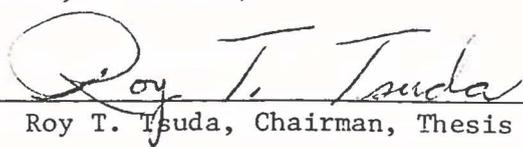


AN ABSTRACT OF THE THESIS of Jeanine Olsen Stojkovich for the Master of Science in Biology presented October 22, 1979.

Title: Revision of the pantropical algal genus Avrainvillea Decaisne  
(Codiales, Codiaceae)

Approved: \_\_\_\_\_

  
Roy T. Tsuda, Chairman, Thesis Committee

Eighteen species of Avrainvillea are recognized in this revision, a reduction from the previous number of twenty-three. Four species occur only in the tropical Atlantic, while ten species occur only in the tropical Indo-Pacific. An additional three species are common to both provinces. One species is reported from southern Australia.

A thorough morphological study of both habit and internal siphon structure was made. Biogeographic data, type material, fresh collections, and standard herbarium specimens were examined.

Habit is useful as a general guide to identification but is best utilized in conjunction with internal anatomy. Significant macroscopic characteristics include type of holdfast, stipe development, branched or nonbranched habit, gregarious or solitary flabella, and, occasionally, size and color.

Internal structure and pattern of the siphons are the most reliable set of differential criteria. Cylindrical, torulose, moniliform, tortuous, or tapered siphons, combined with rounded, pointed, hooked, or clavate apices, and strongly or weakly constricted dichotomies,

contribute to species characterization. Siphon diameter and pseudocortical development are definitely affected by environmental conditions and are not reliable by themselves.

Each species was analyzed for all characteristics. A synonymy, description, discussion, habit photographs, and line drawings are included for each species. A glossary accompanied by microphotographs is also provided.

Four species complexes are recognized: The "lacerata" group, the "sordida" group, the "obscura" group, and the "nigricans" group. A. mazei is placed in synonymy with A. longicaulis, A. atlantica and A. geppii with A. elliotii, A. levis with A. sordida, A. gracillima with A. riukuensis, and finally, A. capituliformis as a new form with A. obscura. Seven ecological forms are also recognized. one new species is described.

Comparison of the effects of light and water motion on the morphology of A. obscura suggest that water motion plays a more significant role, leading to less consolidated thalli and larger average siphon diameters. Torulose characteristics were not affected in these experiments.

REVISION OF THE PANTROPICAL ALGAL GENUS  
AVRAINVILLEA DECAISNE (CODIALES, CODIACEAE)

by

JEANINE OLSEN STOJKOVICH

A thesis submitted in partial fulfillment  
of the requirements for the degree of

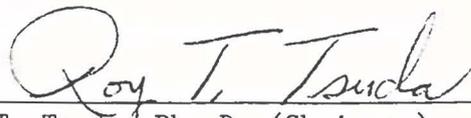
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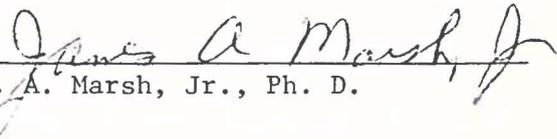
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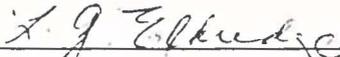
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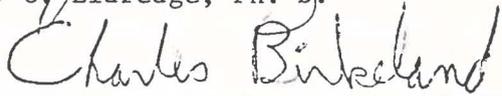
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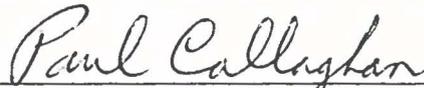
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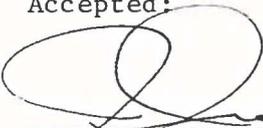


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Chairman, Graduate Council

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## INTRODUCTION

The green algal genus Avrainvillea is found in both hemispheres of the tropical and subtropical domains of the Atlantic, Pacific, and Indian Oceans. Eighteen species of Avrainvillea are recognized in this revision, a reduction from the previous number of twenty-three. Four species occur only in the tropical Atlantic, while ten species occur only in the tropical Indo-Pacific. An additional three species are common to both provinces. One species is reported from southern Australia (Fig. 1).

