Phycologia (1992) Volume 31 (5), 375–418

Systematics of *Avrainvillea* (Bryopsidales, Chlorophyta) in the tropical western Atlantic

D.S. Littler and M.M. Littler

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

D.S. Littler and M.M. Littler. 1992. Systematics of *Avrainvillea* (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia* **31:** 375–418.

Twenty-one specific and infraspecific taxa of the genus *Avrainvillea* from the tropical western Atlantic are treated. Six new species (*Avrainvillea digitata, A. fenicalii, A. fulva, A. hayi, A. silvana, A. sylvearleae*) and seven new intraspecific taxa (*A. asarifolia* var. *olivacea, A. fenicalii* f. *flabellifolia, A. levis* f. *translucens, A. longicaulis* f. *laxa, A. nigricans* f. *floridana, A. nigricans* f. *parva, A. nigricans* f. *spongiosa*) are described. Distinguishing features of the eight pre-existing taxa are clarified, and all 21 taxa are illustrated. Observations of numerous field populations and more than 1500 herbarium specimens form the basis for a discussion of ecological adaptations, reproduction and phylogenetic relationships. A cladistic analysis, based on 24 characters, produced three virtually identical cladograms showing several loosely defined groups. Species with cylindrical blade siphons or expanded siphon apices (*A. mazei, A. hayi, A. sylvearleae, A. geppii*) consistently occurred near the base of the cladogram. The five species with moniliform blade siphons appeared next: *A. nigricans* followed closely by *A. rawsonii* and *A. digitata,* then *A. fulva,* and, lastly, *A. silvana.* Those species with a variety of blade siphon shapes (moniliform, tortuous, and/or cylindrical) formed the final group: *A. longicaulis* followed by *A. asarifolia,* with a tight terminal clade consisting of *A. elliottii, A. fenicalii,* and *A. levis.*

INTRODUCTION

Avrainvillea Decaisne 1842 [Udoteaceae, Bryopsidales (see Silva 1982)] is characterized by uncalcified erect thalli usually composed of three parts: (1) a basal rhizoidal mass (= holdfast) anchored to rock or, more often, immersed in soft substrata such as sand, mud, or peat; (2) an upright corticated stalk (= stipe); and (3) a fan-shaped terminal blade (= flabellum). The blades and stipes are composed of dichotomously branched siphons (= filaments) which, in some cases, taper abruptly near the surface in a pattern of repeated and close-set branching, forming a loosely to tightly woven cortex. Blade siphons are constricted immediately above all major dichotomies. The stipes consist of a medulla of longitudinal siphons surrounded by a cortex of tapered highly branched siphons.

Avrainvillea is distinguished from *Rhipilia* by a lack of short lateral branchlets, each branchlet terminating in a tentaculum or crown (2–6 prongs) that attaches to adjacent siphons. *Avrainvillea* is also similar to *Flabellia,* a genus known only from the Mediterranean, Canary Islands, and Cape Verde Islands; *Flabellia,* however, is generally unistratose with the siphons giving rise to lateral branchlets that terminate in broad interlocking lobes to form a tight cortex. The Caribbean genus *Cladocephalus* is also similar but the lateral branches terminate in highly reduced hyaline apices that interweave to form an extremely tight cortex. The ubiquitous presence of moniliform siphons and the lack of distinct lateral branches are the key characters distinguishing *Avrainvillea* from *Rhipilia, Flabellia,* and *Cladocephalus.* Although siphon arrangement in *Udotea* is somewhat similar to that in *Avrainvillea,* the two genera are not closely related since *Udotea* is calcified, lacks moniliform siphons, has rhizoids that are hyaline and undifferentiated, and has a more differentiated stipe cortex.

The genus *Avrainvillea* was conceived almost simultaneously by two French workers, *Avrainvillea nigricans* Decaisne (1842) having priority by only a few months over *Fradelia fuliginosa* Chauvin (1842). The generic concept of *Avrainvillea* has remained reasonably stable over the years, although early workers occasionally confused it with *Rhipilia, Udotea, Chlorodesmis,* and

other similar genera. Murray & Boodle (1889) were the first to attempt to revise the genus, but with little success because of interpretive errors. Subsequently, the studies of Howe (1905, 1907), Børgesen (1909), Gepp & Gepp (1911), and Olsen-Stojkovich (1985) vastly improved our knowledge of this difficult genus.

As in the case of *Udotea* (Littler & Littler 1990) and *Anadyomene* (Littler & Littler 1991), the need for a monographic treatment of tropical western Atlantic *Avrainvillea* became apparent to us while attempting to use existing works to identify our extensive collections. During a decade of field work, we had accumulated so many unidentifiable entities, particularly from SCUBA depths, that it became obvious that the genus had been inadequately collected and described, particularly in the Caribbean. We therefore made an effort to examine all available western Atlantic material (approximately 1500 specimens) as well as many Indo-Pacific type specimens. The results of this study are presented here.

We deal taxonomically and phylogenetically with only the western Atlantic species of *Avrainvillea*. Treatment of this biogeographic assemblage separate from that of the Indo-Pacific is appropriate, since 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).

MATERIALS AND METHODS

Dried herbarium specimens, liquid-preserved material, and, when available, living plants were examined microscopically after portions were prepared on glass microscope slides for anatomical study. Segments were consistently taken from the mid-holdfast, mid-stipe, mid-blade, and growing margin of each thallus, stained with 1% aniline blue, and mounted using a 20% corn syrup (Karo® Syrup, Corn Products, Inc.) solution in distilled water containing a trace of phenol. When necessary, small pieces of dried plants were soaked in either Aerosol OT Solution (American Cyanamid Co.) or a 20% solution of glycerin for 24 h before microscopic examination. All anatomical drawings were made with a camera lucida on a Zeiss Universal Microscope to ensure accuracy; internal measurements were made with a calibrated ocular micrometer. It was not practical to make all drawings at the same magnification; however, an attempt was made to maintain a constant siphon magnification for groups of similar species to facilitate comparison among them.

The final data matrix, including 14 species of *Avrainvillea* and 24 characters, was analysed phylogenetically using the PAUP 3.0 computer program (Phylogenetic Analysis Using Parsimony; Swofford 1989). The characters were treated independently and not ranked within character groups to avoid having to speculate on primitive versus derived states. If a given character state was not applicable or missing for a 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 the branch and bound (BANDB) algorithm, which guarantees finding all minimum length trees. A consistency index (CI) was calculated for each character, i.e. the range of a character state transition series divided by the number of times that character changes. A CI of 1.0 implies perfect congruence, a CI of 0.33 indicates that the character has changed from state 0 to state 1 (or the reverse) three times on the cladogram. Several other morphological characters were considered at various times in the program (e.g. number of stipes per holdfast, blade thickness, texture, stipe length, holdfast characteristics, blade shape); however, these were ultimately rejected because they were too variable within and among the taxa to be useful for phylogenetic analysis. Autapomorphic characters (i.e. characters unique to a single species) are included even though they do not influence the topology.

In phylogenetic studies, one of the most widely accepted mechanisms to introduce objectivity is use of the outgroup method to assess character polarity. This technique utilizes outgroup comparisons (Wiley 1981), where one or more sister taxa are posited to be most closely related and are chosen to serve as outgroups. We explored the possibility of using several Caribbean species of Bryopsidales [e.g. *Boodleopsis pusilla* (F.S. Collins) W.R. Taylor, Joly et Bernatowicz and *Cladophora prolifera* (Roth) Kützing] as sister taxa. These species were deemed inappropriate because their characteristics were not closely aligned with *Avrainvillea*. For example, the multinucleate *Cladophora* is not coenocytic or moniliform, and *Boodleopsis* lacks moniliform siphons; both of these characters are fundamental to the genus *Avrainvillea*. Thus, a common coenocytic Indo-Pacific species, *Chlorodesmis co-*

mosa Bailey et Harvey, was ultimately chosen as the most appropriate sister taxon because of its close anatomical similarity to *Avrainvillea,* having both moniliform and cylindrical siphons within the thallus.

TERMINOLOGY

The term *filament* is normally defined as a chain of cells attached end to end and is, strictly speaking, incorrectly applied to completely siphonous algae such as *Avrainvillea. Torulose* is a confusing term used by previous workers to describe siphon shape and appears to have had several definitions: (1) twisted or knobby (close in meaning and confusingly similar in pronunciation and spelling to tortuous = twisted or bent; Fig. 1B, E); (2) irregularly swollen at close intervals, a definition which comes extremely close to moniliform (= regularly swollen at close intervals); and (3) with regularly elongate swellings at close intervals (differing from moniliform only in the shape of the swellings, oval versus elongate). Instead of using torulose, we prefer the simpler terms '*slightly moniliform*' (< 20% constriction, see Fig. 3B, E), '*moniliform*' (20–40%, Fig. 7C, D), and '*deeply moniliform*' (> 40%, Fig. 17C, B), since the degree of constriction determines the shape of the bulge.

Siphon apices may be *rounded* (Fig. 3D), *hooked* (Fig. 5F), *clavate* (Fig. 8C, E), or *bulbous* (= capitate; Figs 3C, 5E). The term *clavate* applies to club-shaped apices that expand gradually over a relatively long distance (Fig. 8C, E). *Bulbous* is used for an abrupt expansion at the extreme apex of the siphon (Figs 3C, 5E). Unusually long tapered, pointed apices as described by Børgesen (1909, p. 92, fig. 75f, see also Olsen-Stojkovich 1985, p. 34, fig. 17) appear to be artifacts of preparation. In several weak-walled species (e.g. *Avrainvillea asarifolia, A. elliottii, A. fenicalii*), siphons often stretch and break on dissection. Such drawn-out siphons have the appearance of long tapered apices, but the pointed terminal break may be clearly seen under high magnification. The *medulla* comprises the inner region of the plant, i.e. the internal portion of the blade or the central core of the stipe.

We define *forma* (f.) as a minor deviation from the norm, usually distinguished by a single consistent character, presumably controlled by environmental factors such as irradiance levels or water motion. Because all species of *Avrainvillea* grow erect, overall length measurements (sometimes given as height or tallness) refer to the vertical distance from the substratum to the tip of the thallus (i.e. stipe + blade = frond); the holdfast is not included. Thickness measurements were made consistently at the central regions of blades, stipes, or rhizoidal masses. Abbreviations of herbaria throughout the species treatments are those given in Holmgren *et al.* (1990). The private herbarium of Sylvia A. Earle is abbreviated SEH. An exclamation point (!) is used to designate material we have examined.

OBSERVATIONS

A key to the *Avrainvillea* taxa of the tropical western Atlantic is presented in Appendix I (p. 417).

Avrainvillea asarifolia Børgesen 1909: 34, fig. 4, pl. III

f. *asarifolia*

Fig. 1

LECTOTYPE (designated herein): *Børgesen 1171* (*pro parte*; see also *Avrainvillea nigricans*) (C!), Water Island, St Thomas, US Virgin Islands, 2.i.1906, (marked 'type' not in Børgesen's script). Other syntypes considered were: *Børgesen 1117* (*pro parte*; see also *A. nigricans*) (C!, NY!), Water Island, St Thomas, 23.xii.1905 [two specimens in C, one also marked type (not in Børgesen's script), the other stamped 'original specimen'] and *Børgesen 2081* (C!), Christiansfort, St Jan, 23.iii.1906, also stamped 'original specimen'. The designated lectotype best represents both the external and internal features of the species.

DISTRIBUTION: Florida, Bahamas, Puerto Rico, US Virgin Islands, Martinique, Belize, Atlantic Panama.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Staniard Cay, Andros Island, 5 m deep on sand (*D&M Littler 11169* 16.viii.1986, US). Belize: Southwater Cay, outer ridge above dropoff of the barrier reef, 18–34 m deep on sand (*D&M Littler 13098* 19.ii.1988, US). Martinique: Buoy 'MA 2,' Pointe Borgnesse, 3 m deep in sand pockets on a coral dominated area (*D&M Littler 17172* 22.v.1989, US). Hispaniola: Boca Chica, Santo Domingo, Dominican Republic (*Almodóvar 7162* xii.1974, US).

HABIT: Fronds to 24 cm tall, dark green, solitary or in clusters of 2–5. Mature blades to 11 cm long, 19 cm wide (Fig. 1A), <2 mm thick,

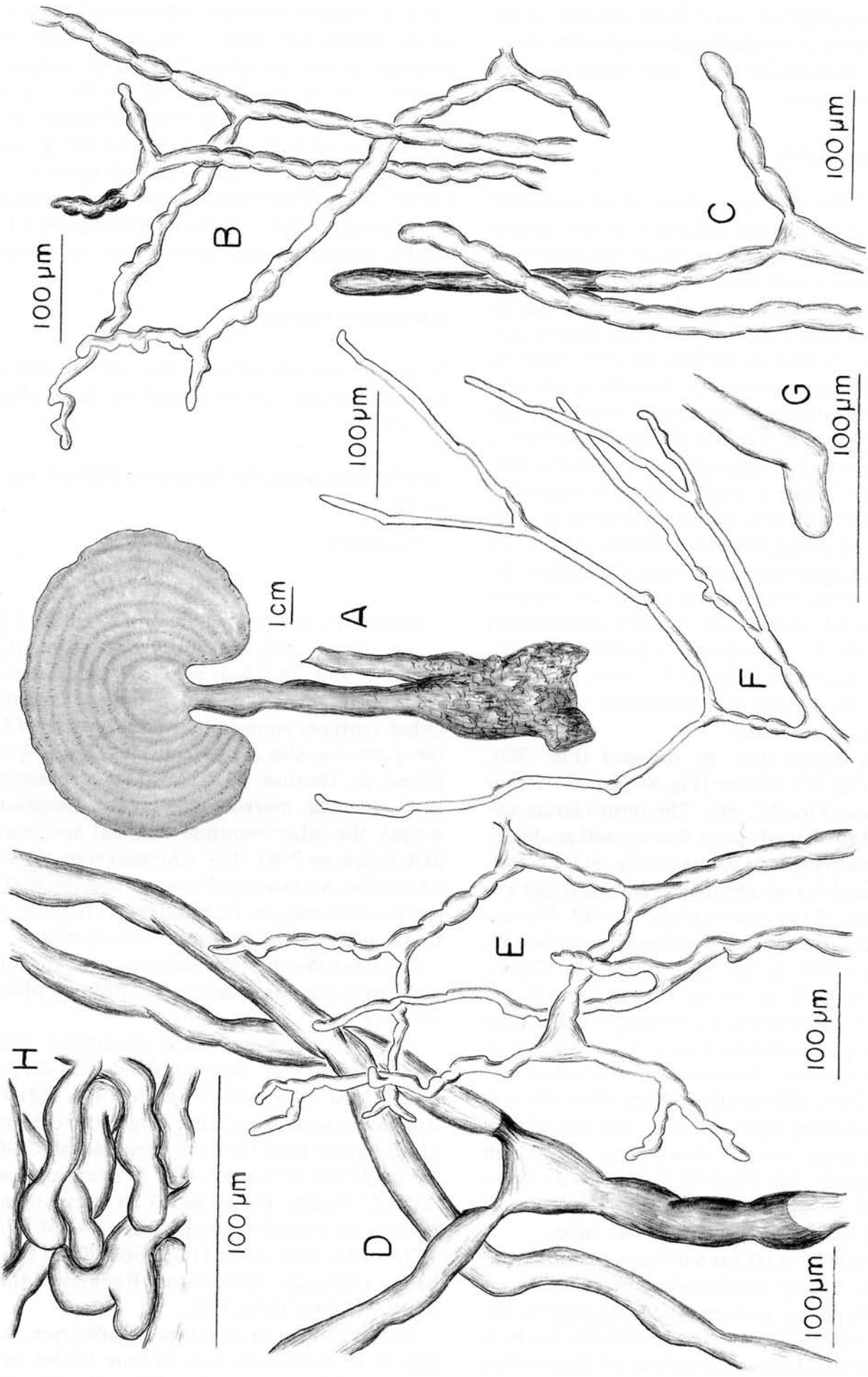

Fig. 1. *Avrainvillea asarifolia* Børgesen. A, habit; B, blade cortical siphons; C, siphons of growing margin; D, stipe medullary siphons; E, stipe cortical siphons; F, rhizoid; G, rhizoid apex; H, cortex of blade showing intertwined nature of surface siphons.

smooth, broadly reniform (kidney-shaped), conspicuously zonate, growing margins lacerate to smoothly rounded, lower margin deeply cordate. Stipe to 15 cm long, 12 mm in diameter, cylindrical or compressed above, not branched, anchored by somewhat bulbous vertical rhizoidal mass.

ANATOMY: Medullary siphons of blade 30–40 (occasionally to 20–30) μm in diameter in deep-water forms, 20–30 μm in diameter in shallow-water forms, slightly moniliform to cylindrical, weak-walled, with supradichotomal swellings or secondary constrictions typically present when cylindrical; siphons forming cortex tapering to 12–20 μm in diameter (Fig. 1B), slightly moniliform and/or tortuous, with rounded apices; distal portion of siphon at growing margins slightly moniliform, 25–40 μm in diameter (Fig. 1C). Medullary siphons of stipe 35–50 μm in diameter (Fig. 1D), slightly moniliform to cylindrical; cortical siphons slightly tortuous and/or slightly moniliform (Fig. 1E), 8–12 μm in diameter. Rhizoids 5–10 μm in diameter (Fig. 1F), cylindrical, frequently terminating in small pad (Fig. 1G).

REMARKS: *Avrainvillea asarifolia* can be identified by its large zonate blade with a deeply cordate lower margin and by its occurrence as individuals or as a cluster of 2–5 fronds from the same holdfast. Internally, fronds have slender slightly moniliform siphons and a distinct cortex comprised of tightly interwoven siphon apices (Fig. 1H). The deep-water (10–20 m) form characteristically has larger medullary siphons and a tighter cortex than the larger shallow-water (< 5 m) form.

In structure, *Avrainvillea asarifolia* is similar to *A. amadelpha* (Montagne) A. Gepp et E.S. Gepp of the western Indian Ocean and Red Sea, both having the tortuous distal blade siphons felted into a thin, tight cortex. However, their growth habits are markedly different. *Avrainvillea asarifolia* is mostly found in soft substrata either singly or in groups of 2–5 with the stipes unbranched. By contrast, *A. amadelpha* is epilithic in cracks and crevices of the reef in large clusters of 25–50 or more blades.

Avrainvillea asarifolia Børgesen

f. *olivacea* f. nov.

Fig. 2

DIAGNOSIS: In structuris anatomicis ad Avrainvilleam asarifoliam f. asarifoliam simila sed in laminis usque ad 12 e massa rhizoideorum proliferatis in laminis transverse ovatis tenuioribus ezonatis et in stipitibus longioribus et angustioribus.

HOLOTYPE: Hidden Creek Lake, Twin Cay, Belize, 0.3–0.6 m deep in a mud/silt or peat substratum (*D&M Littler 13314* 9.ii.1988, US).

DISTRIBUTION: Florida, Bahamas, Cuba, Jamaica, Puerto Rico, US Virgin Islands, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Belize: Grouper Gardens, Twin Cays, 0.5 m deep in organic silt (*D&M Littler 13209* 5.ii.1988, US). Florida: Content Keys, Monroe County, 5 m deep on sand-covered carbonate rock (*D&M Littler 194769b* 13.xii.1987, US). Puerto Rico: Joyuda, Belvedere (*Diaz-Piferrer 7736* 16.ii.1962, US).

REMARKS: *Avrainvillea asarifolia* f. *olivacea* is characteristically gregarious, olive in colour, with little or no zonation, and often with an extremely long stipe also with little or no zonation. It occurs commonly in interior mangrove creeks, ponds, and lakes in areas with rich organic substrata often forming large (to 4 m in diameter) colonies. Internally, f. *olivacea* is virtually identical to f. *asarifolia* (compare siphons of: blade cortex, Figs 2B vs 1B; growing margin, Figs 2C vs 1C; stipe cortex, Figs 2D vs 1E; rhizoids, Figs 2E vs 1F). Externally, plants differ greatly, with the blade of f. *olivacea* generally having a distinctly truncate lower margin (Fig. 2A), while that of f. *asarifolia* has a distinctly cordate base (Fig. 1A). The blades of f. *olivacea* differ from that of f. *asarifolia* in being thinner, not zonate, or with indistinct zonation, often wider than long atop a long, slender stipe. Also, f. *olivacea* usually occurs in clusters of up to 12 upright thalli proliferating from a single rhizoid in contrast with the generally solitary or paired growth form of f. *asarifolia*.

In consideration of consistent differences in external morphology and the lack of intergrades with other taxa, we initially believed this entity to be a separate species. However, its unique habitat and anatomical similarity to *A. asarifolia* f. *asarifolia* prompted us to conduct extensive reciprocal transplant experiments with appropriate controls (Littler *et al.*, unpublished observations). The results showing interconvertibility indicate that this entity is distinct only at the level of *forma*.

Avrainvillea digitata sp. nov.

Fig. 3

DESCRIPTION: Thalli erecti gregarii ad 13 cm longi multipliciter digitati laxe intertexti ezonati estipitati ad basim e massa rhizoideorum magna nascentes; siphones medullares et corticales in diametro 40–55

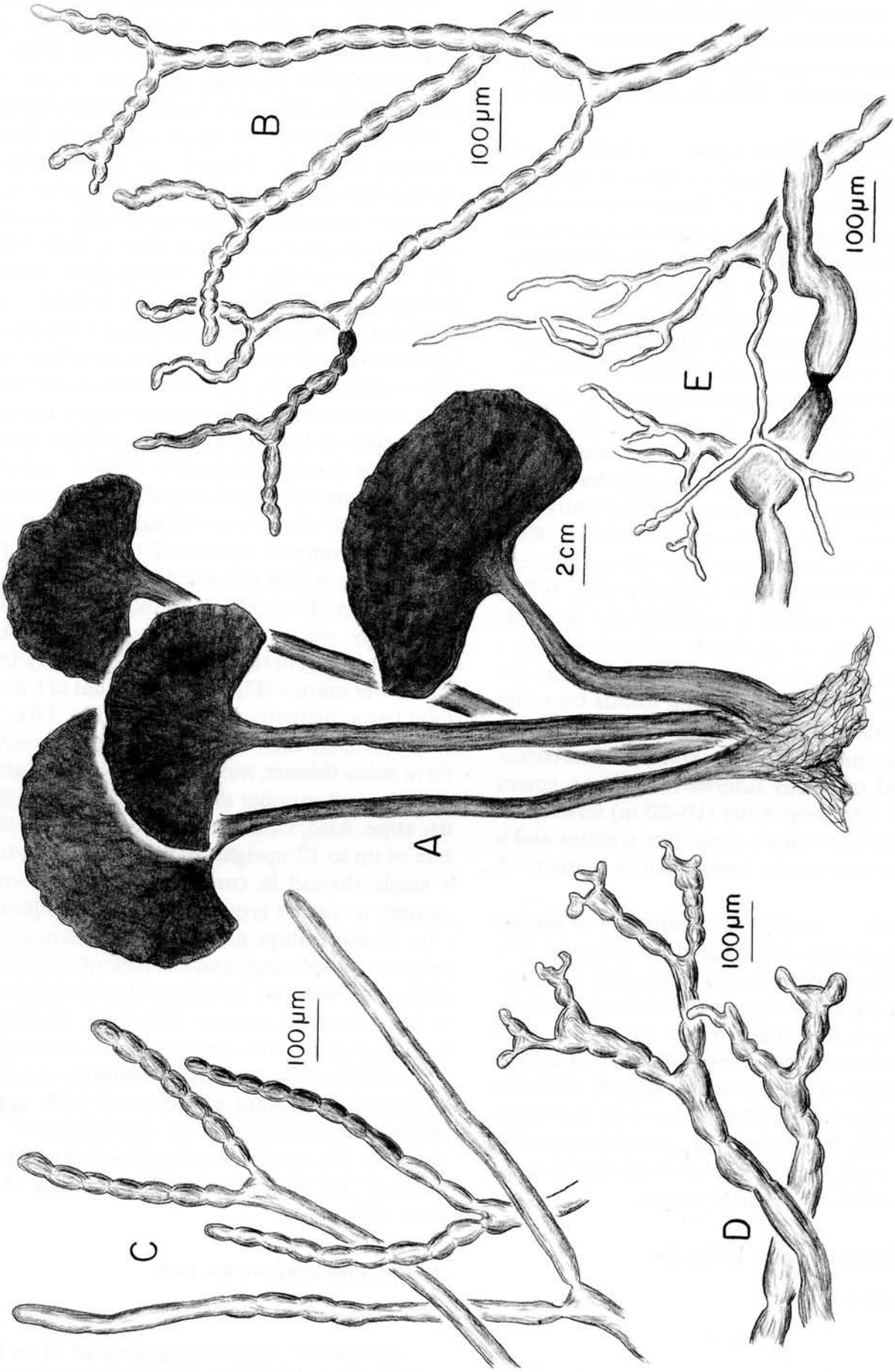

Fig. 2. *Avrainvillea asarifolia* f. *olivacea* f. nov. A, habit; B, blade cortical siphons; C, growing margin siphons; D, stipe cortical siphons; E, rhizoids.

