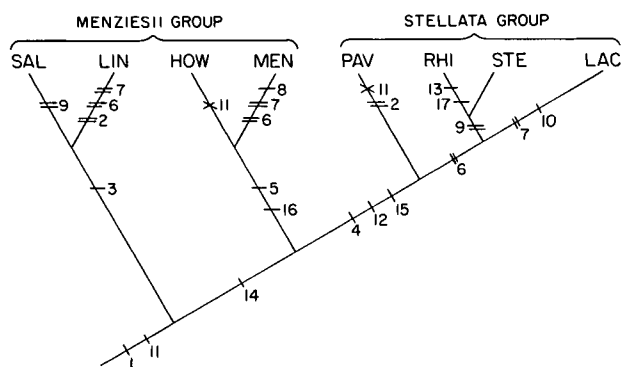


FIG. 57. Representative cladogram depicting phylogenetic relationships among Caribbean species of *Anadyomene*. Four other nearly identical trees were produced, differing only in the independent or grouped placement of *A. saldanhae* and *A. linkiana* proximally, and the placement of *A. pavonina* and *A. lacerata* distally as separate branches. *Microdictyon boergesenii* is the designated outgroup. Numbers on the cladogram correspond to characters in Table 1; taxa abbreviations are in Table 2 matrix. Slashes represent character advances, crosses indicate character reversals or losses, and double lines depict areas of parallel or convergent evolution.

natowicz 49-1545 (MICH)], have elongate vein cells that remain parallel and cohere for up to three cell lengths, and are thus remarkably similar to *A. menziesii*.

Gray's (1866) genus *Cystodictyon* has been used for many years by workers in the Caribbean (e.g. Taylor 1960, Wynne 1986); however, its principal distinguishing character, a perforate blade, is not sufficient to justify generic separation. The chlorophyte genus *Ulva* and the rhodophyte genus *Kallymenia* contain species that are either perforate or eperforate, with an otherwise similar anatomical structure. The internal anatomy of *Cystodictyon* is identical to *Anadyomene* (Heydrich 1894, Wille 1910) and therefore should be included in that genus. The cladistic analysis supports this interpretation, because *A. howei* also has a perforate blade but is evolutionarily closer to *A. menziesii* than to *A. pavonina* (the other perforate species). The combination of the two perforate forms would create a polyphyletic genus and a phylogenetic incongruity.

The representative cladogram (Fig. 57) indicates a grade consisting of two subgroups. The Menziesii group contains the four species that show only polychotomous branching and interstitial cells with tentacula. The Stellata group includes the four species having both pinnate and polychotomous branching and possessing bilobed vein connections. However, we see no utility in emphasizing this division, particularly since the Menziesii group is paraphyletic and could itself be divided into two groups (this would represent a very weak division based on only one character, #14). We therefore support Heydrich (1894) and Wille (1910) in including as members of the monophyletic genus *Anadyomene* all species in the Anadyomeneaceae with blades formed

by the polychotomous branching of vein cells, and intercalary spaces filled (at least in part) by small, polychotomously or pinnately branched cells.

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