A comprehensive examination of the genus has not been undertaken since the Gepp's monograph in 1911. Over the past sixty-five or so years many new species have been added with little attempt made to determine their alliances and possible conspecificity with already existing Avrainvillea species. In addition to problems of inaccessibility and patchy collections, Avrainvillea, shows considerable gross morphologic plasticity. This trait is quite common throughout the family. The degree to which plasticity is determined by genetic or environmental factors is not known and this uncertainty is undoubtedly responsible for the differing concepts of particular species held among different workers from different parts of the world. Species boundaries are often difficult to establish. Geographic clinal patterns result in taxonomic overlap. Such problems are difficult to resolve and show themselves strenuously throughout the genus.

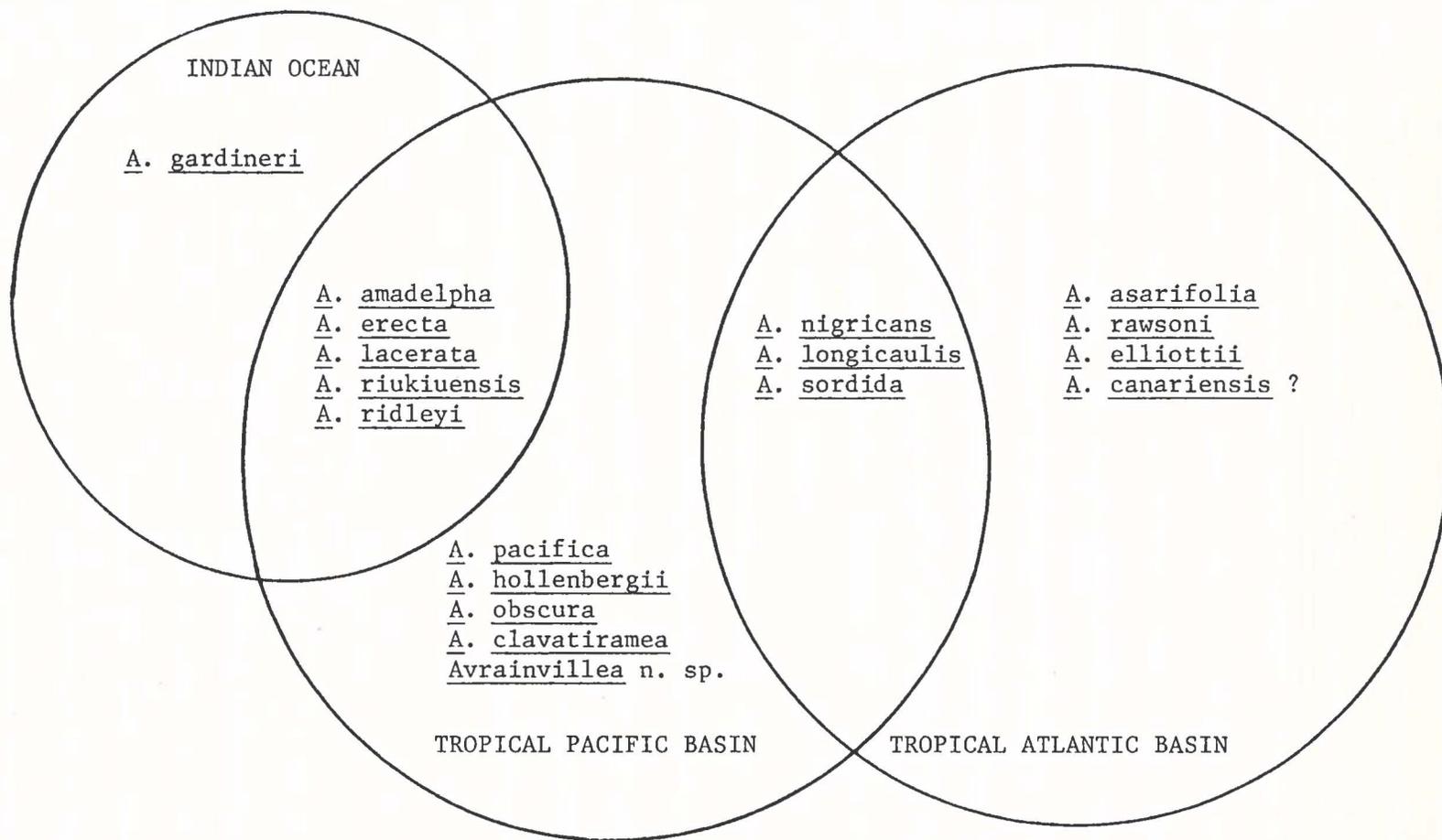


FIG. 1. Biogeographic distribution of the genus Avrainvillea. Intersecting circles indicate that the species is common to both oceans.