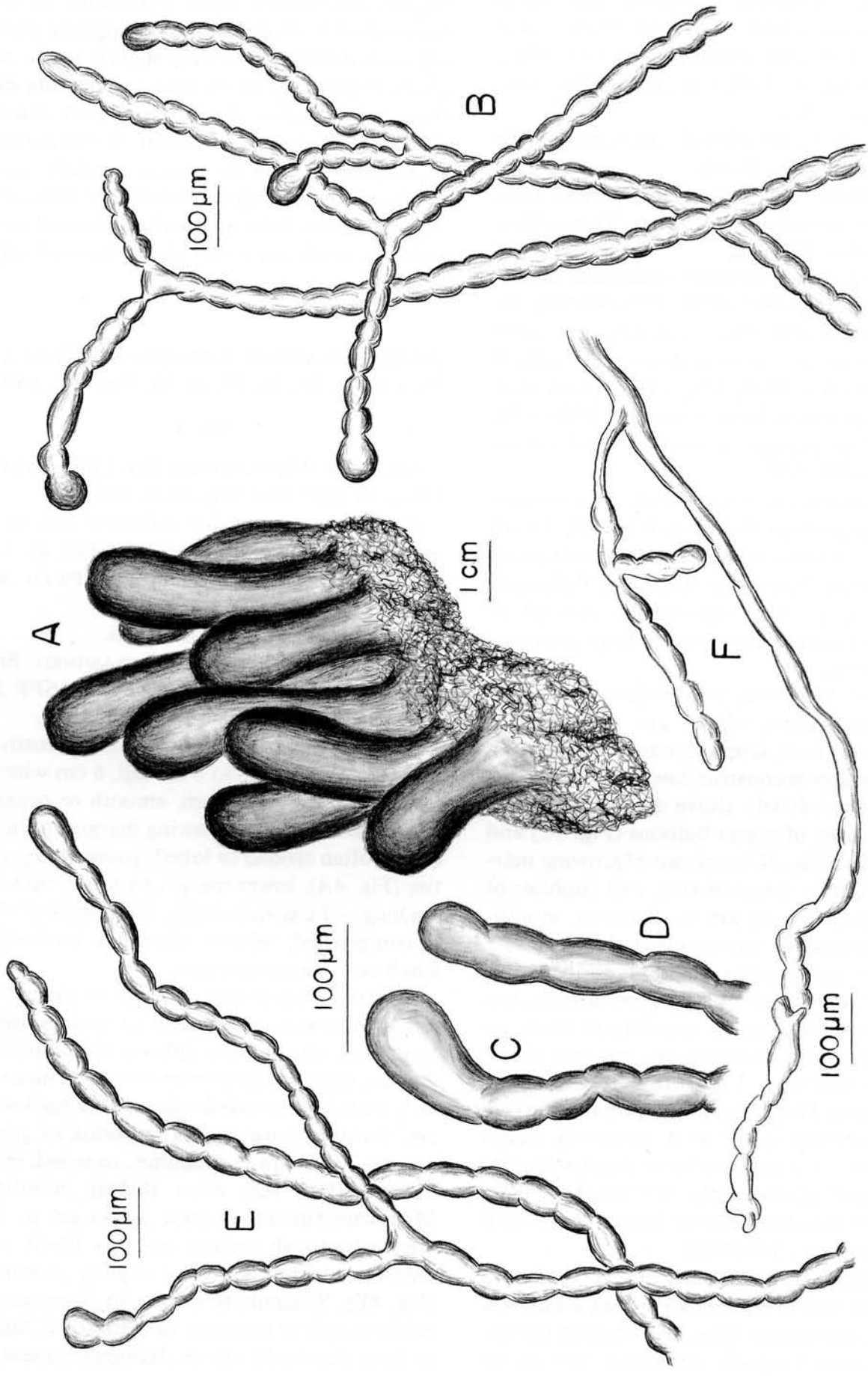

Fig. 3. *Avrainvillea digitata* sp. nov. A, habit; B, siphons of digitate upright; C, bulbous siphon apex; D, rounded siphon apex; E, siphons of growing summit; F, rhizoid.

μm moniliformes apice 60% clavati et 40% rotundati.

HOLOTYPE: Mariguana, Abraham Bay, Bahamas, low-water mark on rocks *Howe 5436* (8.xii.1907, US), also distributed in *Phycotheca Boreali-Americana* #1481 as *Avrainvillea rawsonii* (isotype: NY!).

ETYMOLOGY: *Avrainvillea digitata* is named for its finger-like upright fronds.

DISTRIBUTION: Bahamas, Cuba, Grand Cayman Islands, Jamaica, Puerto Rico, Grenadines, Belize, Atlantic Panama.

REPRESENTATIVE SPECIMENS EXAMINED: Belize: Southwater Cay [16°42′18″N, 87°52′00″W], behind the shallow reef crest, <1 m deep on a sandy rubble substratum forming dense mats (*D&M Littler 19293* 8.vi.1989, US). Cuba: Playa Herradura, Isle of Pines (*Killip 43833* 3.iv.1954, US). Jamaica: Port Morant, 0.3–0.6 m deep (*Howe 6097* 4.iii.1909, NY).

HABIT: Colonies to 13 cm thick, dark brownish-green, gregarious. Fronds to 6 cm tall, 1.5 cm in diameter, loosely woven siphons producing a spongy texture, finger-like without a differentiated stipe (Fig. 3A), occasionally clavate or pointed, not zonate, attached by large prostrate rhizoidal mass.

ANATOMY: Medullary and surface siphons of blade strong-walled, 40–55 μm in diameter, slightly moniliform (approximately 16% reduction in diameter at constrictions), with deep constrictions immediately above dichotomies (Fig. 3B); about 60% of apices bulbous (Fig. 3C) and 40% rounded (Fig. 3D); siphons of growing margin 44–75 μm in diameter (Fig. 3E). Siphons of rhizoidal mass 30–50 μm in diameter, moniliform, cylindrical or tortuous (Fig. 3F).

REMARKS: *Avrainvillea digitata* is easily distinguished by its digitate upright growth form and its often bulbous apex on moniliform blade siphons. Large mats of fronds are typically found in shallow waters (< 1 m), often in dense beds of the seagrass *Thalassia testudinum* Koenig (see Littler *et al.* 1989, p. 69, as *A. rawsonii*). Deep-water forms (> 3 m) may have slender bluntly pointed fronds [*D&M Littler 11478* (US)]. Plants from Puerto Rico have clavate fronds [*Howe 4276* (NY) *Ballantine 2959* (US)].

Externally, *Avrainvillea digitata* is similar to *A. rawsonii*; however, the former has a uniform finger-like appearance (Fig. 3A) whereas the latter has a more irregular, knob-like, peltate, or contorted aspect (Fig. 19A). Internally the two species are also similar. The siphons of the fronds in *A. digitata* are slightly smaller in diameter (mean 48 μm vs 61 μm in *A. rawsonii*) and appear slightly moniliform more frequently. In living material of *A. digitata*, all of the upright siphons are moniliform, albeit only slightly in the medullary region and on occasion appearing cylindrical at the apex; in dried material, older siphons often appear cylindrical. In mature plants of *A. rawsonii*, only the outermost blade siphons are moniliform, many of the interior siphons being cylindrical. Both species lack tapered surface siphons, while each can show bulbous siphon apices.

Avrainvillea elliottii A. Gepp et E.S. Gepp 1911: 35, 138, pl. 11, fig. 99, pl. 12, figs 99a, 100

Fig. 4

HOLOTYPE: Morne Rouge Bay, Grenada (*W.R. Elliott* vi.1887 BM 218-spirit, BM!).

SYNONYM: *Avrainvillea atlantica* Joly et Yamaguishi in Joly *et al.* 1966: 159–160, pl. 1, figs 1–6 [type locality: Ubatuba, São Paulo State, Brazil].

DISTRIBUTION: Grenada, Brazil.

REPRESENTATIVE SPECIMENS EXAMINED: Brazil: Ubatuba, São Paulo State (22.i.1960, SPF 552). Grenada: Morne Rouge Bay (holotype).

HABIT: Fronds to 13 cm tall, olive, mostly solitary. Mature blades to 8 cm tall, 6 cm wide, >4 mm thick, loosely woven, smooth or occasionally wrinkled, zonate growing margins of mature blades often eroded or lobed, young margins entire (Fig. 4A), lower margin truncate. Stipe to 4 cm long, <1 cm in diameter, cylindrical or slightly compressed, seldom branched, anchored by small erect rhizoidal mass.

ANATOMY: Medullary siphons of blade 20–34 μm in diameter, cylindrical to slightly moniliform (Fig. 4B); surface siphons 18–30 μm in diameter, slightly moniliform and/or tortuous (Fig. 4C), with 80% rounded apices, 20% hooked apices, forming loose cortex; siphons of growing margin 20–30 μm in diameter, rounded, seldom bulbous (Fig. 4D), often slightly moniliform. Medullary siphons of stipe 30–44 μm in diameter, cylindrical; cortical siphons 10–28 μm in diameter, tortuous and/or slightly moniliform (Fig. 4E). Rhizoids to 40 μm in diameter, moniliform and/or tortuous, or cylindrical, tapering to long slender (6 μm in diameter) apices (Fig. 4F).

REMARKS: The most distinctive feature of

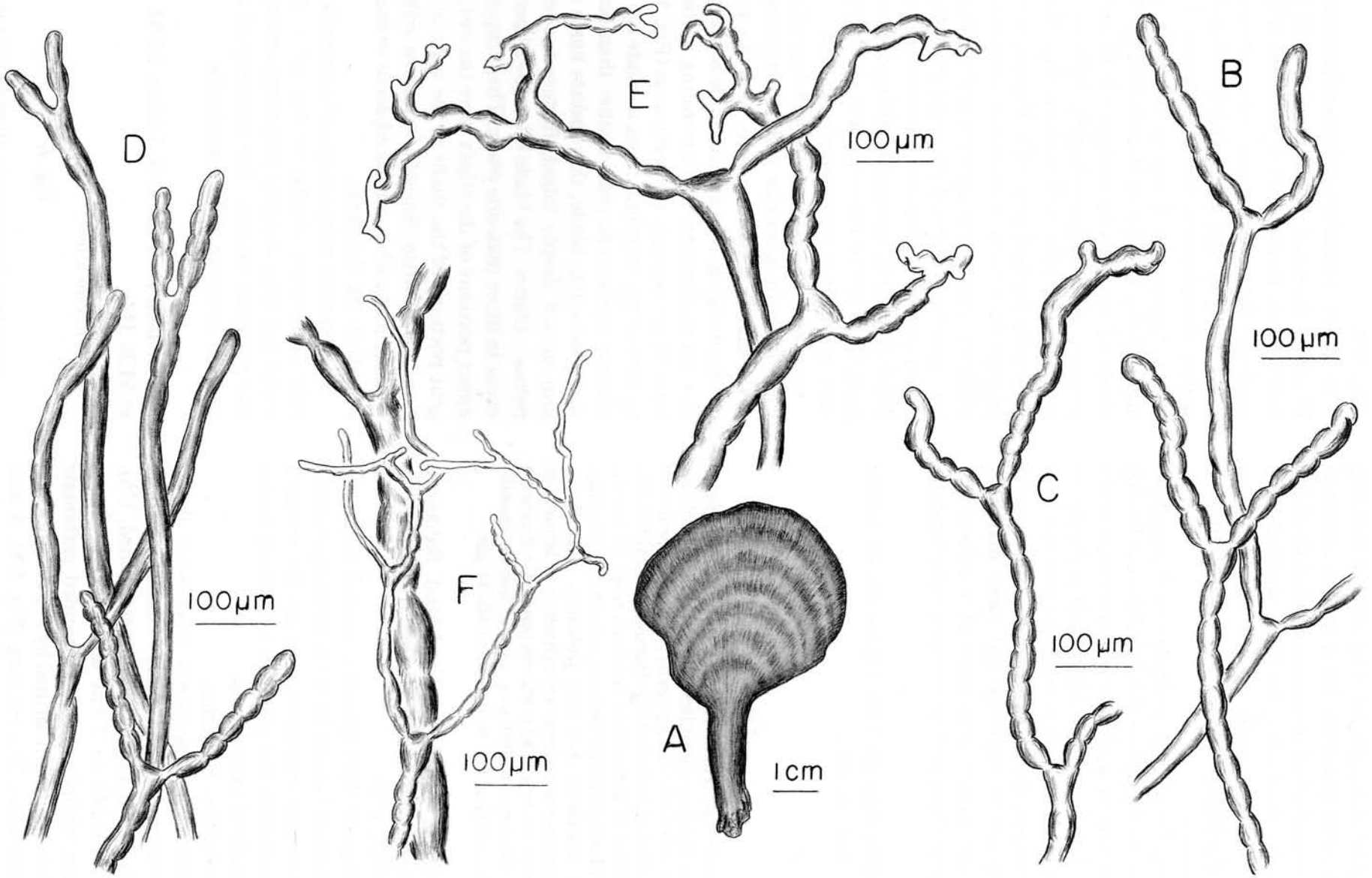

Fig. 4. *Avrainvillea elliottii* A. Gepp et E.S. Gepp. A, habit of immature plant (holotype); B, distal blade siphons; C, proximal blade siphon; D, growing margin siphons; E, cortical stipe siphons; F, rhizoids.

Avrainvillea elliottii is the truncate lower margin of mature blades (see Littler *et al.* 1989, p. 70 for a colour photograph). The distinct banding is also a useful character, but it is often obscured by large quantities of sediments entrapped among the siphons. Internally, the blade siphons have little or no taper with surface siphons being slightly moniliform, while the interior siphons are cylindrical.

Avrainvillea elliottii is similar to *A. asarifolia* in zonation and siphon size but differs in having a smaller and thicker blade with a truncate lower margin. The blade of *A. longicaulis* is similar in size and thickness but is orbicular and not zonate. Moreover, the blade siphons of that species reach 60 μm in diameter and taper markedly toward the surface while those of *A. elliottii* seldom reach 40 μm and are not noticeably tapered.

Avrainvillea fenicalii D.S. Littler, M.M. Littler et M.E. Hay sp. nov.

f. *fenicalii*

Fig. 5

DESCRIPTION: Thalli erecti ad 7 cm longi inferne stipitati distaliter laminiferi, stipitis ramosis vel non ramosis, laminis 5–8 aggregatis 2 cm longis profunde lobatis ferenti, massis rhizoideorum verticalibus columnaribus in sedimentis deorsum ultra 30 cm attingentibus cylindricis ramosis vel non ramosis magnis in diametro 3–4 cm; siphones medullares moniformes vel tortuosi vel cylindrici in laminis in diametro 20–30 μm ad corticem sensim in diametro 8 μm siphones medullares stipitis leniter moniliformes vel cylindrici in diametro 40–51 μm.

HOLOTYPE: Bain Town, Cat Island, Bahamas, 1 m deep in a sandy channel (*Hay 1990-1* 23.vii.1990, US!)

ETYMOLOGY: This species is named in honour of Dr William Fenical for his pioneering research in marine algal chemistry and for the research opportunities he has given us and others on his well-organized expeditions.

DISTRIBUTION: Bahamas.

REPRESENTATIVE SPECIMEN EXAMINED: Bahamas: Williams Island, Andros Island, intertidal (*Dawson 26928* 17.iii.1966 undetermined, US).

HABIT: Fronds to 7 cm tall, dark green but appearing whitish due to entrapped carbonate sediments, capitulum formed by 5–8 deeply lobed blades per stipe, 2–3 cm long (Fig. 5A), 3 mm thick, lobes 5 mm wide, soft-spongy, not zonate. Stipes branched or unbranched, 8 cm long, 1 cm in diameter, terete; arising in clusters (10–30) from an extraordinarily large subterranean rhizoidal column, 3–4 cm in diameter, >30 cm long (Fig. 5B).

ANATOMY: Medullary siphons of capitulum 20–30 μm in diameter, shape varying from slightly moniliform, tortuous to cylindrical (Fig. 5C), swellings due to secondary constrictions characteristically present above constrictions at wide-angled dichotomies; surface siphons forming cortex, tapering to 8 μm in diameter, slightly moniliform, hooked or distorted (Fig. 5D); siphons of the growing margin 16–29 μm in diameter, with approximately 70% of apices rounded (Fig. 5D), 30% bulbous (Fig. 5E) or occasionally hooked (Fig. 5F). Medullary siphons of stipe 40–52 μm in diameter, somewhat moniliform, tortuous or cylindrical (Fig. 5G). Central siphons of vertical rhizoidal column 40–60 μm in diameter, tortuous, moniliform or cylindrical (Fig. 5H), corticating rhizoidal proliferations 8–20 μm in diameter (Fig. 5I), apices clavate, rounded or occasionally hooked.

REMARKS: The external morphology of *Avrainvillea fenicalii* is unique within the genus. Most of the thallus is subterranean, with the branched heads emerging from a massive rhizoidal column 3–4 cm in diameter and extending vertically at least 30 cm beneath the sediments (Fig. 5B). Up to 40% of the rhizoidal mass is made up of proliferous hyaline rhizoids. Rather than bearing a single flabellate blade, this species has a capitulum of 5–8 deeply lobed, flattened, somewhat palmate blades. The blade lobes (3–14 per blade) occur in more than one plane. These capituli and upper portions of the stipes were the only emergent portions of the thalli at the time of collection. *Avrainvillea fenicalii* is known only from *Thalassia testudinum* beds adjacent to mangrove islands in the Bahamas.

The external morphology of *Avrainvillea fenicalii* is remotely similar to that of *A. digitata,* which has large irregular projections from a matlike rhizoidal system. The anatomy of the two species, however, differs markedly.

Avrainvillea fenicalii D.S. Littler, M.M. Littler et M.E. Hay

f. *flabellifolia* f. nov.

Fig. 6

DIAGNOSIS: In structuris rhizoidialibus et interalibus Avrainvilleam fenicalii f. fenicalii simila sed in laminis zonatis margine integris plerumque in apicibus stipitum solitariis differt.

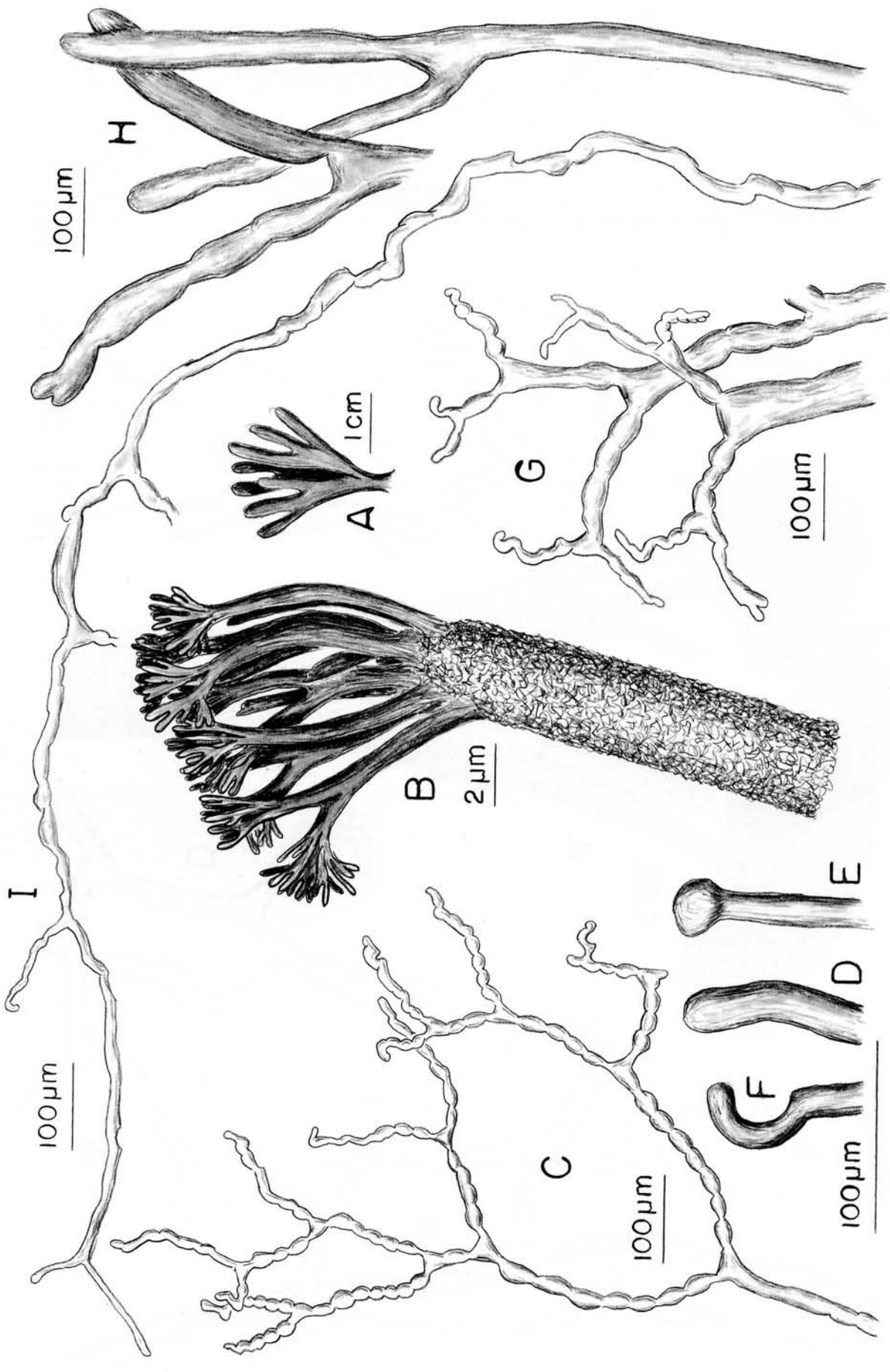

Fig. 5. *Avrainvillea fenicalii* sp. nov. A, bifurcated blade; B, habit illustrating unique large vertical cylindrical rhizoidal mass; C, blade cortical siphon; D, rounded siphon apex; E, bulbous siphon apex; F, hooked siphon apex; G, stipe cortical siphons; H, central rhizoidal mass siphons; I, rhizoidal cortical siphon.