It is well recognized that the use of the typological approach, i.e., the subsequent reliance on a single specimen collected on one occasion, from one location has its shortcomings. In order to minimize this problem, every effort was made to examine as many specimens of a given species as possible. Ideally this included type material, fresh specimens, and, most crucially, as many examples from the known biogeographical range of the species as possible. In most cases alliances and appropriate synonymies were established. In other cases the decision to "split" or "lump" was not clear-cut and the species was retained under the status quo. Further resolution of the genus in the true genetic or ecological sense (Crowson, 1971; Simpson, 1961) cannot be resolved in a herbarium alone.

The main function of this monograph is to present the most up-to-date status of the genus in order to provide the field phycologist with a workable identification scheme; and, to provide the laboratory phycologist with a firm foundation from which to investigate, through whichever preferred means, and to determine the closest approximation to biologic reality.

#### Historical Perspective

Specimens of Avrainvillea are known to have been collected as early as 1722 under the name Fucus bahamensis flabelliformis. During the early 19th century, additional specimens were collected and listed under various names. In 1842, Decaisne and Chauvin began working independently on several specimens which were to be placed in a new genus. Decaisne's Avrainvillea took publication priority over Chauvin's Fradelia to become the valid name. The name Avrainvillea was derived

from a collection belonging to M. d'Avrainville, whose specimens of A. nigricans became the type species for the genus.

Between 1842 and 1889 many new species were described in the genus. Principal contributors included such individuals as M. J. Berkeley, C. Montagne, N. L. Gardiner, J. Zanardini, F. T. Kützing, G. Murray, L. A. Boodle, C. and J. G. Agardh, and W. H. Harvey. It is interesting to note that many of the new Avrainvillea species had previously been described under the genera Udotea and Chlorodesmis.

In 1889, Murray and Boodle made the first attempt to monograph the genus. They were the first to attempt some systematic arrangement of the eight species then recognized and to establish the use of specific diagnostic structures. Their work provides an excellent historical review of the genus to that time.

During the years of the Siboga Expedition to the East Indian Archipelago (1899-1900), Mdm. Weber van Bosse made a large collection of Avrainvillea, and from 1905-1907, Howe recognized four additional species. It was not until 1911, however, that another serious effort was made to monograph the genus. This was carried out by A. and E. S. Gepp. What began as a cataloging of The Siboga Expedition's algal collection, led to a revision and monograph of the entire Codiaceae family. The Gepps took every opportunity to examine as many of the type specimens of Avrainvillea as they could. Most of these are deposited in the Paris, British, and Copenhagen Museums. During the course of their work seven new species were added, bringing the total to sixteen. Notable contributions were also made by Howe (1907). Until now, the Gepp's 1911 monograph has stood as the single most authoritative work on the genus.

## MATERIALS AND METHODS

The bulk of the examinations were carried out on dried herbarium materials, though some specimens were fresh or wet-preserved. Every effort was made to examine as many representative specimens of the species in question from its reported biogeographic range. Type specimens were examined whenever available.

Dried specimens were prepared for microscopic examination by soaking a small piece of the blade in a solution of approximately 25 ml glycerin per 100 ml of a 10% methanol in water solution for a few minutes to several hours. After rehydration and softening, the siphons were teased apart under a dissecting scope with 26-gauge hypodermic needles. The wet mounts could then be examined and measured under a compound microscope. A standard ocular micrometer was employed.

Line drawings were made with a Ken-A-Vision Microprojector. This system enables the worker to make direct tracings from the projected image.

All microscopic measurements are given in micrometers although they are not always annotated as such. Since a range of diameters occurs within an individual specimen, the range of diameters is listed with the average measurement in parentheses, i.e., 8-10-(19-27)-38 would indicate that the bulk of the interior siphons are 19-27  $\mu\text{m}$  in diameter. Occasionally one might see siphons of 38  $\mu\text{m}$  in diameter.

Surface siphons may be as small as 8-10  $\mu$ m. This convention is followed throughout the paper.

A glossary is provided to help clarify the meaning and the author's personal interpretation of certain terms.

An effort to ally species in a natural way has been carried on throughout the paper with the exception of the key, which is wholly artificial.

The format of "specimens examined" sections gives the location, collector and his/her number, date, and herbarium deposition. Breaks in the pattern indicate that the information was not available. The following herbarium abbreviations are employed: University of California, Berkeley (UC); University of Missouri collections now deposited at the University of California, Berkeley (MO in UC); United States National Herbarium, Smithsonian Institution (US); University of South Florida (SF); University of Michigan (MICH); British Museum (BM); University of Copenhagen (C); Philippine National Herbarium (PNH); Hokkaido University (SAP); Kagoshima University (KAG); University of Guam (GUAM); University of São Paulo (SP); University of Adelaide (ADU); personal herbariums of M. S. Doty, University of Hawaii (DOTY), C. J. Dawes, University of South Florida (DAWES), and N. Ogden (OGDEN).

Finally, the early synonymies (pre-1889) have been principally derived from the works of Murray and Boodle (1889) and the Gepps (1911), to which more recent works have been added. All references included in synonymy have been examined by the author with a few exceptions. These references are annotated with an "\*" in the literature cited section. Many of the early synonymies are virtually impossible to verify in a literal sense, owing to very scant Latin

descriptions and inaccessability or loss of the original specimens.  
Because of this, the author accepts the early synonymies of the above  
workers unless specifically stated otherwise.

## RESULTS AND DISCUSSION

Avrainvillea is one of the larger tropical benthic algal genera. It is common both on and over the reef flat in depths ranging from a few centimeters to over sixty meters. The more typical habitats are sandy or muddy areas, especially seagrass beds or reef flat holes, often in association with Halimeda, Udotea, and other siphonous algae possessing large, rhizomatous holdfasts. The alga may occasionally be found in semicryptic habitats where it may attach to more or less rocky substrata.

### Habit

There are four broad habit classifications for Avrainvillea. The first consists of a nonflabellar, cespitose thallus. Little distinction can be made between the rhizome, stipe, and blade. A. rawsoni is the only species which conforms to this habit. The second type consists of a short, gregarious habit involving branched stipes from which numerous fronds originate. A. amadelpha and A. lacerata represent this group. The third type is represented by A. nigricans and A. longicaulis in which the fronds are quite large (up to 20 cm or more), stipitate, and connected sometimes by extensive rhizomal mats (Pl. XI. C), which lead to gregarious populations. Finally, there is the classic habit which consists of solitary plants, having large reniform to cuneate, planar blades, arising from well developed stipes (short to sessile, or quite long), and sandy rhizomes. Most species fall into this category.

A phenomenon seen in this group is the occasional fusion of blades above the substratum. The resulting habit may be quite irregular. Excavation of the stipe and holdfast regions will usually clarify the situation. Fortunately, most of the herbarium materials examined in this study did not exhibit this trait. Members of the "obscura" group seem particularly prone to such fusions (Pl. X. A, B).

Color ranges from nearly black-brown to gray, green, tan, or yellow. Members of the "nigricans" group tend to be dark brown-black, whereas the "obscura" group is largely olive-green. The other groups are more variable in this color distribution. The only reliable use of color is in the identification of A. erecta which always exhibits bright yellow siphons when examined microscopically. The yellow color is not usually evident in the plant's habit.

Blade texture is either papery thin and membranous or quite thick and spongy, often up to a centimeter in thickness. The "lacerata" group illustrates the former and the "nigricans" group the latter. The "obscura" and "sordida" groups generally fall midway but may have individual members representing both extremes. This characteristic is usually discernible even in dried material. Some members of the "obscura" group consist of largely unconsolidated siphons which resemble the paintbrush habit of Penicillus. Avrainvillea, however, is never calcified.

With the exception of A. rawsoni, all Avrainvillea species are stipitate to some degree. They may be stout or quite slender, somewhat flattened or rounded in cross section. Short stipes are generally characteristic of A. erecta, most forms of A. obscura, Avrainvillea n. sp., A. sordida, A. elliottii, and A. gardineri. In some species,

such as A. clavatiramea, A. nigricans, A. asarifolia, and A. longicaulis, the stipes are often very long in proportion to blade size. A third category of stipes is the branched stipes notably characteristic of A. lacerata, A. amadelpa, and A. hollenbergii.