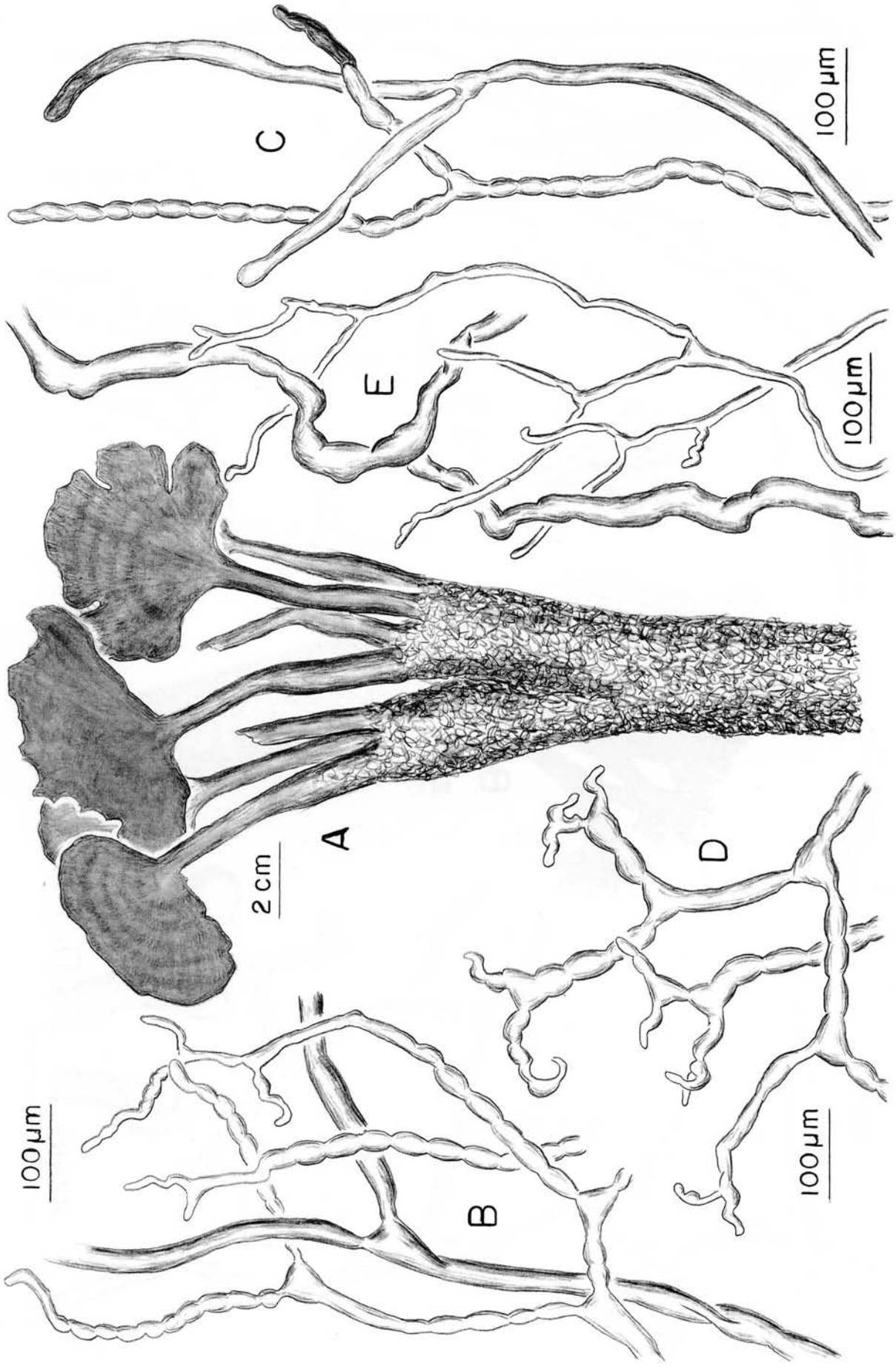

Fig. 6. *Avrainvillea fenicalii* f. *flabellifolia* f. nov. A, habit; B, blade siphons; C, growing margin siphons; D, stipe cortical siphons; E, rhizoidal siphons.

HOLOTYPE: Between Jack's Bay and Isaac Bay, St Croix, US Virgin Islands, in sand with *Thalassia* (*Ogden F1-35* 7.vi.1981, US).

DISTRIBUTION: Puerto Rico, US Virgin Islands.

REPRESENTATIVE SPECIMENS EXAMINED: US Virgin Islands: Smuggler's Cove, St Croix, 2 m deep in sand and coral rubble at the edge of a *Thalassia* bed (*N. Ogden FL-104* 9.vi.1981, US). Puerto Rico: Canyo Santana near Lajas, La Parguera, abundant among *Thalassia* on coarse sand and soft bottom (*Bernatowicz 62–33* 17.i.1962, US).

REMARKS: *Avrainvillea fenicalii* f. *flabellifolia* differs from f. *fenicalii* in the shape of its blade, which has an entire or broadly lobed margin in contrast to the deeply incised blades of f. *fenicalii*. The blade is conspicuously zonate, a feature that in f. *fenicalii* is obscured by the deep laceration of the blade. Siphon shape and size in both forms are virtually identical (compare siphons for: capitulum cortex, Figs 6B vs 5C; stipe cortex, Figs 6D vs 5G; rhizoids, Figs 6E vs 5I, H). Both forms have a distinctive large, pigmented, columnar rhizoidal mass (Fig. 6A, 5B) buried in soft sediments and both are known exclusively from beds of *Thalassia testudinum*.

Avrainvillea fulva (Howe) comb. nov.

Fig. 7

BASIONYM: *Avrainvillea nigricans* f. *fulva* Howe in Collins *et al.* 1908: no. 1480.

HOLOTYPE: Castle Island, Bahamas, 0.3–1.0 m deep inside the reef (*Howe 1480* 22.xii.1907, NY!; isotype: US!).

DISTRIBUTION: Bermuda, Florida, Bahamas, Cuba, Jamaica, Puerto Rico, Guadeloupe, Martinique, Mexico, Venezuela.

REPRESENTATIVE SPECIMENS EXAMINED: Bermuda: Mangrove Bay (20.ii.1913, US 51626). Florida: Monroe County, Content Keys, 1 m deep on sand-covered carbonate rock (*D&M Littler 19471* 23.xii.1987, US). Guadeloupe: Pointe-à-Pitre, Smithsonian-Bredin Caribbean Expedition (29.iii.1956, US 33427). Martinique: Pointe Catherine, 2–5 m deep (*Bucher 1454* 29.viii.1985, US). Puerto Rico: Boca de Infierno, Bahia de Jobos, Aquirre (*Almodóvar 6294* 5.v.1970, US).

HABIT: Thalli to 18 cm tall, golden green to green, solitary or, more often, in clusters of 2–5. Mature blades to 12 cm long, 14 cm wide (Fig. 7A), 2–5 mm thick, loosely woven, coarsely fibrous, wedge-shaped, not zonate, growing margins lacerated and eroded in mature plants, smoothly curved in juveniles (Fig. 7B), base gradually tapering to stipe. Stipe to 6 cm long, thick (to 4.5 cm in diameter), cylindrical, often compressed near blade, unbranched, anchored by massive subterranean rhizoidal system (Fig. 7B).

ANATOMY: Medullary siphons of blade yellow or yellowish brown to clear, 60–120 (occasionally to 140) μm in diameter, moniliform (approximately a 33% reduction in diameter at the constrictions), occasionally cylindrical; surface siphons branching repeatedly, tapering to 20–40 μm in diameter in final two or three dichotomies, moniliform (Fig. 7C); siphons of growing margins 42–55 μm in diameter, not tapered, with few dichotomies (Fig. 7D). Siphons of stipe similar to those of blade, but with more differentiation between surface and interior, medullary siphons 80–130 μm in diameter, moniliform; cortical siphons 20–40 μm in diameter, moniliform and/or tortuous (Fig. 7E). Rhizoids to 85 μm in diameter, moniliform and/or tortuous.

REMARKS: *Avrainvillea fulva* commonly consists of a massive rhizoidal system with several wedge-shaped thick blades. The stipe gradually merges into the blade. *Avrainvillea fulva* commonly grows in moderately shallow waters (1–10 m) on soft substrata rich in organic matter, often sympatrically with *A. nigricans* f. *floridana*.

Avrainvillea fulva has long been confused with *A. nigricans* since both possess moniliform blade siphons. The medullary siphons of the blade of *A. fulva*, however, are three times larger (mean of 101 μm vs 33 μm), have shallower constrictions (33% vs 70% reduction), and a gradual taper (50% or greater reduction in diameter vs <40% reduction in *A. nigricans*) of surface siphons. Blades of the two species are usually different, those of *A. fulva* arising from a massive base, while those of *A. nigricans* are less than 2 mm thick, broadly reniform to suborbicular, and terminal on a solitary narrow stipe arising from a bulbous anchor.

Avrainvillea fulva is also similar to *A. silvana*, but the medullary siphons of its blade are larger (mean diameter 102 μm vs 66 μm). Also, *A. fulva* develops a rough-textured loose blade while that of *A. silvana* is tightly woven and smooth.

Avrainvillea geppii Børgesen 1913: 87, figs 71, 72

Fig. 8

HOLOTYPE: Maho Bay, St Jan, US Virgin Islands, 16 m deep (*Børgesen 2011* 17.iii.1906, C!).

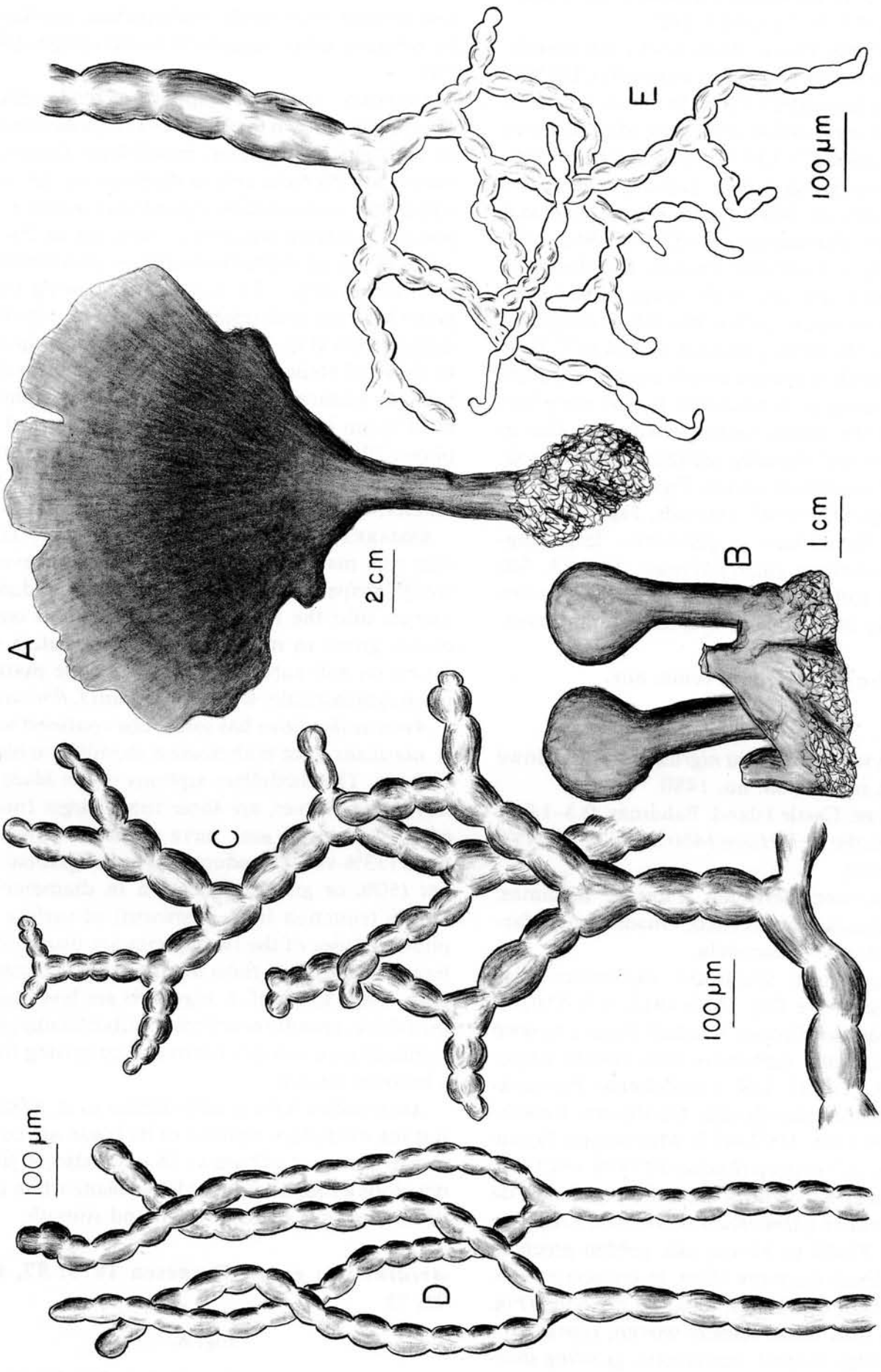

Fig. 7. *Avrainvillea fulva* (Howe) comb. nov. A, habit of mature plant; B, habit of juvenile illustrating massive holdfast giving rise to more than one upright; C, blade siphons; D, blade growing margin siphons; E, stipe cortical siphon.

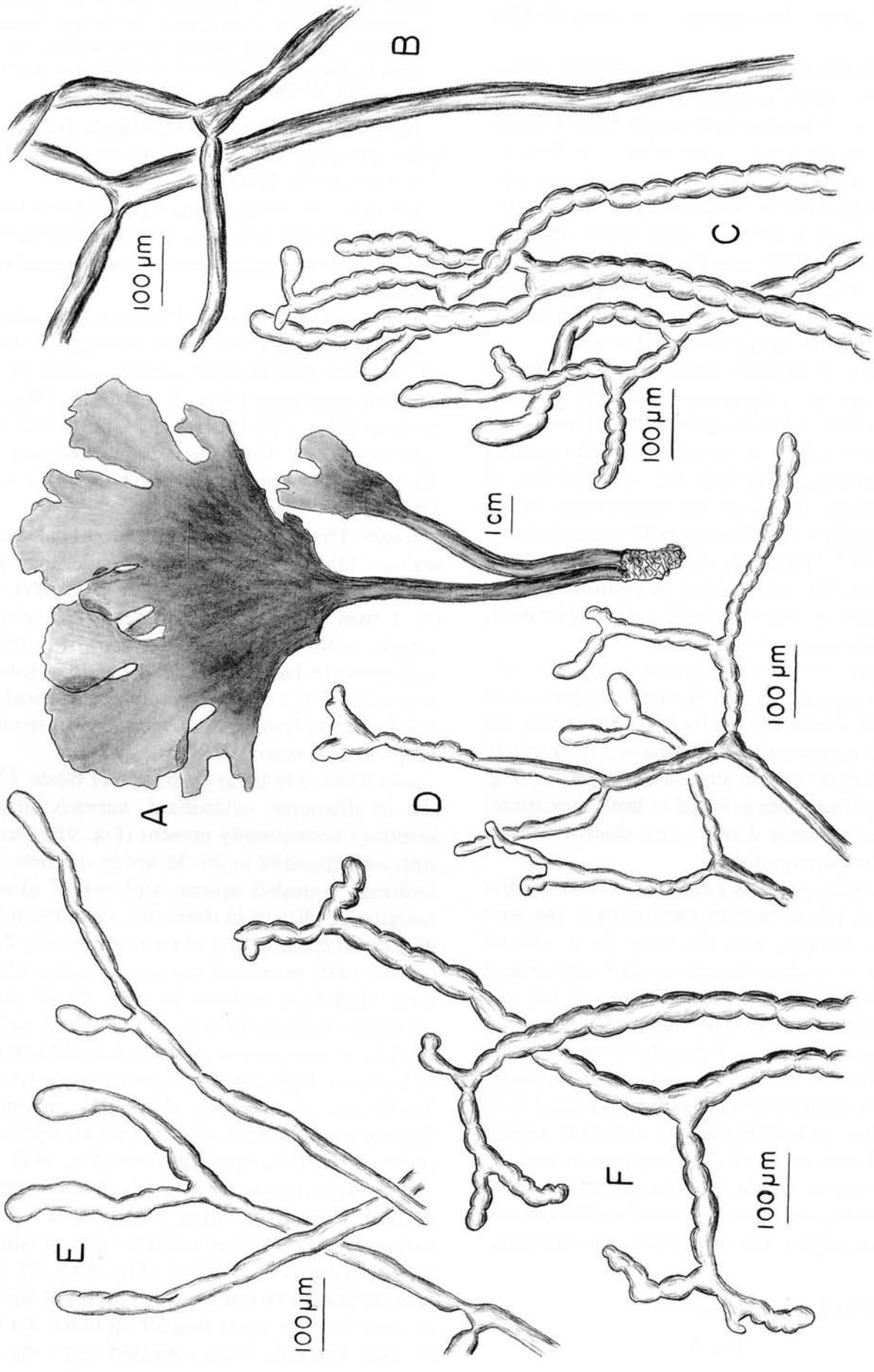

Fig. 8. *Avrainvillea geppii* Børgesen. A, habit; B, blade medullary siphons; C, lower blade cortical siphons; D, upper blade cortical siphons; E, growing margin siphons; F, stipe cortical siphons.

DISTRIBUTION: Florida, US Virgin Islands.

REPRESENTATIVE SPECIMEN EXAMINED: Florida: Monroe County, Key Largo, 2 m deep (HBFH 3254).

HABIT: Thalli to 20 cm tall, dark greenish-brown proximally, lighter greenish-brown distally, solitary or 2 or 3 arising from single base. Mature blades to 10 cm long, 13 cm wide (Fig. 8A), 1–2 mm thick, loosely woven with rough but uniform texture, ovate to wedge-shaped, not zonate, growing margins lacerate with lobed indentations extending 30% into the blade, with attenuate base (Fig. 8A). Stipe to 10 cm long, 5 mm in diameter, cylindrical, unbranched, anchored to substratum by small rhizoidal clump.

ANATOMY: Medullary siphons of blade 30–40 μm in diąmeter, cylindrical to slightly moniliform (Fig. 8B); surface siphons 20–40 μm in diameter, moniliform to cylindrical, with rounded and expanded apices (Fig. 8C, D); siphons of growing margin to 28–40 μm in diameter, cylindrical to slightly moniliform, with expanded apices (Fig. 8E). Medullary siphons of stipe 40–50 μm in diameter, moniliform to cylindrical (Fig. 8F); siphons of cortex 18–25 μm in diameter, moniliform and/or tortuous.

REMARKS: *Avrainvillea geppii* is known only from two specimens and is therefore presumed to be rare. Plants are easily identified from the expanded apices of the siphons which occur in approximately 75% of the surface siphons (Fig. 8C, D, E). The blade is lobed in both specimens, lighter and thinner distally and slightly thicker and darker proximally.

Avrainvillea geppii is similar to *A. elliottii,* but its blade is lobed, thin and not zonate, the base gradually merging with the stipe. In *A. elliottii* the blade is seldom lobed, thicker and zonate with a truncate base. The siphons of the two species are similar in size, but *A. geppii* has far more expanded apices, the siphons of *A. elliottii* being generally consistent in diameter throughout. Olsen-Stojkovich (1985) synomynized these two species, understandably so with only a single specimen (the type) of *A. geppii* known and the close similarity of the internal structure. With the discovery and examination of additional material of *A. geppii,* the differences are apparent.

Avrainvillea hayi sp. nov.

Fig. 9

DESCRIPTION: Thalli erecti ad 12.5 cm longi solitarii, laminis maturis ovatis zonatis tenuibus (< 1 mm) dense intertextis base truncatis vel cuneatis margine leviter lobatis; siphones laminalis medullares cylindrices in diametro 20–30 μm corticales cylindrici sensim in diametro 26–36 μm; siphones stipitatis medullares leniter moniliformes vel tortuosi in diametro 28–40 μm corticales in diametro sensim ad 10–18 μm.

HOLOTYPE: Galeta Pointe, Galeta Island, Atlantic Panama, 13.3 m deep on sand plain (*Hay 256* 14.ix.1978, US!).

ETYMOLOGY: *Avrainvillea hayi* is named for the collector, Dr Mark E. Hay, in appreciation of his adeptness at searching out new and unusual specimens.

DISTRIBUTION: Atlantic Panama, Colombia.

REPRESENTATIVE SPECIMENS EXAMINED: Atlantic Panama: Galeta Point, Galeta Island, 16.6 m deep on sand plain (*Hay 34* 9.ii.1978, US); 13.3 m deep (*Hay 728* 13.v.1979, US); (*Kilar 2322* 8.ix.1979, US). Columbia: Bahia Gairaca, 13–20 m on sand bottom (*Sims 88-003* 17.v.1988, US).

HABIT: Thalli to 12.5 cm tall, bright pale green, solitary. Mature blades slightly broader than long, ovate, 9 cm long, 10.5 cm wide (Fig. 9A), thin (< 1 mm thick), tightly interwoven, smooth, zonate, with smoothly lobed growing margins and truncate base. Stipe to 4 cm long (mostly shorter), 0.3–0.5 cm in diameter, cylindrical, unbranched, anchored in sedimentary substrata by deep vertical rhizoidal mass.

ANATOMY: Medullary siphons of blade 22–30 μm in diameter, cylindrical, supradichotomal swellings occasionally present (Fig. 9B); surface siphons expanded to 26–36 μm in diameter, cylindrical, rounded apices; siphons of growing margins 25–30 μm in diameter, cylindrical (Fig. 9C); distal 0.5 mm end of siphon typically larger (24–42 μm), proximal portions smaller (22–30 μm). Medullary siphons of stipe 28–40 μm in diameter, cylindrical (Fig. 9D); cortical siphons 10–18 μm in diameter, slightly moniliform and/or tortuous. Medullary siphons of rhizoidal mass 30–50 μm in diameter (Fig. 9F), cylindrical, slightly moniliform and/or tortuous, tapering in cortex to 10–20 μm in diameter (Fig. 9G).

REMARKS: *Avrainvillea hayi* is characterized by a large, thin, oval, often lobed blade with an extremely narrow stipe and a unique, small, vertically cylindrical holdfast (Fig. 9A). Of those species that have uniformly cylindrical siphons, *A. hayi* has the most slender siphons. To date, *A. hayi* has only been collected from the deep subtidal on sand plains in Atlantic Panama and Colombia.

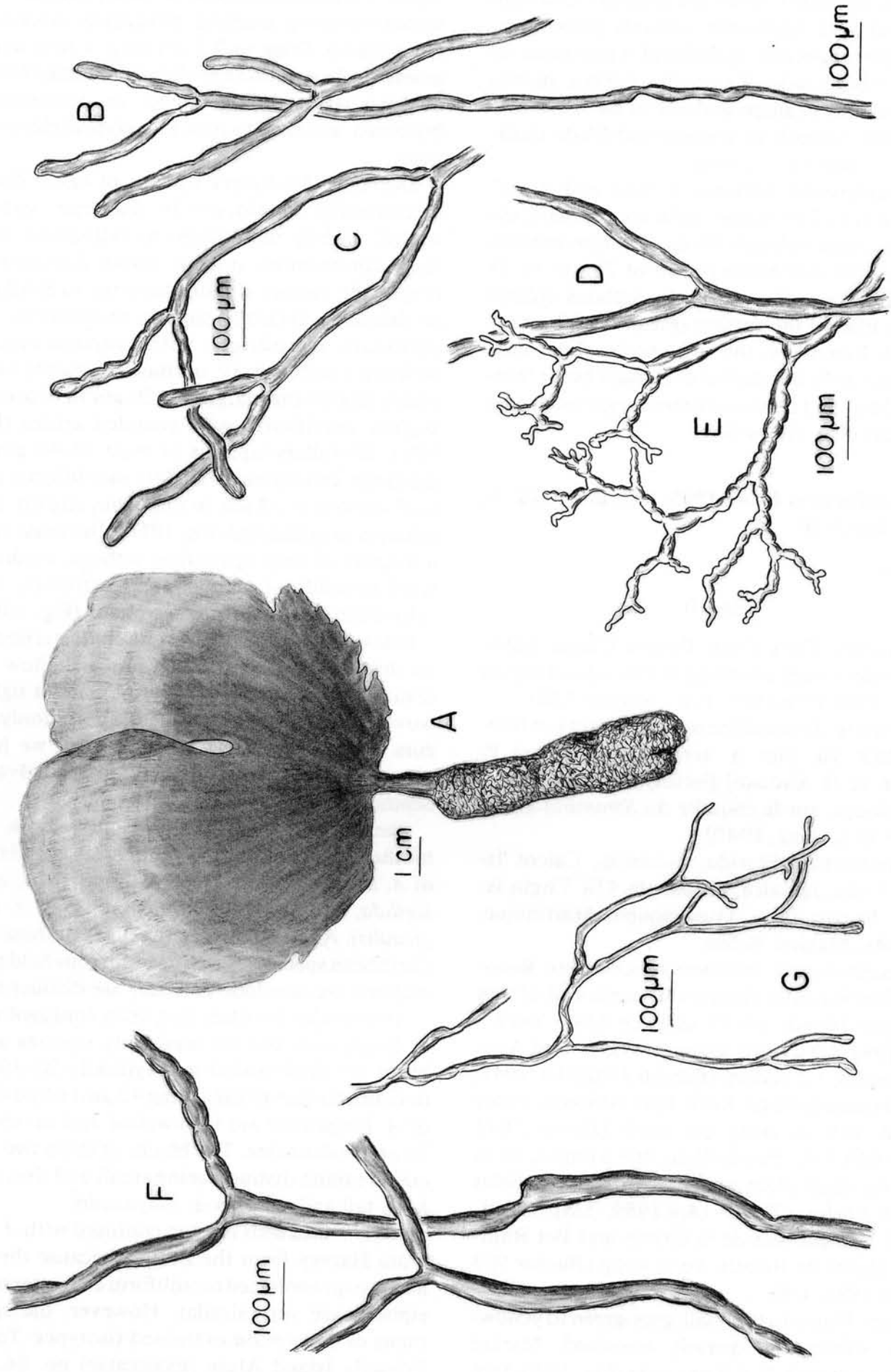

Fig. 9. *Avrainvillea hayi* sp. nov. A, habit; B, blade siphons; C, growing margin siphons; D, stipe medullary siphon; E, cortical stipe siphon; F, siphons of central portion of rhizoidal mass; E, rhizoidal cortical siphon.

Avrainvillea hayi is similar to *A. mazei* internally but its blade siphons are smaller (22–44 μm vs 30–60 μm). Moreover, actively growing siphons are uniformly cylindrical while those of *A. mazei* often taper. Externally, the two species differ not only in shape and size of blade but also in texture (smooth vs fibrous) and blade thickness (< 2 mm vs > 2 mm).

The differences between *A. hayi* and *A. sylvearleae* are more subtle. Both species have cylindrical blade siphons. Those of *A. hayi* are narrower in the mid-blade (mean of 28 μm vs 41 μm) while in both species the siphons enlarge slightly toward the surface (means of 37 μm vs 52 μm). Externally, the two species differ considerably, with the thallus of *A. hayi* being thinner, zonate, and from 2–3 times longer and wider than that of *A. sylvearleae.*

Avrainvillea levis Howe 1905; 565, pl. 23, fig. 1, pl. 26, figs 8–10

f. *levis*

Fig. 10

HOLOTYPE: Cave Cays, Exuma Chain, Bahamas, under a rock overhang in low littoral region (*Howe 3996* 19.ii.1905, NY!; isotype: US!).

SYNONYM: *Avrainvillea sordida* Murray et Boodle 1889: 70. [not *A. sordida* (Montagne) P. Crouan et H. Crouan] [lectotype; Basse Terre, Guadeloupe, sur la coquille du *Strombus gigas,* (*Mazé 30* no date, BM!)].

DISTRIBUTION: Florida, Bahamas, Caicos Islands, Cuba, Jamaica, Hispanola, UK Virgin Islands, Puerto Rico, Guadeloupe, Martinique, Grenada, Mexico, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: San Salvador Seamount, north end of San Salvador Island, 67–73 m deep (*JSL 1493-7* 18.x.1983, US). Haiti: Dame Marie toward Anse D'Hainault, 1.2 m deep (*Bartlett 17829* 1.v.1941, US). Jamaica: Coral Reef, Port Antonio, Navy Island, 0.6 m deep on sand (*Howe 5881* 25.ii.1909, US). Puerto Rico. Isle Monito, 40 m deep on sand plain attached to small pebbles (*D&M Littler 17048b* 14.v.1989, US). Martinique: between Îlet de la Grotte and Îlet Ramville, Havre de Robert, 16 m deep (*Bucher 983* 25.viii.1985, US).

HABIT: Plants to 6 cm tall, grey-green to yellow-green, solitary or sparsely branched. Mature blades to 4 cm tall, 6.5 cm wide (Fig. 10A), thin (< 1 mm thick), tightly woven with a smooth compact surface, reniform to obovate, base slightly cordate, not zonate or faintly zonate, with smooth-growing margins, irregularly eroded in older blades. Stipe to 2.5 cm long, 4 mm in diameter, subcylindrical or slightly flattened (often concave when dried), simple or occasionally branched, attached to rock by a conical rhizoidal mass.

ANATOMY: Medullary siphons of blade 25–35 (occasionally to 40) μm in diameter, strong-walled, slightly moniliform to cylindrical, long leggy constrictions present above dichotomies (Fig. 10B); surface siphons tapering to 8–12 μm in diameter, typically slightly moniliform, occasionally cylindrical, with rounded apices, forming a tight cortex; ultimate segments of siphons of growing margin 12–20 μm in diameter, slightly moniliform with rounded apices (Fig. 10C). Medullary siphons of stipe 30–40 μm in diameter, cylindrical to slightly moniliform; cortical siphons 8–12 μm in diameter, slightly moniliform to cylindrical (Fig. 10D). Rhizoidal mass a mixture of large cylindrical siphons, medium-sized moniliform siphons, and extremely thin cylindrical and/or tortuous siphons (Fig. 10E).

REMARKS: *Avrainvillea levis* is characterized by its thin, tough blade, which has a shallow but distinctly cordate base (Fig. 10A), and a tightly woven outer cortex. This species commonly occurs in shallow waters (< 1 m), but we have observed it at a depth of 125 m on San Salvador Seamount in the Bahamas.

Avrainvillea levis has previously been enmeshed in the confusing nomenclatural history of *A. longicaulis* (see Gepp & Gepp 1911, as *A. sordida,* and Olsen-Stojkovich 1985, as *A. longicaulis*). After examining the types of these two Caribbean species, as well as numerous field populations, we conclude that they are distinct taxa.

Avrainvillea levis has long been confused with *A. longicaulis,* but the medullary siphons of its blade are thick-walled and typically 20–30 μm in diameter (never exceeding 40 μm) while those of *A. longicaulis* are thin-walled and up to 60–70 μm in diameter. The blades of these two species are quite distinct, being small and thin in *A. levis,* tall and thick in *A. longicaulis.*

Avrainvillea levis is often confused with *A. lacerata* Harvey from the Pacific, because the size and less-pronounced moniliform character of the siphons are very similar. However, the specimens of *A. lacerata* examined (isotypes: Tonga, Friendly Island Algae [Exsiccatae] no. 86, leg. W.H. Harvey BM!, NY!, MEL!) are usually re-

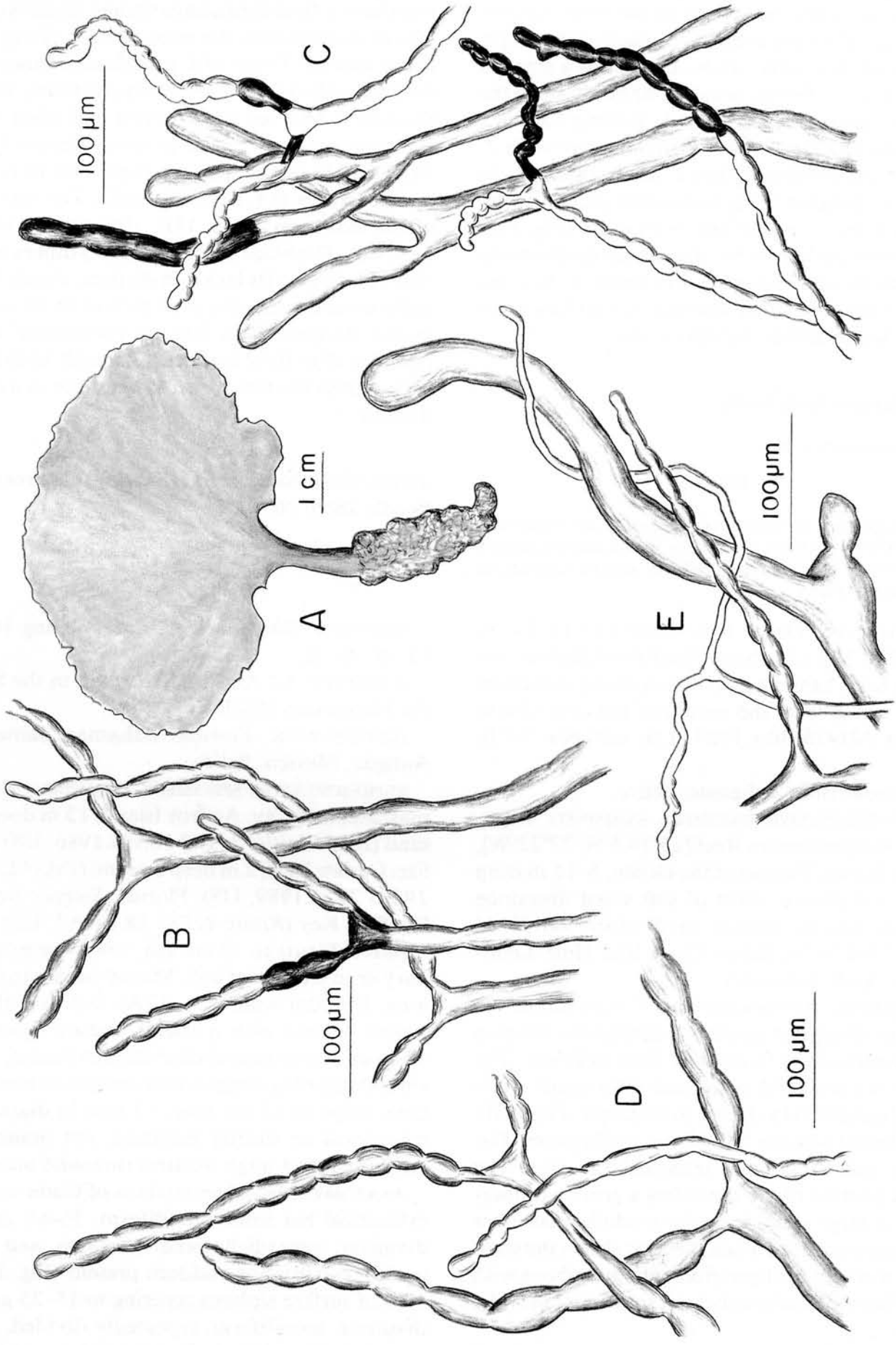

Fig. 10. *Avrainvillea levis* Howe. A, habit; B, blade siphons; C, growing margin siphons; D, stipe siphons; E, rhizoids.

peatedly and irregularly branched with clusters of blades, whereas *A. levis* typically is solitary or occasionally branches once at the base. *Avrainvillea lacerata* has a distinctly lacerated margin and is never zonate, while *A. levis* has a smooth margin and is faintly zonate. The holdfasts of the two are also different, with *A. lacerata* having a compact emergent mat or bulbous mass while *A. levis* most commonly has a small almost nonexistent holdfast with occasional plants developing a small conical rhizoidal mass (Fig. 11A illustrates the largest holdfast found on the many specimens we examined). Internally *A. lacerata* has no defined cortex whereas *A. levis* has a distinct, tough, tightly woven cortex.

Avrainvillea levis Howe

f. *translucens* f. nov.

Fig. 11

DIAGNOSIS: In structuris anatomicis ad Avrainvilleam levis f. levis simila sed in dispositionis siphonis laxiore in laminis tenuiore et in stipitis longiore et tenuiore differt.

HOLOTYPE: Great Blue Hole [17°18′54″N, 87°32′10″W], Lighthouse Reef Atoll, Belize, 10–50 m deep hanging from silt-covered carbonate walls which form the mouth of the cave (*D&M Littler 12147b* 30.v.1987, US; isotypes: UCB, BM).

DISTRIBUTION: Bahamas, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Washerwoman Reef [23°39.5′N, 77°22′W], Sister Rocks, Tongue of the Ocean, 5–15 m deep at cave entrance, walls of soft silted limestone and calcareous muddy sand (*Earle 68-10-11* 23.ii.1968, SEH). Belize: Great Blue Hole, Lighthouse Atoll (holotype).

REMARKS: *Avrainvillea levis* f. *translucens* occurs as abundant pendant populations fringing the mouth of the Great Blue Hole in Belize. The blade is composed of at least 60% small, often hyaline siphons (5–10 μm in diameter; Fig. 11B), 20% larger siphons (20–30 μm in diameter; Fig. 11B), and about 20% intermediate sizes. The lower portion of the blade has a greater proportion of large siphons in the medulla than does the upper portion, while the stipe shows the standard medulla configuration of large siphons with a surface of loosely entwined small siphons (Fig. 11D).

The thalli tend to be larger than those of *A. levis* f. *levis* (15 cm vs 6 cm tall) with mature blades to 7 cm tall, 9 cm wide (Fig. 11A), extremely thin (< 1 mm thick), loosely woven, and translucent. Both forms have slender siphons (20–30 μm in diameter), the most slender of any Atlantic species. Those of f. *translucens,* however, are thin-walled and cylindrical to tortuous, while those of f. *levis* are thick-walled and often moniliform. Siphons of the growing margin (Fig. 11C) tend to be smaller than those that form the distinct cortex in f. *levis* (Fig. 10C). The rhizoids of the two forms (Figs 11E, 10E) appear to be identical. The blade of f. *translucens* differs from that of f. *levis* in its lack of a distinct, tightly knit outer cortex, rendering it so thin as to be translucent. Because thalli that are transitional with regard to all of these features can readily be found, we interpret the two forms as extremes in a continuum.

Avrainvillea longicaulis (Kützing) Murray et Boodle 1889: 70

f. *longicaulis*

Fig. 12

BASIONYM: *Rhipilia longicaulis* Kützing 1858: 13, pl. 28, II.

HOLOTYPE: Ad Antillas [Antigua], in the Sonder Herbarium (MEL!).

DISTRIBUTION: Florida, Bahamas, Jamaica, Antigua, Mexico, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Staniard Cay, Andros Island, 13 m deep on sand (*D&M Littler 11172* 16.viii.1986, US). Belize: Curlew Reef, 2 m deep on sand (*D&M Littler 19293* 27.vi.1989, US). Florida: Siegner Beach, Big Pine Key (*Killup 41781* 18.i.1952, US).

HABIT: Plants to 13 cm tall, yellow-green, solitary or in clusters of 3–5. Mature blades to 6 cm long, 10.5 cm wide (Fig. 12A), >3 mm thick, loosely woven with a coarse texture (granular when dry), spatulate to obovate, not zonate, with smooth growing margins and cuneate to truncate base. Stipe to 12 cm long, 13 mm in diameter, cylindrical or slightly flattened, not branched. Anchored by a large, vertical rhizoidal mass.

ANATOMY: Medullary siphons of blade mostly cylindrical but some moniliform, 35–60 μm in diameter, supradichotomal swellings and secondary constrictions seldom present (Fig. 12B); 10% of surface siphons tapering to 15–25 μm in diameter, moniliform, repeatedly divided, with rounded apices (Fig. 12B); dark siphons of growing margin 25–35 μm in diameter, light siphons

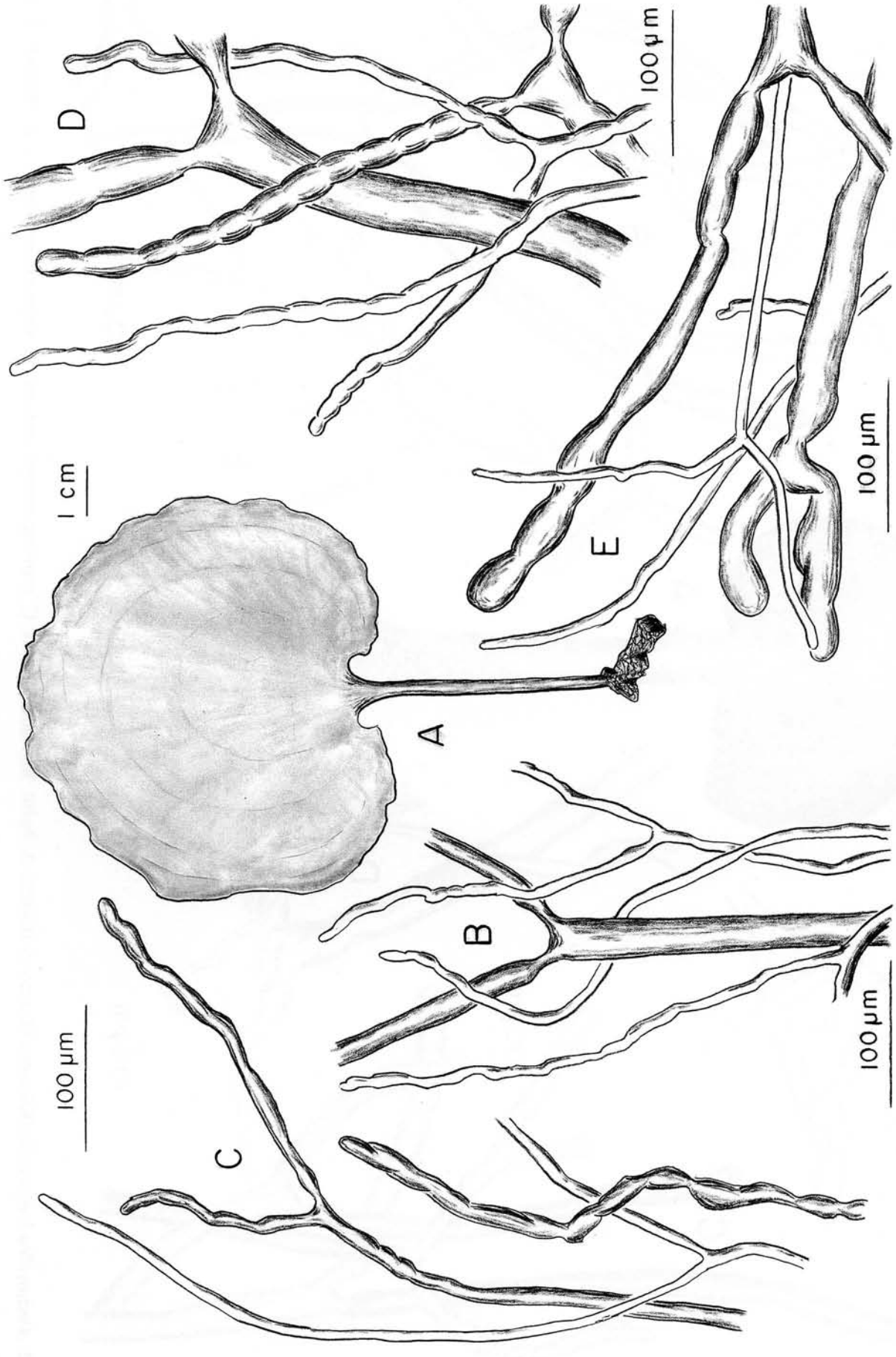

Fig. 11. *Avrainvillea levis* f. *translucens* f. nov. A, habit; B, large blade siphons intermixed with smaller blade siphons; C, growing margin siphons; D, larger stipe medullary siphon and tapered stipe cortical siphons; E, rhizoids.

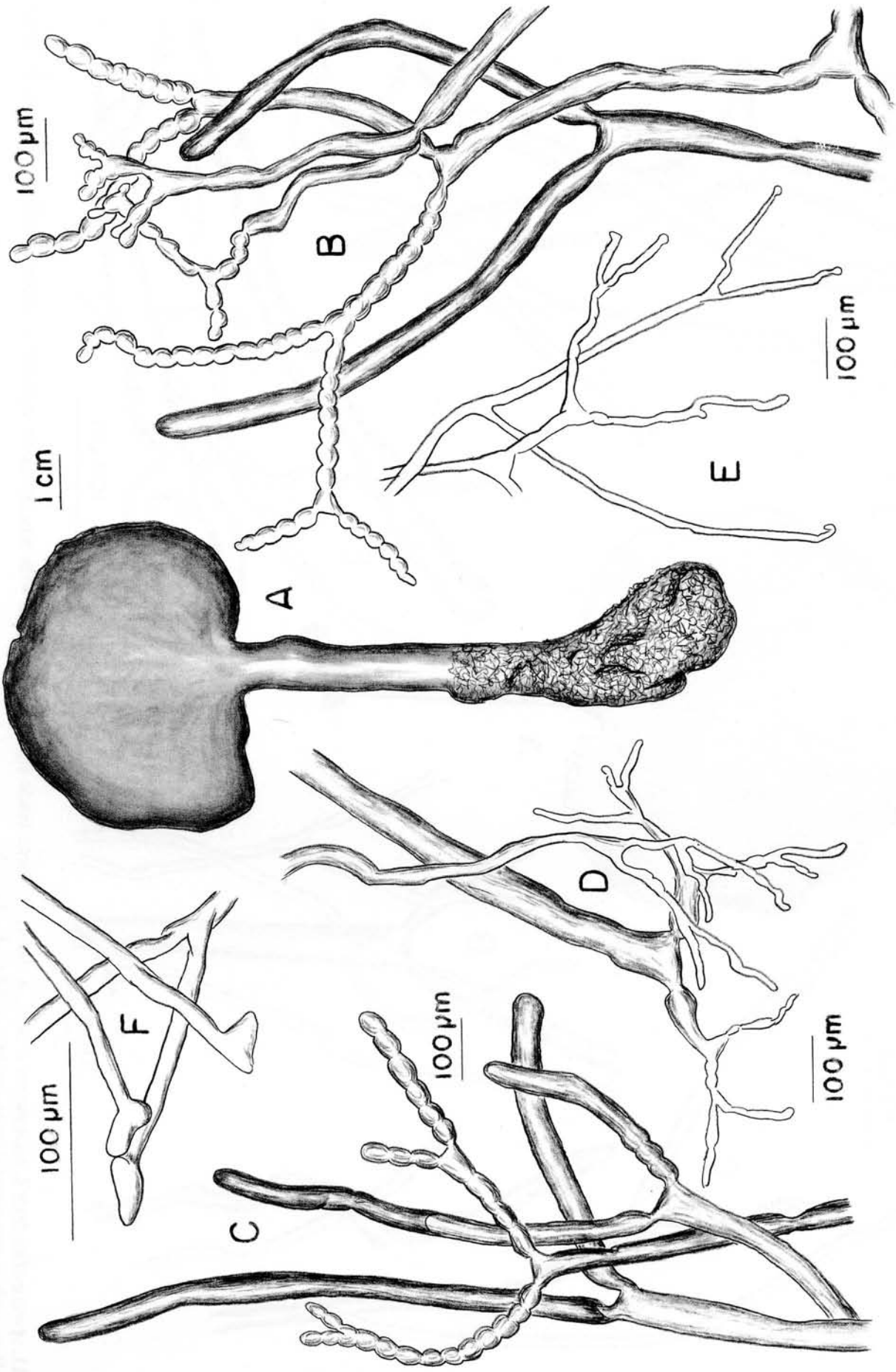

Fig. 12. *Avrainvillea longicaulis* (Kützing) Murray et Boodle. A, habit; B, blade siphons; C, growing margin siphons; D, stipe cortical siphons; E, rhizoids; F, rhizoid apices.

28–42 μm in diameter, both with rounded apices (Fig. 12C). Medullary siphons of stipe 38–46 μm in diameter, cylindrical; cortical siphons 8–12 μm in diameter, moniliform and/or tortuous (Fig. 12D). Rhizoids fine (5–10 μm in diameter), hyaline, irregular to cylindrical (Fig. 12E), terminating in expanded pads (Fig. 12F) or bulbous apices.

REMARKS: The blade of *Avrainvillea longicaulis* is broadly oval with a truncate lower margin (Fig. 12A), extremely thick and spongy, and with tapered moniliform siphons that form either no cortex (often only 10% of the surface siphons being tapered and moniliform) or an exceedingly thin, loosely woven, outer cortex. The thalli are typically anchored in open sandy or seagrass areas of shallow (1–4 m), pristine waters.

Avrainvillea longicaulis has had a long and confusing history as discussed by Gepp & Gepp (1911; as *A. sordida*) and Olsen-Stojkovich (1985; as *A. longicaulis*). Although these authors considered *A. longicaulis* to be conspecific with *A. levis,* our study of type specimens and field populations supports the recognition of both species. A comparison of the two is given under *A. levis. Avrainvillea mazei,* which Howe (1905, 1907) considered synonymous with *A. longicaulis,* is almost identical at the growing margin (where Howe indicated that he made his examination), but its blade is normally cuneate and has tapered moniliform siphons only in the extreme basal portion of the blade adjacent to the stipe.

Avrainvillea longicaulis (Kützing) Murray et Boodle

f. *laxa* f. nov.

Fig. 13

DESCRIPTION: Thalli erecti ad 30 cm longi gregarii, laminis obovatis leniter zonatis tenuibus (< 1 mm) laxissime intertextis base cuneatis vel leniter cordatis margine leviter lobatis vel laceratis, stipitis longis saepe ramosis; siphones laminalis medullares cylindrices in diametro 20–60 μm, corticales in partibus laminis 30% inferioribus hyalini leniter moniliformes vel tortuosi in diametro sensim 8–25 μm; siphones stipitatis medullares cylindrici in diametro ad 40 μm corticales moniliformes vel tortuosi in diametro 10–20 μm.

HOLOTYPE: Tobacco Range, Belize, in the upper creek channel at the northeastern mangrove island, 1 m deep on a fine organic silt bottom (*D&M Littler 19345* 19.vi.1989, US).

DISTRIBUTION: Florida, Bermuda, Cuba, Puerto Rico, Antigua, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bermuda: Walsingham Pond, Hamilton Island (*Bernatowicz 50–47* 9.xi.1950, US). Florida: Penicamp Park, Monroe County, Key Largo (*Diaz-Piferrer 1905* 17.vii.1976, US). Puerto Rico: La Parguera, Guayacan Island (*Norris 14999* 21.v.1987, US).

REMARKS: Thalli of *Avrainvillea longicaulis* f. *laxa* have an exceptionally long stipe (to 26 cm) and a blade that is thin, loosely woven at the margins and with a gracefully curving cuneate lower portion (Fig. 13A). Medullary siphons in mature blades are 40–60 μm in diameter and cylindrical (Fig. 13B). Surface siphons taper to 8 μm in diameter as in f. *longicaulis,* but only in the lower third of the blade (Fig. 13C). Siphons of the growing margin are cylindrical, often dark, and thick-walled with a diameter of 20–30 μm (Fig. 13D). *Avrainvillea longicaulis* f. *laxa* commonly grows in nutrient-rich areas such as the shallow waters (< 2 m) within interior lagoons of mangrove islands, while f. *longicaulis* grows in pristine seagrass habitats.

Originally, we believed that this unique form, without intergrades, was a separate species. However, its distinctive habitat and anatomical similarity to *A. longicaulis* f. *longicaulis* prompted us to conduct reciprocal transplant experiments. The results showed a clear pattern of interconvertibility between the two entities (Littler *et al.,* unpublished observations) justifying designation only at the level of forma.

The cylindrical siphons at the growing margin of *Avrainvillea longicaulis* f. *laxa* are almost identical to those of *A. mazei,* being darkly pigmented and narrower than the lighter, large siphons below. These two species differ, however, in that the distal portions of the siphons of *A. longicaulis* f. *laxa* are tapered and slightly moniliform and/or tortuous throughout the blade while those of *A. mazei* are neither tapered nor moniliform at the mid-blade, differentiation not appearing until the stipe–blade interface. This difference in surface siphons accounts for the smooth blade of *A. longicaulis* f. *laxa* and the coarse fibrous blade of *A. mazei.*

Avrainvillea mazei Murray et Boodle 1889: 70

Fig. 14

LECTOTYPE: Plage des Basses, Marie Galante (Grand Bourg), Guadeloupe (*Mazé 65* 21.ii.1870, BM!).

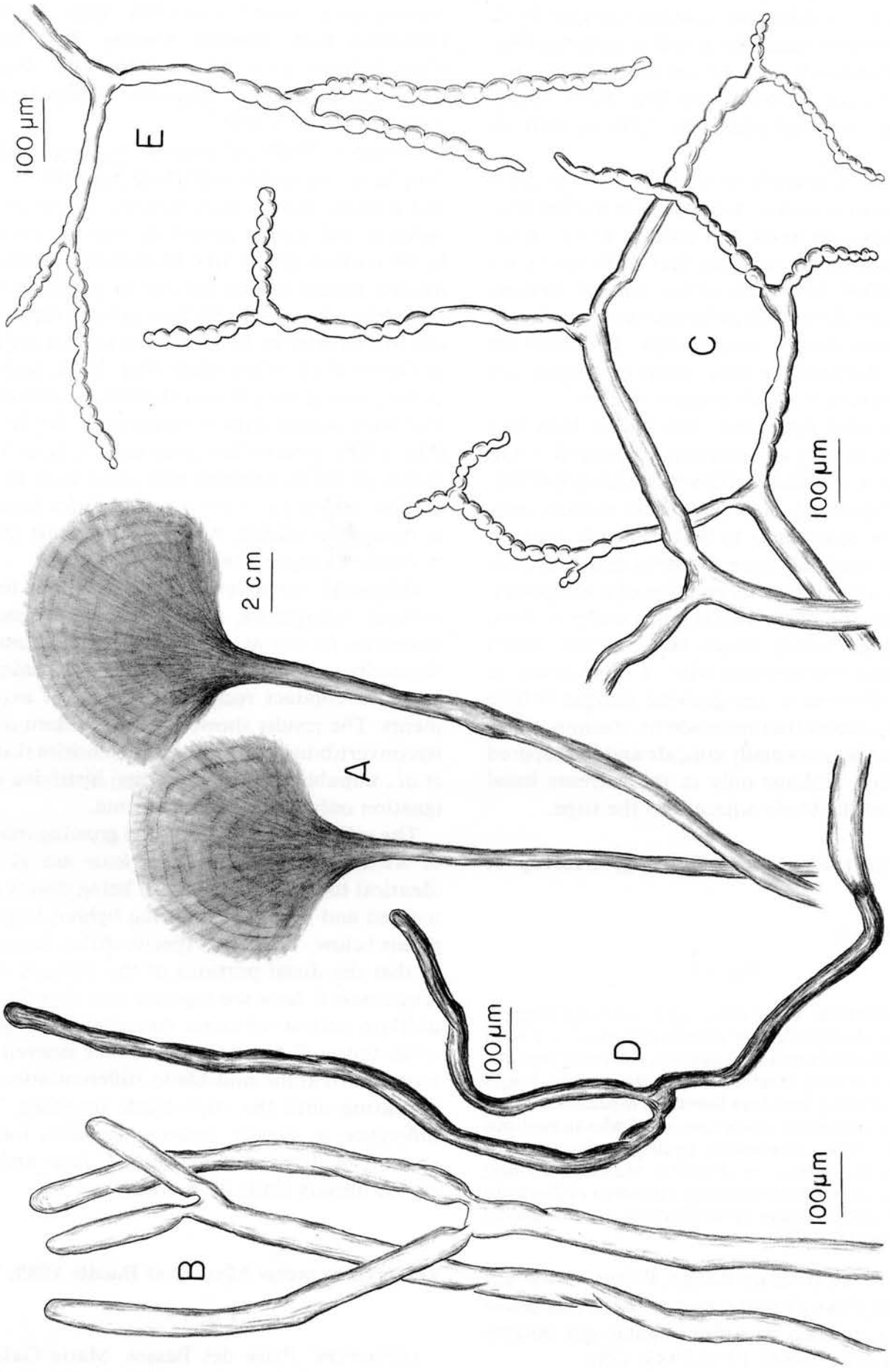

Fig. 13. *Avrainvillea longicaulis* f. *laxa* f. nov. A, habit; B, distal blade surface siphons; C, proximal blade surface siphons; D, growing margin siphon; E, stipe cortical siphon.

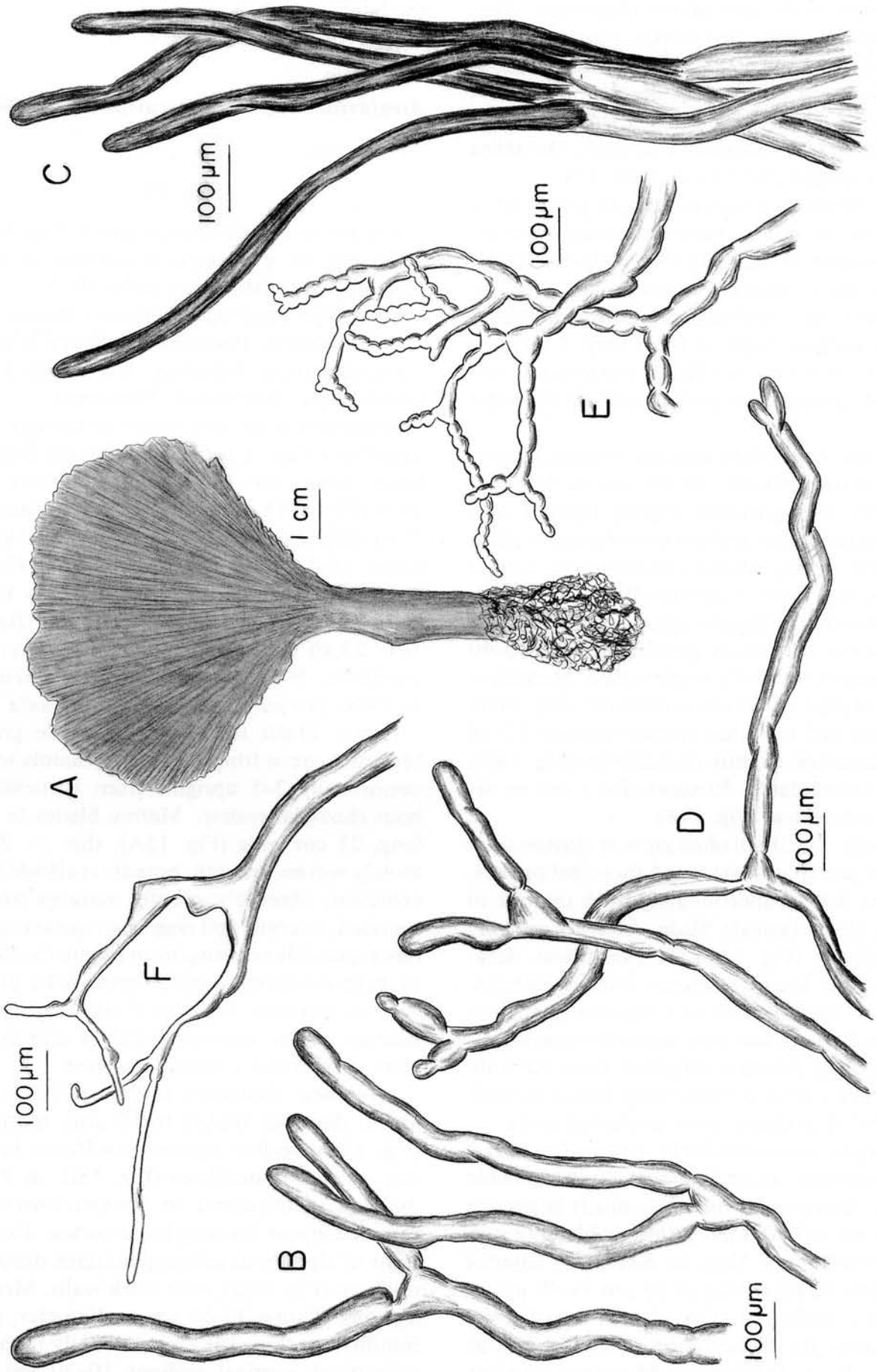

Fig. 14. *Avrainvillea mazei* Murray et Boodle. A, habit; B, blade siphons; C, growing margin siphons illustrating darkly pigmented slender apices; D, stipe medullary siphons; E, stipe cortical siphons; F, rhizoid.

DISTRIBUTION: Bermuda, Florida, Bahamas, Jamaica, Guadeloupe, Belize, Costa Rica.

REPRESENTATIVE SPECIMENS EXAMINED: Bermuda: Achilles Bay, St Georges Island (*Bernatowicz 53-420* 13.vi.1953, US). Florida: Content Keys, Monroe County, 5 m deep on sand-covered carbonate rock (*D&M Littler 19745a* 13.xii.1987, US). Mexico: Cozumel, Quintana Roo (*Hernández 294* 11.viii.1966, US).

HABIT: Thalli to 13 cm tall, bright green, often solitary or several in close proximity. Mature blades cuneate, to 7 cm tall, 9 cm wide (Fig. 14A), >2 mm thick, loosely woven, coarse, and fibrous, not zonate, with smooth or slightly ragged growing margins. Stipe to 8 cm long, 1.2 cm in diameter, cylindrical to slightly compressed, unbranched, anchored by a small conical rhizoidal base.

ANATOMY: Medullary siphons of blade brown, 50–60 μm (occasionally 40–80 μm) in diameter (Fig. 14B), strong-walled, slightly tapered, and deeply pigmented at actively growing apices only, cylindrical, rarely slightly moniliform and/or tortuous, supradichotomal swellings or secondary constrictions characteristically present above dichotomies; siphons of growing margin 30–40 μm diameter (Fig. 14C), thick-walled. Medullary siphons of stipe 55–70 μm in diameter (Fig. 14D), cylindrical and tortuous; surface siphons 12–18 μm in diameter, slightly moniliform (Fig. 14E), loosely consolidated. Rhizoids 8–12 μm in diameter, cylindrical (Fig. 14F).

REMARKS: The thalli often grow in clusters arising from partially intertwined rhizoidal masses. The stipe is disproportionately thick relative to the size of the cuneate blade. Actively growing blade siphons (Fig. 14C) are cylindrical, dark, and narrower than the mature interior siphons, which are thick-walled and frequently slightly tortuous. Both mature and immature siphons often have their contents shrunken from the wall. *Avrainvillea mazei* is commonly found in shallow (0.5–5.0 m deep), wave-protected areas.

The species most similar to *Avrainvillea mazei* is *A. sylvearleae,* which also has cylindrical blade siphons. However, *A. mazei* is much larger (13 cm vs 6 cm tall) and has a thicker blade (2 mm vs <1 mm thick). Also, its medullary siphons are slightly larger (mean of 56 μm vs 40 μm in diameter), darker, and usually with a distinct bulge above the dichotomies, a feature not as apparent in *A. sylvearleae.* Moreover, slightly moniliform surface siphons cover the entire stipe in *A. mazei,* but only the lower portion of the stipe in *A. sylvearleae.* The similarity of *Avrainvillea mazei* to *A. longicaulis* is discussed under the latter species.

Avrainvillea nigricans **Decaisne 1842: 108**

f. *nigricans*

Fig. 15

HOLOTYPE: Îles de Saintes près la Guadeloupe, 1842, leg. *M. d'Avrainville,* labelled as *Avrainvillea nigra* in Decaisne's script (PC!).

SYNONYM: *Fradelia fuliginosa* Chauvin 1842: 124. [HOLOTYPE: Pernambuco, Brazil (CN)].

DISTRIBUTION: Bahamas, US Virgin Islands, Guadeloupe, Martinique, Honduras.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Cave Cays, Exuma Chain, under rock overhang near low-water mark (*Howe 3982* 19.ii.1905, NY). Guadeloupe: Îles les Saintes, 1–15 m deep (*Bucher 1575* 22.viii.1985, US). Honduras: Media Luna Reef, Media Luna Cay, 10–20 m deep (*Hay 1172b* 24.v.1981, US), US Virgin Islands: Water Island, St Thomas (*Børgesen 1117* 23.xii.1905 *pro parte*; see also *Avrainvillea asarifolia,* NY); 30 m deep (*Børgesen 1171* 2.i.1906, *pro parte*; see also *A. asarifolia,* NY).

HABIT: Thalli to 30 cm tall, pale green to brownish-green fringed in black, mainly solitary, occasionally 2–5 uprights from vertically bulbous rhizoidal system. Mature blades to 15 cm long, 23 cm wide (Fig. 15A), thin (< 2 mm), loosely woven, smooth, broadly reniform to suborbicular, obscurely zonate; margins smoothly rounded, lacerate, and ragged or containing small lobes (possibly resulting from regrowth after having been wounded by herbivorous fish), base cordate to truncate. Stipe to 9 cm long, typically shorter, narrow (approximately 4 mm in diameter), cylindrical, seldom branched.

ANATOMY: Medullary siphons of blade 30–40 μm in diameter (rarely to 50 μm), moniliform (Fig. 15C); surface siphons 20–30 μm in diameter, deeply moniliform (Fig. 15B, to 70% reduction in diameter at constrictions), with rounded apices forming loose cortex; distal portions of siphons at growing margins deeply moniliform (Fig. 15D), with thick walls. Medullary siphons of stipe 30–60 μm in diameter, slightly moniliform (Fig. 15E), occasionally (about 5%) cylindrical; cortical siphons 10–20 μm in diameter, deeply moniliform (Fig. 15E). Rhizoids 40–50 μm in diameter, moniliform, tapering to

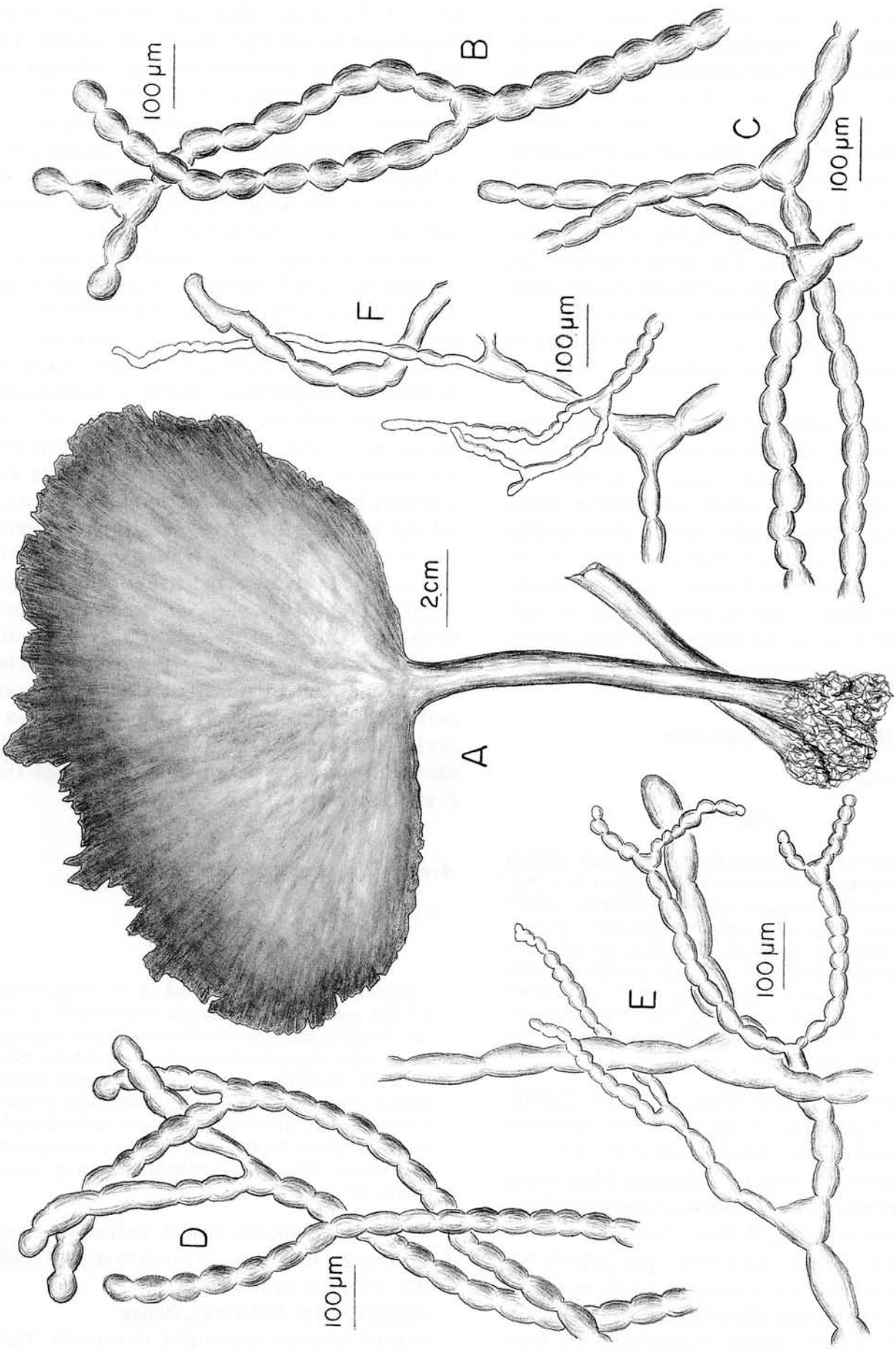

Fig. 15. *Avrainvillea nigricans* Decaisne. A, habit; B, blade cortical siphons; C, blade medullary siphons; D, growing margin siphons; E, large stipe medullary siphon and tapered stipe cortical siphon; F, rhizoids.

7–12 μm in diameter (Fig. 15F), few fine hyaline cylindrical apices.

REMARKS: At one time, all specimens of *Avrainvillea* with flabellate blades and moniliform blade siphons were assigned to *A. nigricans.* Howe (in Collins *et al.* 1908) was the first to recognize that several entities were involved. *Avrainvillea nigricans* f. *nigricans,* as revealed by the type specimen, has deeply to slightly moniliform siphons, those in the blade being 30–40 μm in diameter, tapering slightly at the surface to 20 μm in diameter. The surface siphons are entangled to form a loose cortex but can generally be separated easily by dissection. *Avrainvillea nigricans* f. *nigricans* grows in moderately deep to deep water (15–45 m) on sand-covered rock substrata.

Avrainvillea nigricans is a highly variable species with many different growth forms occurring as intergrades in a wide range of habitats. To describe this complex species adequately, therefore, we have designated as *formas* those entities in the myriad of shapes and sizes that are dependent upon specific habitats, such as interior mangrove lakes. There is a continuum of variation within all of the forms described herein, precluding their recognition as species.

Avrainvillea nigricans **Decaisne**

f. *floridana* f. nov.

Fig. 16

DESCRIPTION: Thalli erecti ad 9 cm longi solitarii, laminis cuneiformibus ezonatis crassibus (2–3 mm) base attenuatis, margine rotundatis laceratis, stipitis ad 2.5 cm longis ad 1 cm latis cylindricis raro ramosis; siphones laminalis medullosi moniliformes in diametro 32–50 μm corticalis profunde moniformes in diametro 32–50 μm; siphones stipitatis medullosi leniter moniliformes vel cylindrici in diametro 38–54 μm corticalis profunde moniliformes in diametro 28–42 μm.

HOLOTYPE: Content Keys, Monroe County, Florida, 2 m deep on sand-covered carbonate rock (*D&M Littler 19442* 15.xii.1987, US).

DISTRIBUTION: Florida, Bahamas, Martinique.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Bucaroon Bay, Wilson City, Great Abaco Island, 2.5 m deep (22.x.1969, US 26267); San Salvador Island, 2–3 m deep on sandy and rocky bottoms, calm water (*Booth, Lammert, Chichester A-43* ii.1973, SEH). Martinique: Pt Dunkerque, Ste Anne, 2 m deep on sand (*D&M Littler 11541* 17.vii.1986, US).

REMARKS: The siphons of *Avrainvillea nigricans* f. *floridana* are slightly to deeply moniliform. Those of the blade are 30–40 μm in diameter and do not taper toward the surface. The surface siphons, which do not fuse with one another or become entangled and thus do not form a distinct cortex, can be separated easily by dissection. *Avrainvillea nigricans* f. *floridana* grows in shallow to moderately deep waters (1–30 m) anchored in soft substrata rich in organic matter, often in the same habitats as *A. fulva.*

Avrainvillea nigricans f. *floridana* is most easily confused with f. *nigricans,* from which it differs in having a blade that is both thicker (> 2 mm) and coarser than the papery blade of f. *nigricans.* The blades of the two forms also differ in shape and appearance, that of f. *floridana* being cuneate and not zonate while that of f. *nigricans* often tends to be reniform (Fig. 15A) with a truncate to slightly cordate lower margin and a distinct black zonation. Anatomical differences are more subtle. In f. *floridana* the blade siphon size is quite uniform (30–40 μm in diameter, Fig. 16C) and shows less constriction of the surface siphons (Fig. 16B), while f. *nigricans* has slightly tapered, smaller surface siphons (< 30 μm and only occasionally reaching 40 μm in diameter) with deeper constrictions (70% reduction compared with approximately 46% reduction in f. *floridana*). Stipe and rhizoid siphons are virtually identical (compare siphons for: stipe, Figs 16E, F vs 15E; rhizoids, Figs 16G vs 15F).

Avrainvillea nigricans **Decaisne**

f. *parva* f. nov.

Fig. 17

DESCRIPTION: Thalli erecti ad 16 cm longi solitarii, laminis reniformibus ezonatis tenuibus (< 1 mm) base cordatis margine rotundatis laceratis, stipitis ad 9 cm longis angustis ad 4 mm latis cylindricis rariter ramosis; siphones laminalis medullares moniliformes in diametro 20–40 μm corticales profunde moniformes in diametro 20–40 μm; siphones stipitatis medullares leniter moniliformes vel cylindrici in diametro 30–60 μm corticales profunde moniliformes in diametro 10–20 μm.

HOLOTYPE: Tobacco Range, Belize, northwest fracture area, 6 m deep on mangrove peat (*D&M Littler 19302* 9.vi.1989, US).

DISTRIBUTION: Bahamas, Belize.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas, Staniard Cay, Andros Island, 5 m deep on sand (*D&M Littler 11167* 16.viii.1986, US). Be-

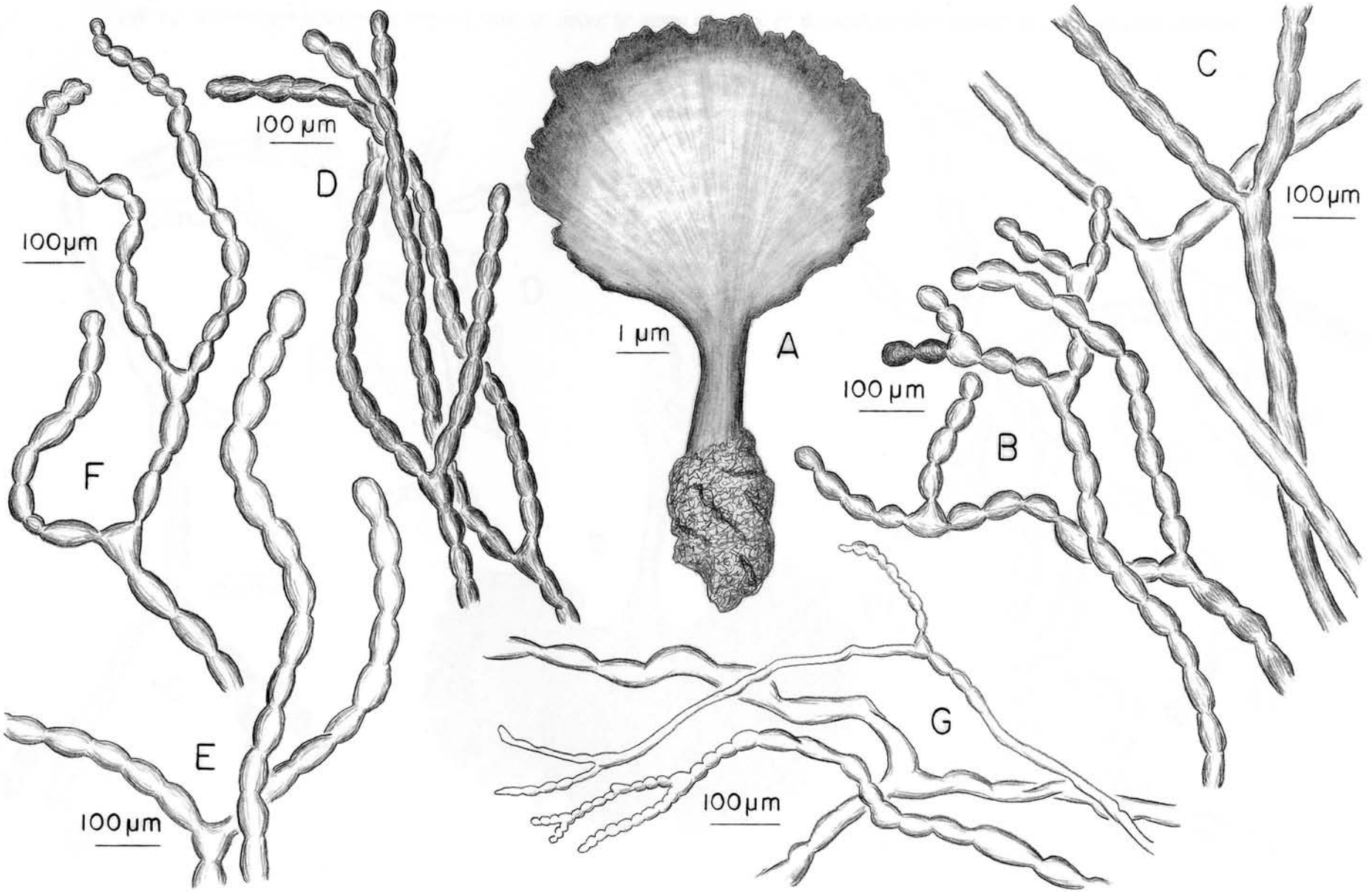

Fig. 16. *Avrainvillea nigricans* f. *floridana* f. nov. A, habit; B, blade cortical siphons; C, blade medullary siphons; D, growing margin siphons; E, medullary siphons; F, stipe cortical siphon; G, rhizoids.

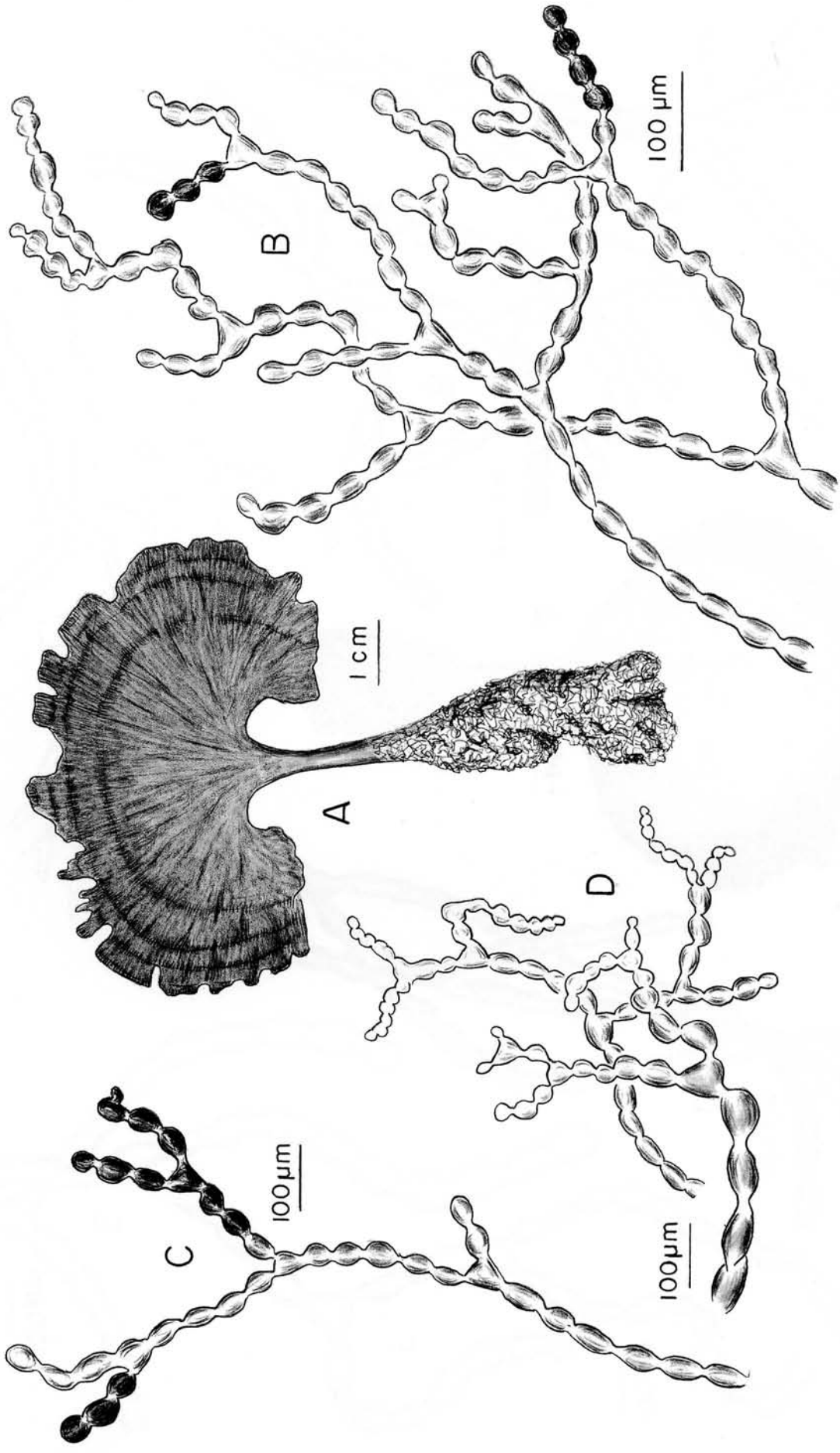

Fig. 17. *Avrainvillea nigricans* f. *parva* f. nov. A, habit; B, blade siphons; C, growing margin siphon; D, stipe cortical siphons.

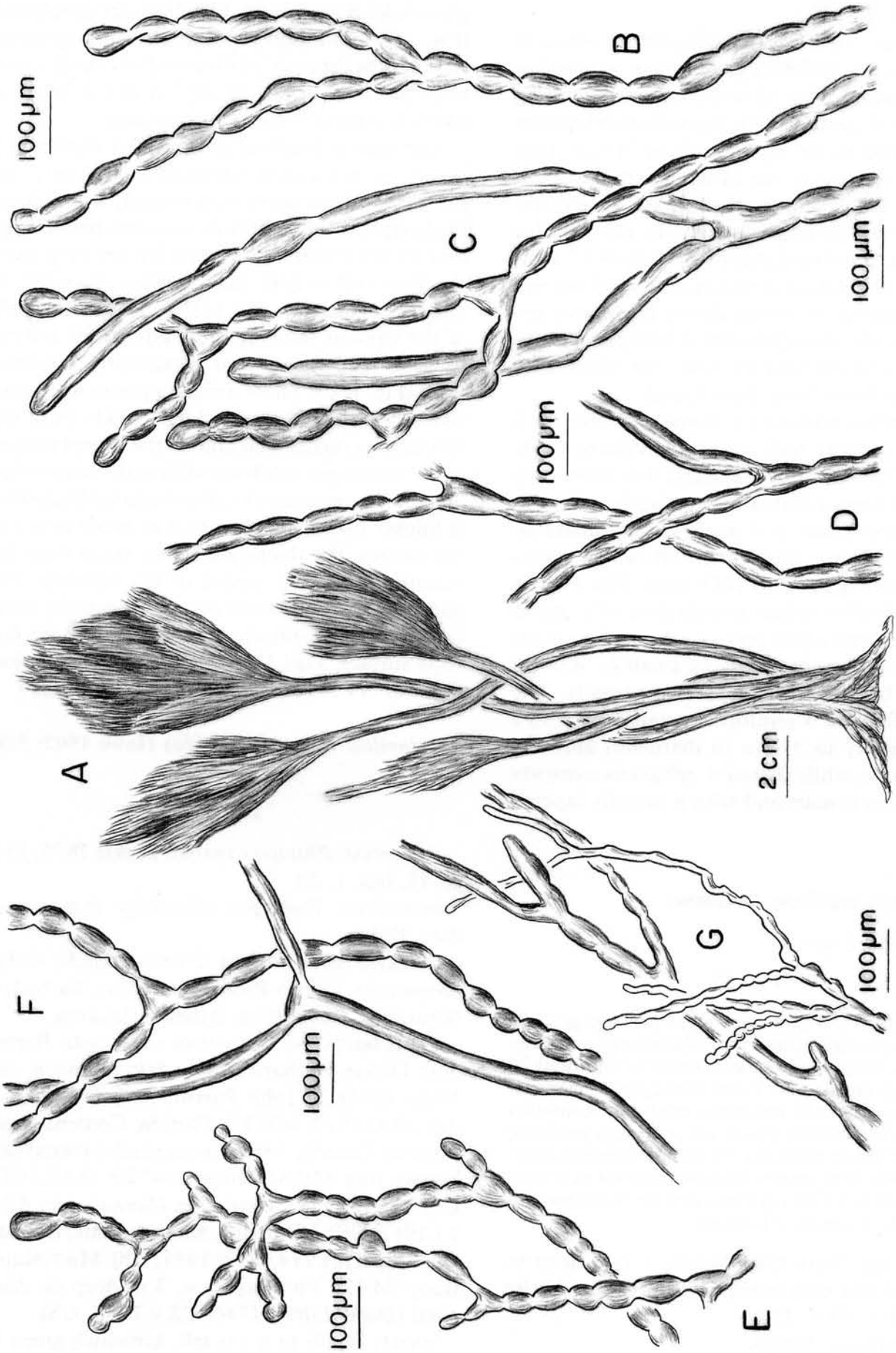

Fig. 18. *Avrainvillea nigricans* f. *spongiosa* f. nov. A, habit; B, growing margin siphon; C, blade cortical siphons showing moniliform shape occurring in 95% of the siphons and the cylindrical/moniliform shape occurring in only 5% of the siphons; D, blade medullary siphons; E, stipe cortical siphons; F, stipe medullary siphons; G, rhizoids.

lize: Tobacco Range, northwest fracture area, 6 m deep on mangrove peat (*D&M Littler 13290* 20.ii.1988, US).

REMARKS: *Avrainvillea nigricans* f. *parva* is small, solitary, and dark green, often outlined in blackish-green, this distinct coloration being caused by areas of darkly pigmented cytoplasm concentrated at the siphon apices. *Avrainvillea nigricans* f. *parva* is one of the few members of the genus displaying distinct darkened lines radiating from the stipe outward to the margins (Fig. 17A). It is found mostly in shallow (< 2 m) waters in population densities of several per m^2. Future material or manipulative taxonomic experiments may prove that these populations represent a separate species, since no intergrades with other forms have been found.

Avrainvillea nigricans f. *parva* is similar to f. *nigricans* in that both have moniliform blade siphons (30–40 μm in diameter) that taper only slightly to form a cortex that is tightly woven in f. *parva* and looser in f. *nigricans* (compare siphons for: blade surface, Figs 17B vs 16B; growing margin, Figs 17C vs 16D; stipe, Figs 17D vs 16E, F). Shallow-water populations of f. *parva* are often intermingled with *A. silvana.* The thalli of both entities are relatively small (*c.* 4.0–5.5 cm tall), but are easily separated visually. The blade of f. *parva* is reniform, zonate, and with a thin (typically to 3 mm in diameter) abruptly tapered stipe, while that of *A. silvana* is narrowly cuneate, not zonate, and with a broadly tapered stipe.

Avrainvillea nigricans Decaisne

f. *spongiosa* f. nov.

Fig. 18

DESCRIPTION: Thalli erecti ad 36 cm longi gregarii, laminis obovatis ezonatis crassiusculus (5 mm) base cuneatis margine rotundatis laceratis, stipitis ad 20 cm longis angustis ad 4 mm latis cylindricis rariter ramosis; siphones laminalis medullares moniliformes in diametro 20–40 μm corticales profunde moniformes in diametro 20–40 μm; siphones stipitatis medullares leniter moniliformes vel cylindrici in diametro 30–60 μm corticales profunde moniliformes in diametro 10–20 μm.

HOLOTYPE: Twin Cay, Belize, <1 m deep in mangrove lake with heavy siltation (*D&M Littler 21028* 13.vi.1991, US).

DISTRIBUTION: Belize.

SPECIMEN EXAMINED: Belize: Twin Cay (HOLOTYPE).

REMARKS: *Avrainvillea nigricans* f. *spongiosa* occurs in abundance in interior lakes of mangrove islands in Belize. The thalli are gregarious (Fig. 18A), tall, and olive green, often growing among other species of *Avrainvillea.* To date this form has been collected only in Belize but it is likely to have a broader distribution.

The siphon shape of *Avrainvillea nigricans* f. *spongiosa* is virtually identical to that in f. *nigricans,* both forms having strongly moniliform blade siphons of a uniform diameter between 30 and 40 μm (compare siphons for: growing margin, Figs 18B vs 15D; blade surface, Figs 18C vs 15B; blade interior, Figs 18D vs 15C). About 5% of the siphons forming the blade cortex are cylindrical with occasional moniliform constrictions (Fig. 18C). These unique siphons were consistently observed in this form. Aside from the similarities mentioned above, the morphologies of the blades are markedly different. *Avrainvillea nigricans* f. *spongiosa* has an elongated blade that is thicker (3–5 mm) than that of other forms of the species. The thickened blades result from the exceptionally loose weave of the siphons. The stipe and rhizome structure are essentially identical to that in f. *nigricans* (compare siphons for: stipe surface, Figs 18E vs 15E; siphon interior, Figs 18F vs 15E; rhizoids, Figs 19G vs 15F).

Avrainvillea rawsonii (Dickie) Howe 1907: 510, pl. 30

Fig. 19

BASIONYM: *Rhipilia rawsonii* Dickie 1875: 151, pl. 11, figs. 1, 20.

HOLOTYPE: Barbados (*Governor Rawson* no date, BM!).

DISTRIBUTION: Florida, Caicos Islands, Cuba, Hispaniola, Puerto Rico, Martinique, Barbados, Nicaragua, Costa Rica, Atlantic Panama.

REPRESENTATIVE SPECIMENS EXAMINED: Barbados: Dickie Herbarium, no date, *Rawson and Watts* (BM); St John Parish, Bath (*Taylor 72-215* 24.xi.1972, MICH). Florida: Content Keys, Monroe County, 5 m deep on sand-covered carbonate rock (*D&M Littler 194720* 13.xii.1987, US). Puerto Rico: Guajataca (*Bernatowicz 62-2* 1.i.1962, US). Nicaragua: Seranna Bank, reef flat, 1 m deep (*Hay 1141* 23.v.1981, US). Martinique: Buoy 'MA2', Pte Borgnesse, 3 m deep on dead coral (*D&M Littler 17160* 22.v.1989, US).

HABIT: Thalli to 6 cm tall, brownish green to black-green, gregarious in large mats. Mature blades knurled, knobbed or irregular in shallow

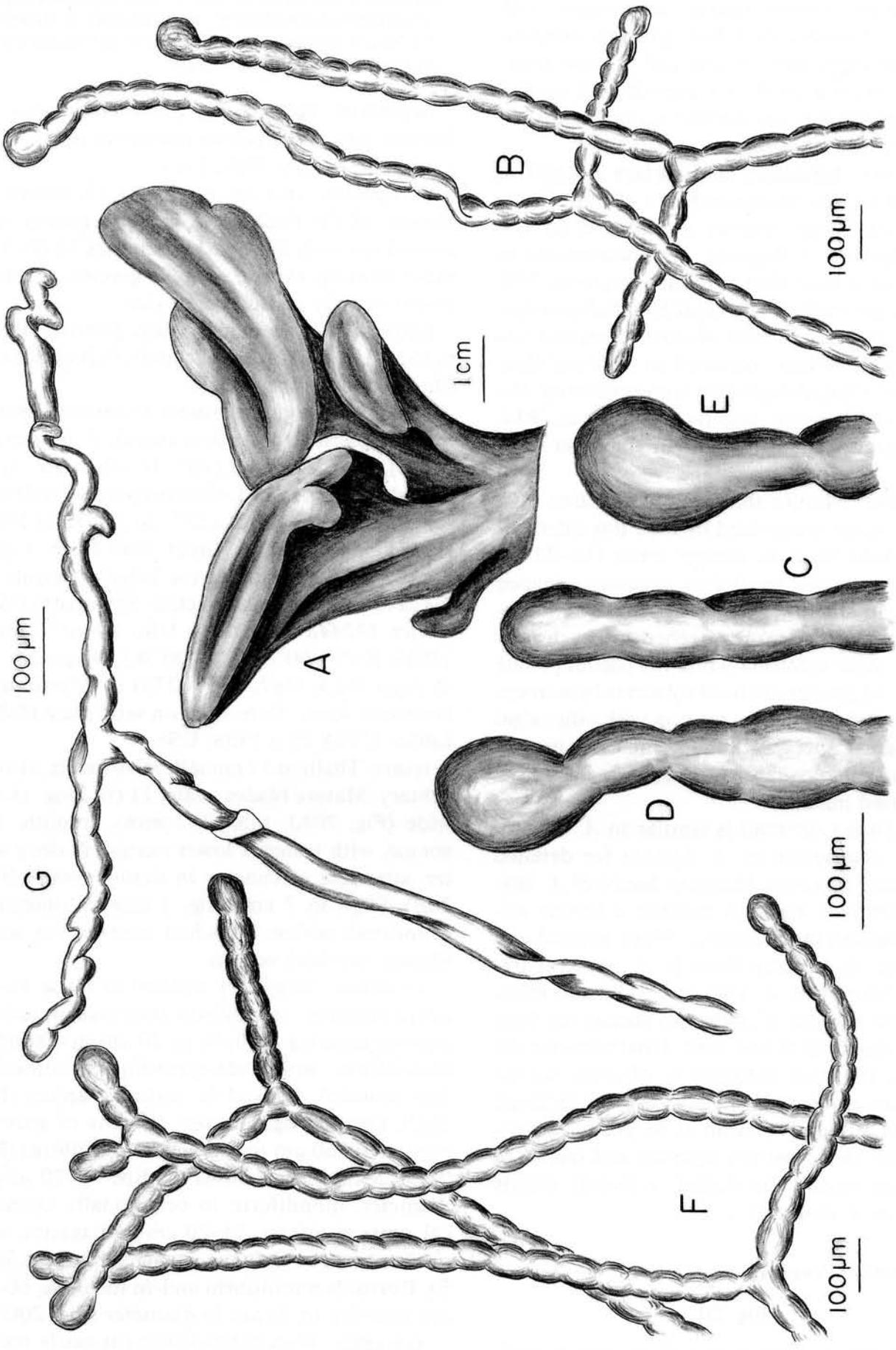

Fig. 19. *Avrainvillea rawsonii* (Dickie) Howe. A, habit; B, blade siphons; C, rounded siphon apex; D, and E, bulbous siphon apices; F, growing margin siphons; G, rhizoid.

water, thick-spatulate or pseudopeltate in deeper water (Fig. 19A), to 5 cm tall, 5 cm wide, 3 cm thick, loosely woven, spongy, not zonate, with smoothly rounded or lobed growing margins. Stipe tapering widely, cylindrical to oval, commonly branched (in deep water) or with no distinct stipe present (in shallow water), anchored by large prostrate rhizoidal mat.

ANATOMY: Medullary and surface siphons of blade 50–65 μm (occasionally to 80 μm) in diameter (Fig. 19B), slightly moniliform (*c.* 10–12% reduction in diameter at constrictions) to cylindrical in shrivelled or dried specimens, 50% rounded apices (Fig. 19C) and 50% bulbous apices (Fig. 19D, E), siphons of growing margin 50–80 μm in diameter, rounded or bulbous (Fig. 19F). Cortical and medullary siphons of stipe 38–75 μm in diameter, slightly moniliform. Rhizoids cylindrical, 38–66 μm in diameter (Fig. 19H).

REMARKS: Mature thalli of *Avrainvillea rawsonii* are easily recognized by their lop-sided, almost peltate form in deeper water (10–25 m) (Fig. 19A) or their knurled or irregularly shaped uprights in shallow water (< 1 m). The knob-like form tends to grow attached to beach rock or other solid substrata while the pseudopeltate form grows attached to hard substrata by a creeping rhizoidal mat in competition with other algal and seagrass species. Siphon walls are usually weak and often collapsed or appearing cylindrical in dried material.

Avrainvillea rawsonii is similar to *A. digitata* (see the description of *A. digitata* for detailed discussion); however, blades or knobs of *A. rawsonii* often fuse with one another, a feature seldom observed in *A. digitata.* When pressed and dried, the deep-water form of *A. rawsonii* frequently resembles *A. fulva* externally and internally. The siphons of these two species are both slightly moniliform and their distal portions are of nearly the same diameter (*c.* 60 μm), but the medullary siphons of *A. fulva* are much larger (mean of 101 μm vs mean of 56 μm in *A. rawsonii*) and show distinct tapering and increased branching toward the surface, a feature clearly lacking in *A. rawsonii.*

Avrainvillea silvana sp. nov.

Fig. 20

DESCRIPTION: Thalli erecti a 17 cm longi solitarii, laminis late ovatis ezonatis tenuibus (1–2 mm) base truncatis margine laceratis, haptero rhizoidealis fibroso; siphones laminales medullares moniliformes in diametro 45–70 μm corticales moniliformes vel tortuosi in diametro sensim 20 μm; siphones stipitis medullares moniliformes vel cylindrici in diametro 50–70 μm corticales moniliformes vel tortuosi saepe hyalini in diametro 15–20 μm.

HOLOTYPE: Tobacco Range, Belize, northwest fracture area, 1 m deep on mangrove peat (*D&M Littler 19348* 9.vi.1989, US!).

ETYMOLOGY: *Avrainvillea silvana* is named in honour of Dr Paul Silva who has greatly improved not only our own systematics works, but those of many others, with his precise, accurate and extremely instructive advice.

DISTRIBUTION: Bahamas, Cuba, Jamaica, Puerto Rico, US & UK Virgin Islands, St Barthélemy, Martinique, Belize, Brazil.

REPRESENTATIVE SPECIMENS EXAMINED: Bahamas: Staniard Cay, Andros Island, 5 m deep on sand (*D&M Littler 11167* 16.viii.1986, US); Grand Bahama Island, 42 m deep (collected from the Johnson-Sea-Link-1327, S134, 22.iii.1983, HBFH 5543). Belize: Great Blue Hole, Lighthouse Reef Atoll, under the ledge or mouth of the cave attached to a stalactite, 50 m deep (*D&M Littler 12244a* 21.v.1987, US). Brazil: Station 1701A [01°57′00″S, 37°46′00″W], Dragagem, 57 m deep (12.x.1967, SPF 027511). Martinique: Diamond Rock, 52 m deep on sand plain (*D&M Littler 17218* 23.v.1989, US).

HABIT: Thalli to 17 cm tall, olive-green, mostly solitary. Mature blades ovate, 11 cm long, 16 cm wide (Fig. 20A), thin (1–2 mm), smooth, not zonate, with truncate lower margin in deep water, attenuate or cuneate in shallow water (Fig. 20B). Stipe to 7 cm long, 7 mm in diameter, cylindrical, seldom branched, anchored by small fibrous rhizoidal system.

ANATOMY: Medullary siphons of blade 45–80 μm in diameter, moniliform, thin-walled; surface siphons tapering abruptly to 20 μm in diameter, moniliform, with wide-spreading dichotomies, and rounded, hooked or tortuous apices (Fig. 20C), forming tight cortex; siphons of growing margin 30–60 μm in diameter, moniliform (Fig. 20D). Medullary siphons of stipe 50–70 μm in diameter, moniliform to occasionally cylindrical; cortical siphons 15–20 μm in diameter, moniliform and/or tortuous, often hyaline (Fig. 20E, F). Rhizoids moniliform and/to tortuous, 60–80 μm tapering to 20 μm in diameter (Fig. 20G).

REMARKS: *Avrainvillea silvana* is easily recognizable by the distinctive lacerate margin of its blade. Occasionally the invaginations result in a

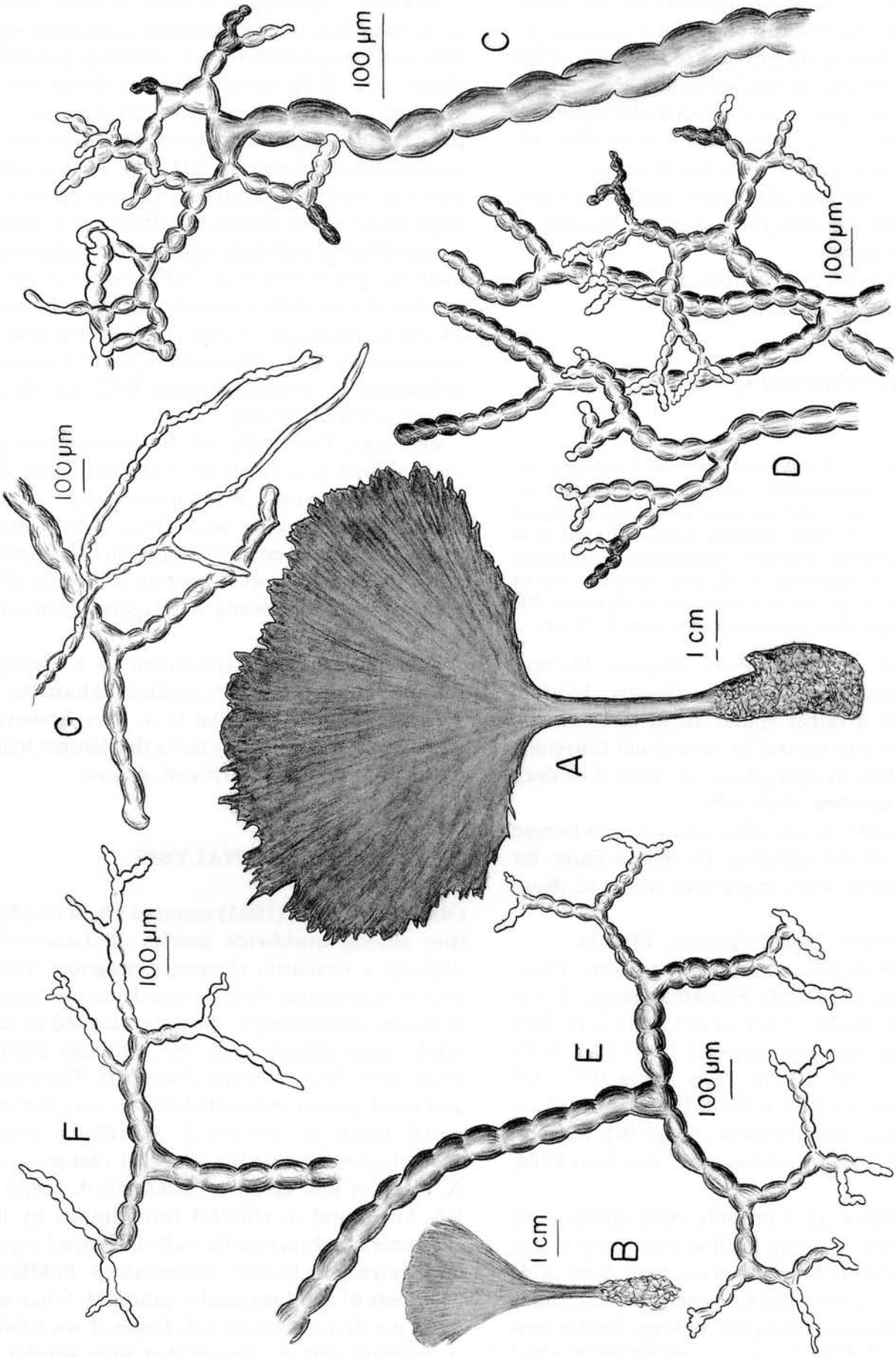

Fig. 20. *Avrainvillea silvana* sp. nov. A, habit of mature deep-water plant; B, habit of mature shallow-water plant; C, blade siphon depicting larger moniliform medullary siphon with abrupt and rapid taper and increased branching at cortex; D, growing margin siphons; E, upper stipe siphon; F, lower stipe siphon illustrating elongated apices that become rhizoids; G, rhizoids.

ragged margin of strap-shaped proliferations [*Norris 17037* (US), *Norris 16954* (US)]. The consistently moniliform siphons of the blade covered by a tightly knit cortex that appears immediately behind the growing margin (Fig. 20D) are characteristic of this species. The cortex of the stipe is so tightly intertwined that it is difficult to separate during dissection. *Avrainvillea silvana* is found over a wide depth range (1–117 m) on either deep sand plains or shallow, shaded, nutrient-rich habitats such as in the vicinity of mangrove islands.

The similarity of *A. silvana* to *A. fulva* is discussed under the latter.

***Avrainvillea sylvearleae* sp. nov.**

Fig. 21

DESCRIPTION: Thalli erecti parvi ad 6 cm longi solitarii vel approximati, laminis orbicularibus vel obovatis zonatis base truncatis vel cuneatis margine integris vel laceratis, haptero rhizoidealis parvo et denso; siphones laminales medullares et corticales cylindrici in diametro 32–48 μm; siphones stipitis cylindrici vel leniter moniliformes in diametro 40–50 μm in partibus proximalibis sensim 8–14 μm.

HOLOTYPE: Wilson's Pier, Alligator Harbor, Saint Teresa Beach, Franklin County, Florida, mixed with a rather sparse stand of *Thalassia testudinum* interrupted by occasional limestone rocks 60–100 m from shore, on rock 2 m deep (*Earle* no number 1962, US).

ETYMOLOGY: *Avrainvillea sylvearleae* is named in honour of the collector, Dr Sylvia Earle, for her pioneering work in gaining access to deep-sea biotas.

DISTRIBUTION: North Carolina, Florida.

REPRESENTATIVE SPECIMENS EXAMINED: Florida: Saint Teresa Beach, Franklin County, 1.5 m deep (*Roth St-20-67* 5.vii.1967, US); 2 m deep on sand and rock bottom (*Roth Fl-57* 20.v.1975; 14.x.1976, US); 1.6 m deep (25.ix.1977, US 25319; *Roth Fl-34* 4.x.1980, US). North Carolina: Onslow Bay [34°19'N, 76°53'W], Carteret County, 29 m deep (*Schneider 2946* 3.vii.1984, MICH).

HABIT: Plants to 6 cm tall, dark green, most often solitary or living in close proximity to one another. Mature blades to 5 cm long, 5 cm wide (Fig. 21A), 1 mm thick, loosely woven, finely fibrous, orbicular to slightly oblong, faintly zonate, with somewhat lacerate growing margins and truncate to cuneate base. Stipe to 2 cm long (more commonly 1 cm), 2–5 mm in diameter, cylindrical, unbranched, anchored by small, dense, pyramidal rhizoidal mass.

ANATOMY: Medullary siphons of blade 32–50 μm in diameter, often subparallel, cylindrical with thin walls, supradichotomal swellings generally absent (Fig. 21B); surface siphons 40–48 μm in diameter, cylindrical, with rounded apices; siphons of growing margin 44–60 μm in diameter, with rounded apices (Fig. 21C, D), a few slightly bulbous. Medullary siphons of upper portion of stipe 40–50 μm in diameter, cylindrical to slightly moniliform, with little differentiation between medulla and cortex (Fig. 21E); cortex of lower portion of stipe differentiated, surface siphons 8–14 μm in diameter, slightly moniliform and/or tortuous (Fig. 21F). Rhizoids 85 μm in diameter, cylindrical to tortuous, apices 8–12 μm in diameter, cylindrical (Fig. 21G).

REMARKS: The thallus of *Avrainvillea sylvearleae* consists of a small (to 6 cm tall), thin, orbicular blade with a short narrow stipe atop a small conical rhizoidal mass (Fig. 21A). It has a limited but persistent distribution in more northern latitudes than other species of *Avrainvillea* and is found commonly in seagrass communities.

The similarity of *A. sylvearleae* to *A. mazei* is discussed under the latter species. Externally, *A. sylvearleae* appears similar to *A. levis*; however, *A. sylvearleae* completely lacks the distinct blade cortex that is characteristic of *A. levis*.

PHYLOGENETIC ANALYSIS

Olsen-Stojkovich (1985) assessed phenetic affinities among worldwide species of *Avrainvillea* utilizing a similarity clustering program. Three major assemblages were revealed and one smaller cluster. Macroscopic characters tended to correlate more closely with the resultant assemblages than did anatomical characters. The largest and most closely associated cluster was the 'obscura' group [*A. obscura* J. Agardh, *A. erecta* (Berkeley) A. Gepp et E.S. Gepp, *A. clavatiramea* A. Gepp et E.S. Gepp, *A. gardineri* A. Gepp et E.S. Gepp and *A. elliottii*] being linked by the character of solitary thalli, well-developed stipes, and extensive buried rhizomatous holdfasts. Members of the 'longicaulis' group (*A. longicaulis, A. pacifica* A. Gepp et E.S. Gepp, *A. asarifolia, A. lacerata* and *A. amadelpha*) were similar in their well-developed branched stipes and emergent holdfasts; however, the microscopic char-

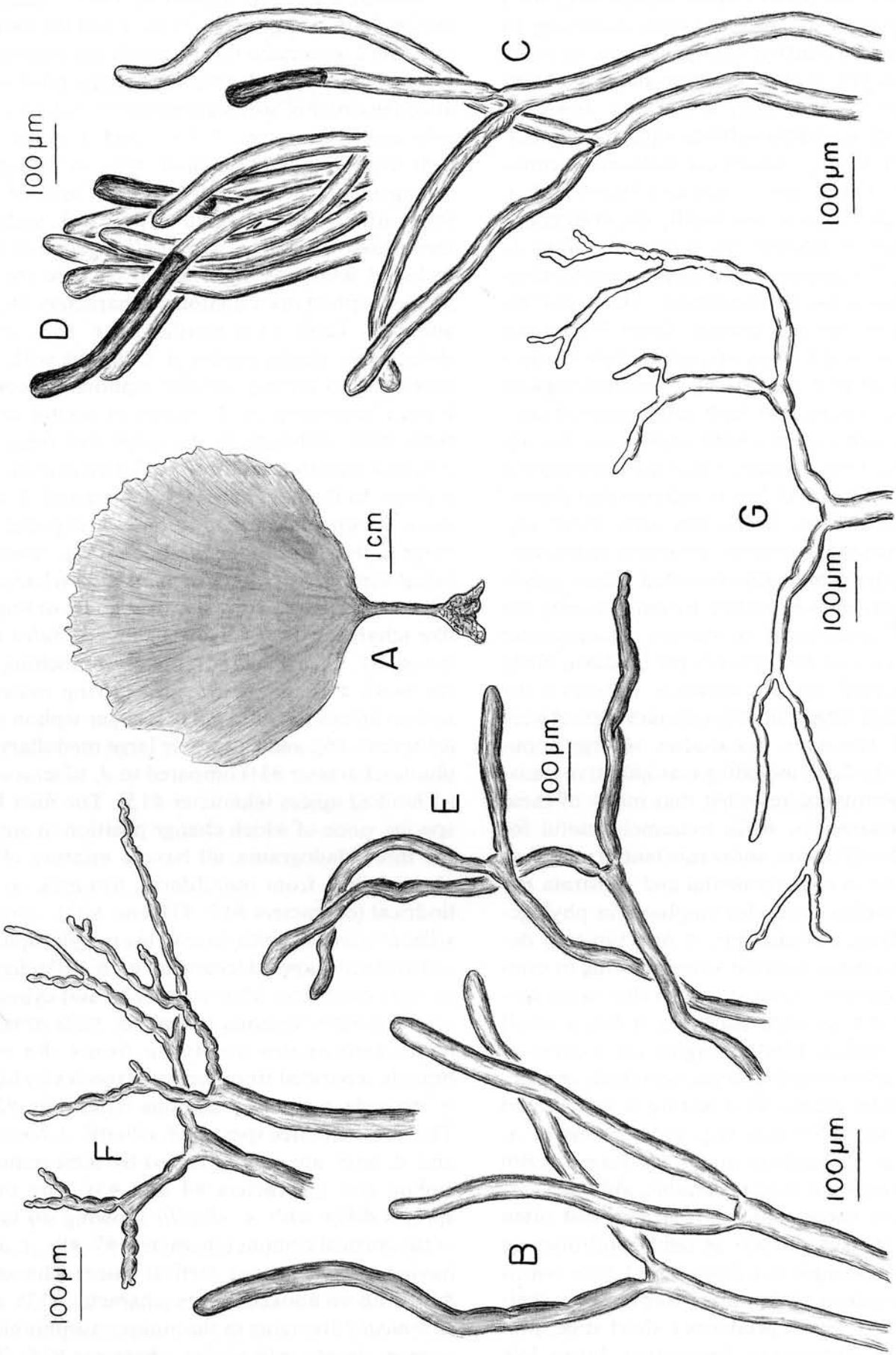

Fig. 21. *Avrainvillea sylvearleae* sp. nov. A, habit; B, blade siphons; C, and D, growing margin siphons; E, upper stipe siphons; F, lower stipe siphons; G, rhizoid.

acters tended to produce inconsistencies. For example, the 'nigricans' group (*A. nigricans, A. mazei* and *A. rawsonii*) was characterized by dark spongiose thalli characteristically occurring in patches with extensive emergent mats as holdfasts. However, the blade siphon shape confused this cluster with *A. nigricans* and *A. rawsonii,* both having moniliform blade siphons, while *A. mazei* has strictly cylindrical siphons. A minicluster of *A. riukiuensis* (Dickie) Howe and *A. hollenbergii* Trono was linked by the presence of small siphon diameters and finally, *A. ridleyi* A. Gepp et E.S. Gepp formed a single-member cluster that was remotely connected to both the 'nigricans' and 'obscura' groups. Olsen-Stojkovich (1985) also used subsets of separate microscopic (anatomical) and macroscopic (morphological) characters, stating that both sets produced similar clustering patterns with only a few species moving to other clusters when the microscopic characters were used. She concluded that the external macroscopic characters were more important than the internal microscopic characters.

The cladistic analysis presented herein represents a significant departure by emphasizing the utility of anatomical characters. Macroscopic features (i.e. number of stipes per holdfast, blade thickness, blade texture, zonation, features of the margin, stipe length, holdfast characteristics) were also used. However, our studies of large populations in the field, including manipulative transplant experiments, revealed that many of these external characters, while extremely useful for general identification, show substantial variation in response to environmental and substrata parameters which precludes emphasis in phylogenetic analysis. For example, *A. levis* typically develops a bulbous holdfast when growing in sand or soft sediment; however, when this same species is found on hard substrata it has a small conical holdfast. Blade margins are extremely variable, often rounded in younger thalli and lacerate in older plants. This feature is also altered with habitat differences (e.g. loose forms of *A. longicaulis, A. asarifolia,* and *A. nigricans* in calm waters). Length of stipe is variable, although certain species show some consistency, and often depends on factors such as light conditions or depth. One example is *A. longicaulis* f. *laxa,* which usually develops a long stipe except in very shallow waters, where it produces a short stipe, presumably in response to desiccation during low water. In marked contrast, the internal anatomical characters have proven to be relatively conservative and show little variation as a function of habitat.

The PAUP analysis (Swofford 1989), utilizing the 24 characters given in Table 1 and the matrix in Table 2, generated three equally parsimonious trees, all similar with only inconsequential variations in order of species placement. *Avrainvillea sylvearleae, A. mazei, A. hayi,* and *A. geppii* appear at the bases of all three trees in the same arrangement depicted in Fig. 22. Three of the four initial species have cylindrical siphons throughout the blade. *Avrainvillea geppii* is also included with this basal group because its expanded siphon apex anatomy (characters #8, #9 and #11, Table 1) is similar to *A. hayi,* even though one might expect it to group with the other species having variable siphons. The next branch consisting of *A. nigricans* occurs in all three trees, although in the other two trees the position is shifted slightly (see dotted lines) tying it closer to the next pair, *A. rawsonii* and *A. digitata. Avrainvillea rawsonii* and *A. digitata* diverge in the shape of the thallus, with *A. rawsonii* being somewhat peltate or knob-like (character #3) and *A. digitata* consistently digitate or finger-like (character #2). All trees show *A. fulva* followed by *A. silvana* individually branching off the main axis due to *A. fulva* having rounded siphon apices (character #14), larger siphon size (character #6), and extremely large medullary siphons (character #5) compared to *A. silvana* with its hooked apices (character #13). The final five species, none of which change position in any of the three cladograms, all have a mixture of siphon shapes, from moniliform, tortuous, to cylindrical (characters #17, #18 and #21). *Avrainvillea longicaulis,* with its growing margin siphons not distinctly tapered (character #10), little change in their diameters (character #12), and cylindrical medullary siphons (character #22) appears next. *Avrainvillea asarifolia* forms the next branch, separated from the basal species by highly variable medullary siphons (character #20). The terminal three species, *A. elliottii, A. fenicalii* and *A. levis,* are closely linked by their reduced siphon size (characters #4 and #5). The three species differ with *A. elliottii* showing no taper of the cortical siphons (characters #7, #9), *A. levis* having solely rounded cortical apices (character #14) with no hooked apices (character #13), and *A. fenicalii* diverging in the autapomorphic character of deeply split blades (character #23). The consistency index for the entire tree is rather low at CI 0.45 and if one examines trees one step

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

0. Upright siphons free and unconsolidated (0); upright siphons consolidated into some distinct shape (1) [Autapomorphy for outgroup].
1. Upright other than flattened blade (0); upright flattened blade (1) [CI = 1.00].
2. Upright digitate (0); upright other than digitate (1) [Autapomorphy].
3. Upright peltate (0); upright other than peltate (1) [Autapomorphy].
4. Medullary siphons generally <35 μm in diameter (0); medullary siphons generally >35 μm in diameter (1) [CI = 0.50].
5. Medullary siphons other than 30–60 μm in diameter (0); medullary siphons primarily 30–60 μm in diameter (1) [CI = 0.25].
6. Medullary siphons 50–140 μm in diameter (0); medullary siphons <50 μm in diameter (1) [CI = 0.50].
7. Cortical siphons do not have a greater than 50% taper (0); cortical siphons have a greater than 50% taper (1) [CI = 0.50].
8. Cortical siphons not expanded (0); cortical siphons expanded (1)—this feature is not to be confused with bulbous apices [CI = 1.00].
9. Cortical siphons show no or little change in diameter (0); cortical siphons show major change in diameter (1) [CI = 0.33].
10. Siphons of growing margin not distinctly tapered (0); siphons of growing margin distinctly tapered (1) [CI = 0.50].
11. Siphons of growing margin not expanded (0); siphons of growing margin clearly expanded (1) [CI = 1.00].
12. Siphons of growing margin showing little or no change in diameter (0); siphons of the growing margin showing major change in diameter (1) [CI = 0.50].
13. Cortical apices of siphons other than tortuous or hooked in shape (0); cortical apices of the siphons tortuous, often hooked in shape (1) [CI = 0.50].
14. Cortical apices solely rounded (0); cortical apices other than rounded (1) [CI = 0.33].
15. Cortical apices of siphons never or seldom bulbous (0); over 25% of apices of cortical siphons bulbous (1) [CI = 1.00].
16. Cortical siphons not deeply (< 50% reduction) moniliform (0); cortical siphons deeply (> 50% reduction) moniliform (1) [CI = 1.00].
17. Cortical siphons not solely moniliform (0); cortical siphons solely moniliform (1) [CI = 0.50].
18. Cortical siphons highly variable, ranging from moniliform, tortuous, to cylindrical (0); cortical siphons consistently moniliform or cylindrical (1) [CI = 0.50].
19. Cortical siphons solely cylindrical (0); cortical siphons other than cylindrical (1) [CI = 0.50].
20. Medullary siphons highly variable from moniliform, tortuous, to cylindrical (0); medullary siphons not highly variable, consistently uniform (1) [CI = 0.33].
21. Medullary siphons <90% moniliform (0); medullary siphons >90% moniliform (1) [CI = 0.50].
22. Medullary siphons <90% cylindrical (0); medullary siphons >90% cylindrical (1) [CI = 0.33].
23. Outer margin not deeply and abundantly lobed (0); outer margin incisions with greater than a 50% depth proximally for the numerous lobes (1) [Autapomorphy].

longer many of the nodes collapse, indicating the ambiguity and overlap of many of the entities. This ambiguity of key characteristics throughout the genus is why it has been and will continue to be a taxonomically difficult group. The high degree of morphological plasticity is reflected in the large number of taxonomic forms which are required to clarify the systematics of the genus. In interpreting the overall pattern of the cladogram, the species do group, to a limited extent, based on the unifying character of siphon shape. Thus, one would surmise that this character has been significant in the evolution of the genus.

ECOLOGICAL ADAPTATIONS

Sufficient material, representing a broad spectrum of anatomical forms and habitats, has been examined to enable us to make limited correlations concerning ecological adaptations. Although more than 1500 herbarium specimens and countless field populations were examined, little evidence of large herbivore damage was apparent. Most species of *Avrainvillea* occur in areas of relatively low current and wave energy. An effective strategy for avoiding predation is to grow in environments lacking three-dimensional structure that could serve as shelter for grazers (i.e. refugia escapes *sensu* Littler & Littler 1988). Nearly all *Avrainvillea* populations grow in deep water or on sand plains, in seagrass beds, mangrove lakes, or vertical reef faces; habitats that do not provide large grazers protection from their carnivorous predators. For example, in deeper waters *A. asarifolia* often occurs in open sand pockets, whereas, in the shallow reef environment, this same species grows exclusively in cracks and crevices where herbivorous fish would find it difficult to locate and awkward to graze. By contrast, *A. longicaulis,* a species found in shallow open sand or seagrass (*Thalassia testudinum*) beds, is chemically defended from reef fish (Hay *et al.* 1990) by the presence of avrainvilleol, a brominated diphenylmethane deriva-

Table 2. Matrix of characters from which the cladogram (Fig. 22) was derived (character absent = 9). CHL, *Chlorodesmis comosa* (outgroup); RAW, *Avrainvillea rawsonii*; DIG, *A. digitata*; NIG, *A. nigricans*; FUL, *A. fulva*; SIL, *A. silvana*; MAZ, *A. mazei*; SYL, *A. sylvearleae*; HAY, *A. hayi*; LON, *A. longicaulis*; ELL, *A. elliottii*; FEN, *A. fenicalii*; ASA, *A. asarifolia*; LEV, *A. levis*; GEP, *A. geppii*. Character numbers as in Table 1. * = autapomorphic character

	Characters[1]																							
Taxa	0 *	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16 *	17	18	19	20	21	22	23 *
CHL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
RAW	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0
DIG	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0
NIG	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0
FUL	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0
SIL	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	1	0	1	1	1	0	0
MAZ	1	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0
SYL	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
HAY	1	1	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0
LON	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	1	1	1	0	1	0
ELL	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
FEN	1	1	1	1	0	1	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1
ASA	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0
LEV	1	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
GEP	1	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0

[1] Characters are explained in Table 1.

tive (Sun *et al.* 1983). Although *A. longicaulis* is chemically resistant to fish predation, at the same time it constitutes the exclusive diet for the ascoglossan gastropod *Costasiella ocellifera* and the crab *Thersandrus compressus* (Hay *et al.* 1990). The gastropod sequesters avrainvilleol from its host and uses the compound as an effective defence against predatory fish. The crab, however, does not appropriate avrainvilleol but is camouflaged when on *Avrainvillea* by being identical in colour and texture, and thus avoids predation. To date, *A. longicaulis* is the only member of the genus to show interesting secondary chemistry, which may reflect a predominance of escape strategies in the genus. However, natural product surveys for western Atlantic species of *Avrain-*

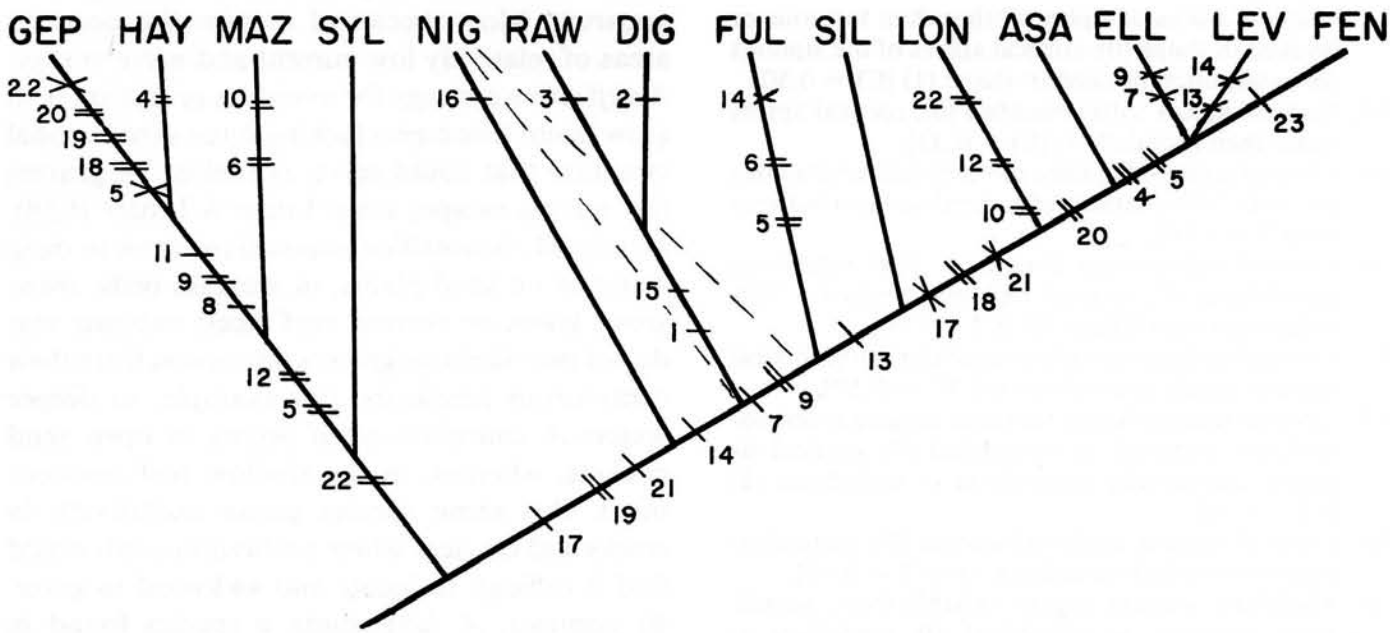

Fig. 22. Representative cladogram depicting phylogenetic relationships among Caribbean species of *Avrainvillea*. Two other nearly identical trees were produced, differing only in the placement of *A. nigricans* (other placements shown by dotted lines). *Chlorodesmis comosa* is the designated outgroup. 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.

villea have been hampered by the lack of an adequate taxonomy. We anticipate that the present treatment will facilitate more accurate chemical screening and stimulate taxonomically accurate ecological studies.

A process possibly related to defence against herbivory is the entrapment of silt- and sand-sized particles of carbonate among the siphons of those species of *Avrainvillea* that possess large siphons and lack a well-formed cortex. Presumably, such inorganic particles could lower palatability and digestibility, particularly in the case of the smaller grazing invertebrates. There is a clear positive correlation between the abundance of large, strongly moniliform siphons and the degree of sediment accumulation. We hypothesize that the moniliform siphon anatomy produces conduit-like passages and represents an adaptation for increasing seawater circulation throughout the thallus. Sediment accumulation is a result of the associated transport/entrainment processes. This leads to the question of why epiphytic algal spores, transported by these same hydrodynamic processes, do not become entrapped and germinate to overgrow the host thalli. We speculate that the enigmatic paucity of epiphytes on healthy *Avrainvillea* could reasonably be a result, in part, of allelopathy or the removal of epiphytes by grazing invertebrates (e.g. crustaceans). An interesting additional hypothesis which we are testing is that *Avrainvillea* and some other Bryopsidales (e.g. *Penicillus, Udotea, Cladocephalus*), by means of cytoplasmic streaming that is unimpeded by crosswalls in siphons, possess a unique ability to translocate resources rapidly from an older epiphytized or wounded thallus to a young frond emanating from the same rhizoidal mass. The older thallus then becomes senescent. This sequence could represent a mechanism for shedding the epiphyte load.

Giant-celled siphonous algae are thought to be adapted to habitats of low light energy (Raven *et al.* 1979), and large cell or siphon sizes should be indicative of shade plants. This is logical because there is less structural wall material to intercept the light received (Littler & Littler 1980, structural hypothesis). In accordance with this hypothesis, the medullary siphons in the blades of deep-water populations of both *Avrainvillea asarifolia* and *A. silvana* are relatively enlarged. Additionally, *A. nigricans* f. *nigricans,* a plant found in deeper water or shaded habitats, is thinner and much elongated compared with *A. nigricans* f. *parva,* suggesting processes analogous to etiolation in vascular plants. However, *A. nigricans* f. *nigricans,* as well as the deepest occurring species *A. levis* (< 1 to 125 m), shows no difference in siphon size as a function of depth. The latter, although among the thinnest, contains the smallest blade siphons of the western Atlantic species. Also, we have found no consistent relationship between siphon wall thickness and shade acclimation/adaptation in western Atlantic *Avrainvillea.* As in the case of *Udotea* (Littler & Littler 1990), the patterns for *Avrainvillea* are both supportive and contradictory of current theories of plant adaptive-geometry (Horn 1971; Raven *et al.* 1979; Hay 1986). The conspicuous exceptions indicate that one must be cautious when interpreting the adaptive significance of large siphon size in the order Bryopsidales.

REPRODUCTION

Little is known about reproduction in *Avrainvillea* from the western Atlantic. Sporic reproduction has been observed both in the field and from dried specimens and seems somewhat similar to that of *Udotea.* Specific surface siphons of the blade first become thin, thus forming a stalk, then swell and enlarge in diameter (often 2–3 times that of the subtending siphons) producing single somewhat clavate reproductive structures. These darken as the cytoplasm concentrates and eventually cleaves into 3–8, initially misshapen, ovoid bodies. The resultant spores are then released from the apex of the structure and presumably germinate [see Howe (1907) for a detailed description of the formation and release of spores in *A. fulva*]. One mature pressed specimen of *A. asarifolia* [*D&M Littler 13098* (US)] possesses similar clavate reproductive structures as does a single specimen of *A. asarifolia* f. *olivacea* [*Hill 13485* (NY)]. The occurrence of this form of reproduction appears to be rare within the genus.

Vegetative reproduction and persistence are presumed important but virtually unstudied. As an example of persistence, Olsen-Stojkovich (1985) found that the holdfasts accounted for as much as 90% of the total thallus in some species, enabling plants to lose uprights under unfavourable conditions, later replacing them with one to several new young blades depending on the growth habit of the species. For instance, during periods of physical disturbance, such as storms, random grazing by fishes, and other stochastic events, the more delicate stipes and blades be-

come vulnerable, but the subterranean rhizoidal mass can serve as a perennating portion. We have also observed this regenerative process in several species from the tropical western Atlantic (e.g. *A. asarifolia, A. fenicalii, A. fulva, A. hayi, A. longicaulis, A. nigricans* f. *spongiosa*) and the remains of the old uprights are often apparent as stubs surrounding, or surrounded by, newly forming upright thalli on the massive columnar holdfasts (Figs 1A, 5B, 6A, 7B). Vegetative reproduction by rhizome-like rhizoidal extensions similar to those known in *Udotea* (Littler & Littler 1990) have not been previously documented for *Avrainvillea.* However, we observed a propensity for *A. longicaulis* f. *laxa, A. nigricans* f. *spongiosa,* and *A. asarifolia* f. *olivacea* to proliferate laterally from elongated stipes partially buried in organic sediments to form large, 0.5-m-thick, clonal mounds several metres in diameter. These three taxa, localized in calm, back-water, interior habitats of mangrove systems, are characterized by exceptionally loose arrangements of the blade siphons. Both *A. digitata* and *A. rawsonii* can spread laterally by their creeping mat-like bases to cover large areas of shallow back reefs, often overgrowing and smothering other algae and seagrasses.

In general, psammophytic macroalgae such as *Avrainvillea* and *Udotea* do not appear to have mechanisms for long-distance dispersal such as shown by hitch-hiking boat foulers, pelagic algae, or macrophytes with long-lived resistant spores. This leads to reproductive isolation and may explain why few species of Caribbean *Avrainvillea* are found in the Pacific Ocean and vice versa. Records of Pacific *Avrainvillea* in the western Atlantic that we have investigated are the result of mistaken identifications, which is understandable given the relatively large numbers of 'pair species' [e.g. *A. levis* (Atlantic) and *A. lacerata* (Pacific), *A. asarifolia* (Atlantic) and *A. amadelpha* (Pacific)] and the previous absence of ample taxonomic collections.

ACKNOWLEDGEMENTS

We thank Barrett L. Brooks for valuable field, library, and laboratory assistance throughout this project and W.D. Lee and S.A. Reed for providing field assistance. We sincerely appreciate V.A. Funk's expertise in helping with the cladistic interpretations. Gratitude is extended to B.E. Lapointe and W. Fenical for inviting us to participate on their NSF-sponsored cruises throughout the southern Yucatán Peninsula and the Greater and Lesser Antilles, H.E. Robinson for the Latin translations, and D.H. Nicolson for assistance in interpreting the rules of botanical nomenclature. The comments of P.C. Silva were of great help in fine-tuning the manuscript. We are grateful for the invitation by D.L. Ballantine to participate in the Distinguished Visiting Scientist lecture series that allowed us to collect important living Puerto Rican material. Field work was supported by grants from the Research Opportunities Fund of the Smithsonian Institution, the Smithsonian Marine Station at Link Port, Florida, (SMS Contribution #300), and the Caribbean Coral Reef Ecosystem Program of the National Museum of Natural History (CCRE Contribution #356).

REFERENCES

ADEY W.H. 1976. Crustose coralline algae as microenvironmental indicators for the tertiary. In: *Historical Biogeography, Plate Tectonics, and the Changing Environment* (Ed. by J. Gray & A.J. Boucot), pp. 459–464. Oregon State University Press, Corvallis.

BØRGESEN F. 1909. The species of Avrainvilleas hitherto found on the shores of the Danish West Indies. *Videnskabelige Meddelelser fra den naturhistoriske Forening i. Kjøbenhavn* **1908:** 27–44, pl. III.

BØRGESEN F. 1913. The marine algae of the Danish West Indies. Part 1. Chlorophyceae. *Dansk Botanisk Arkiv* **1** (4): 1–160.

CHAUVIN F.J. 1842. *Recherches sur l'Organisation, la Fructification et la Classification de Plusieurs Genres d'Algues.* A. Hardel, Caen, 132 pp.

COLLINS F.S., HOLDEN I. & SETCHELL W.A. (Eds) 1908. *Phycotheca Boreali-Americana, Exsiccatae.* Fascicle XXX. Malden, Massachusetts.

DECAISNE M.J. 1842. Essai sur une classification des algues et des polypiers calciferes de Lamouroux. *Annales des Sciences Naturelles, Botanique, Séries* 2, **17:** 297–380, pls. 14–17; **18:** 89–199.

DICKIE G. 1875. On the marine algae of Barbadoes. *Journal of the Linnean Society of London, Botany* **14:** 146–152.

GEPP A. & GEPP E.S. 1911. The Codiaceae of the Siboga Expedition including a monograph of Flabellarieae and Udoteae. In: *Siboga-Expeditie Monographie* (Ed. by M. Weber) **62:** 1–150, 22 pls. E.J. Brill, Leiden.

HAY M.E. 1986. Functional geometry of seaweeds: ecological consequences of thallus layering and shape in contrasting light environments. In: *On the Economy of Plant Form and Function* (Ed. by T.J. Givnish), pp. 635–666. Cambridge University Press, Cambridge.

HAY M.E., DUFFY J.E., PAUL V.J., RENAUD P.E. & FENICAL W. 1990. Specialist herbivores reduce their susceptibility to predation by feeding on the chem-

ically defended seaweed *Avrainvillea longicaulis*. *Limnology and Oceanography* **35:** 1734–1743.
HOLMGREN P.K., HOLMGREN N.H. & BARNETT L.C. 1990. Index Herbariorum. Part 1: the Herbaria of the world. *Regnum Vegetabile* **120:** 1–693.
HORN H.S. 1971. *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, 144 pp.
HOWE M.A. 1905. Phycological studies—II. New Chlorophyceae, new Rhodophyceae, and miscellaneous notes. *Bulletin of the Torrey Botanical Club* **32:** 563–586, pls. 23–29.
HOWE M.A. 1907. Phycological studies—III. Further notes on *Halimeda* and *Avrainvillea*. *Bulletin of the Torrey Botanical Club* **34:** 491–516, pls. 25–30.
JOLY A.B., CORDEIRO M., YAMAGUISHI N. & UGADIM Y. 1966. New marine algae from southern Brazil. *Rickia* **2:** 159–181.
KÜTZING F.T. 1858. *Tabulae Phycologicae*. Vol. 8. Privately published, Nordhausen, 48 pp., 100 pls.
LITTLER D.S. & LITTLER M.M. 1990. Systematics of *Udotea* species (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia* **29:** 206–252.
LITTLER D.S. & LITTLER M.M. 1991. Systematics of *Anadyomene* species (Anadyomenaceae, Chlorophyta) in the tropical Western Atlantic. *Journal of Phycology* **27:** 101–118.
LITTLER D.S., LITTLER M.M., BUCHER K.E. & NORRIS J.N. 1989. *Marine Plants of the Caribbean*. Smithsonian Institution Press, Washington, DC, 263 pp.
LITTLER M.M. & LITTLER D.S. 1980. The evolution of thallus form and survival strategies in benthic macroalgae: field and laboratory tests of a functional-form model. *American Naturalist* **116:** 25–44.
LITTLER M.M. & LITTLER D.S. 1988. Structure and role of algae in tropical reef communities. In: *Algae and Human Affairs* (Ed. by C.A. Lembi & J.R. Waaland), pp. 29–55. Cambridge University Press, New York.
MURRAY G. & BOODLE L.A. 1889. A systematic and structural account of the genus *Avrainvillea* Decne. *Journal of Botany* **27:** 67–72, pls. 288–289; 97–101.
OLSEN-STOJKOVICH J. 1985. A systematic study of the genus *Avrainvillea* Decaisne (Chlorophyta, Udoteaceae). *Nova Hedwigia* **41:** 1–68.
RAVEN J.A., SMITH, F.A. & GLIDEWELL S.M. 1979. Photosynthetic capacities and biological strategies of giant-celled and small-celled macro-algae. *New Phytologist* **83:** 299–309.
SILVA P.C. 1982. Chlorophyceae. In: *Synopsis and Classification of Living Organisms*. Vol. 1 (Ed. by S.P. Parker), pp. 133–161. McGraw-Hill, New York.
SUN H.H., PAUL V.J. & FENICAL W. 1983. Avrainvilleol: a brominated diphenylmethane derivative with feeding deterrent properties from the tropical green alga *Avrainvillea longicaulis*. *Phytochemistry* **22:** 743–745.
SWOFFORD D.L. 1989. *Phylogenetic Analysis Using Parsimony*. Illinois Natural History Survey, Champaign, Illinois, 1-1 to 6-2 pp.
WILEY E.O. 1981. *Phylogenetics, the Theory and Practice of Phylogenetic Systematics*. John Wiley, New York, 439 pp.

Accepted 28 *March* 1992

APPENDIX I

Key to the tropical western Atlantic *Avrainvillea* taxa

[Where appropriate, siphon size and various other supplementary characters have been added in brackets to the key to make it more comprehensive and easier to use.]

(1) Fronds digitate (finger-like) or somewhat clavate (club-shaped) [siphon apices often bulbous, medullary siphons of blade slightly moniliform, 40–55 μm in diameter] ..... *A. digitata*
(1) Fronds flattened, peltate (umbrella-shaped) or expanded 2
  (2) Fronds thickened and peltate or expanded and knob-like [medullary siphons slightly moniliform, 50–65 μm in diameter, siphon apices often bulbous] ..... *A. rawsonii*
  (2) Uprights flattened and paddle-shaped 3
(3) Blades clustered (5–8) atop stipes [blade siphons moniliform to cylindrical, 20–30 μm in diameter, siphon apices tapered to 8 μm in diameter] ..... *A. fenicalii* f. *fenicalii*
(3) Blades borne singly on stipes 4
  (4) Blade siphons moniliform throughout 5
  (4) Blade siphons not moniliform throughout 10
(5) Blade siphons with extreme taper toward surface of frond 6
(5) Blade siphons with little or no taper toward surface of frond 7
  (6) Frond thick, blade siphons gradually tapering to form a loose cortex, medullary siphons of blade 60–140 μm in diameter ..... *A. fulva*
  (6) Frond thin, blade siphons tapering abruptly to form a tightly knit cortex, medullary siphons of blade 45–80 μm in diameter ..... *A. silvana*

(7) Blade siphons consistently 30–40 μm in diameter, apices not forming a tightly knit cortex, blade generally not zonate, lower margin of blade cuneate (wedge-shaped) 8
(7) Blade siphons generally 20–40 μm in diameter, apices forming a tightly knit cortex blade often zonate, lower margin of blade often cordate (deeply lobed) 9
(8) Blades loosely woven, rounded to slightly oval, generally with no zonation ..... *A. nigricans* f. *floridana*
(8) Blade extremely loosely woven, much longer than wide, with faint zonation ..... *A. nigricans* f. *spongiosa*
(9) Blade medium sized (to 9 cm tall), with distinct zonation, lower margin of blade cordate, cortex tightly knit ..... *A. nigricans* f. *parva*
(9) Blade large (to 30 cm tall), with faint or no zonation, lower margin of blade seldom cordate, cortex loosely woven ..... *A. nigricans* f. *nigricans*
(10) Blade siphons cylindrical throughout 11
(10) Blade siphons partly moniliform and/or tortuous 13
(11) Dried blades fibrous, thick (2–3 mm), actively growing siphons darkly pigmented and smaller in diameter than older siphons (30–40 μm vs 40–80 μm) ..... *A. mazei*
(11) Dried blades not fibrous, thin (1–2 mm), actively growing siphons generally not darkly pigmented and not smaller in diameter than older siphons 12
(12) Fronds to 12.5 cm tall, blade <1 mm thick, growing margin often smoothly lobed, cortical siphons slightly larger (26–36 μm in diameter) than medullary siphons (22–30 μm in diameter), those of the growing margin small (25–30 μm in diameter) ... *A. hayi*
(12) Fronds to 6 cm tall, blade 1–2 mm thick, growing margin smoothly rounded or lacerate (ragged), cortical and medullary siphons approximately the same diameter (32–48 μm), those of growing margin slightly expanded (44–60 μm in diameter) ..... *A. sylvearleae*
(13) Distal half of blade containing only cylindrical siphons (20–60 μm in diameter), proximal half with occasionally tapered moniliform siphons (8–25 μm in diameter) at surface, [stipe typically much elongated (to 26 cm), blade extremely thin (< 1 mm), siphons loosely woven at margins] ..... *A. longicaulis* f. *laxa*
(13) Distal and proximal portions of blade having cylindrical siphons grading to moniliform and/or tortuous at surface 14
(14) Blades medium thick to thick (> 2 mm) 15
(14) Blades thin (< 2 mm) 16
(15) Blades thick (> 4 mm), spongy, orbicular, not zonate, medullary siphons to 70 μm in diameter, with few tapered (to 15 μm in diameter) siphons at surface of frond, uprights 1–3 ..... *A. longicaulis*
(15) Blades medium thick (2–3 mm), not spongy, broadly oval, zonate, medullary siphons to 30 μm in diameter, tapering (to 8 μm in diameter) at surface of frond, uprights 4–10 ..... *A. fenicalii* f. *flabellifolia*
(16) Distal portion of blade lacking compact cortex 17
(16) Distal portion of blade with compact cortex 18
(17) Siphons in distal portion and at surface of blade extremely fine (5–8 μm), elsewhere to 30 μm, blade <1 mm thick ..... *A. levis* f. *translucens*
(17) Siphons in distal portion and at surface of blade expanded (28–40 μm), blade 1–2 mm thick ..... *A. geppii*
(18) Base of blade truncate (cut straight across), siphons with little or no taper at surface of blade, cortical siphons 8–10 μm in diameter 19
(18) Base of blade cordate; siphons tapered at surface of blade, cortical siphons 8–10 μm in diameter 20
(19) Stipe short and thick, blade >2 mm thick, zonate ..... *A. elliottii*
(19) Stipe long and narrow, blade thin, not zonate ..... *A. asarifolia* f. *olivacea*
(20) Fronds large (to 24 cm tall), blade zonate, with deeply cordate base, cortical siphons moniliform and/or tortuous, 12–20 μm in diameter ..... *A. asarifolia* f. *asarifolia*
(20) Fronds small (to 6 cm tall), blade not zonate, with shallowly cordate base, cortical siphons generally moniliform, 8–12 μm in diameter ..... *A. levis*