Blade size and shape vary tremendously within individuals as well as within species. Reniform, obovate, cuneate, rotundate, rhomboid, and various combinations thereof cover all cases. The blades are predominantly planar structures with the exception of certain A. obscura members and A. rawsoni. As mentioned above, plants exhibiting multiply fused thalli may not be planar. Frond size ranges from a few to more than 20 cm in diameter. Members of the "nigricans" group tend to be larger than members of the other groups, but this is filled with individual exceptions and is best left as an academic generalization rather than as a useful field guide.

The holdfast is simply a continuation of the stipe siphons into or over the substratum. These siphons are coarser and usually embedded with sand grains. Siphon structure in the holdfast region has not been used as a taxonomic guideline. Holdfast type falls into two categories, both of which are affected by local conditions of the substratum. The first is characterized by the "nigricans" group. The rhizome forms a thick mat, often 5-6 cm thick which tends to spread horizontally over rubbly substrata. The second type is more characteristic of the "obscura" group. In this group the rhizome penetrates deeply into the sand for up to 20 cm where it then bends ninety degrees and may run another several centimeters (Pl. XI. B). In such species, the subterranean portion of the plant is many times larger than the photosynthetic portion. Members of the "sordida" and "lacerata" groups have more bulbous

holdfasts which may exhibit either of the previously mentioned types with some modification. Unfortunately, few herbarium specimens have much of their holdfasts intact.

In general then, habit is useful only in the broadest sense. A few species are readily identified in the field but most, at best, can be put in one of the four habit categories. Knowledge of the species' distribution and, better yet, the community, are the best field aids.

### Siphon Structure

The internal anatomy of Avrainvillea consists exclusively of interwoven, coenocytic siphons which are dichotomously branched in varying degrees toward their apices. The genus does not exhibit lateral branchlets as in Rhipilia, for example. The combined structure and pattern of the siphons are the single most reliable way to speciate the genus, and serve as the primary basis for the designation of species complexes. Siphons may be cylindrical, torulose, or moniliform; tapering or isodiametric toward their apices; attenuated or ramified near the surface of the blade; strongly or weakly constricted at their dichotomies; rounded, clavate, tapered, hooked, or thread-like at their apices; and finally, tortuous or nontortuous near the surface. A glossary is provided for clarification of these terms. Siphon color may range from transparent, olive, brown, or yellow. Siphon diameters are subject to environmental variation and are useful in a general way only. Members of the "lacerata" and "sordida" groups generally have smaller average siphon diameters than members of the "nigricans" and "obscura" groups. Surface ramification and pseudocortical development are useful but are affected environmentally to some extent. They are best used as supportive rather than negative evidence.

In practice a combination of several characteristics delineates a particular species. Differences between closely allied species are admittedly subtle and require careful examination. It is recognized that the use of a statement such as, "Species A is more torulose than Species B" is of little help when one possesses only specimens of Species A. Unfortunately, there is no way to completely avoid this. Study of siphon structural drawings, combined with habit and geographic locale will rectify the ambiguity in most cases.

#### Species Complexes

Avrainvillea may be divided into four large complexes based predominantly on siphon structure, rather than habit. This is an important point, since members within a complex often do not resemble one another in habit, e.g., A. rawsoni and A. nigricans. The four complexes are the "lacerata", "sordida", "obscura", and "nigricans" groups (Fig. 2).

The "lacerata" group includes A. lacerata, A. amadelpa, A. gardineri, A. pacifica, A. riukuensis, and A. hollenbergii. This group is confined to the Indo-Pacific. All members of the group have papery, thin blades with the exception of A. pacifica. A. lacerata, A. amadelpa, and A. hollenbergii are characterized by branched stipes and a few to many fronds; whereas A. gardineri, A. pacifica, and A. riukuensis are more typically solitary in habit.

Siphon structure is predominantly cylindrical in the deeper portions of the blade, becoming tapered towards the surface and often tortuous and lightly torulose. The siphons are transparent to olive and rarely exceed 28  $\mu\text{m}$ . The tapering characteristic is variable becoming as small as 3-4  $\mu\text{m}$  in A. hollenbergii and A. riukuensis, the

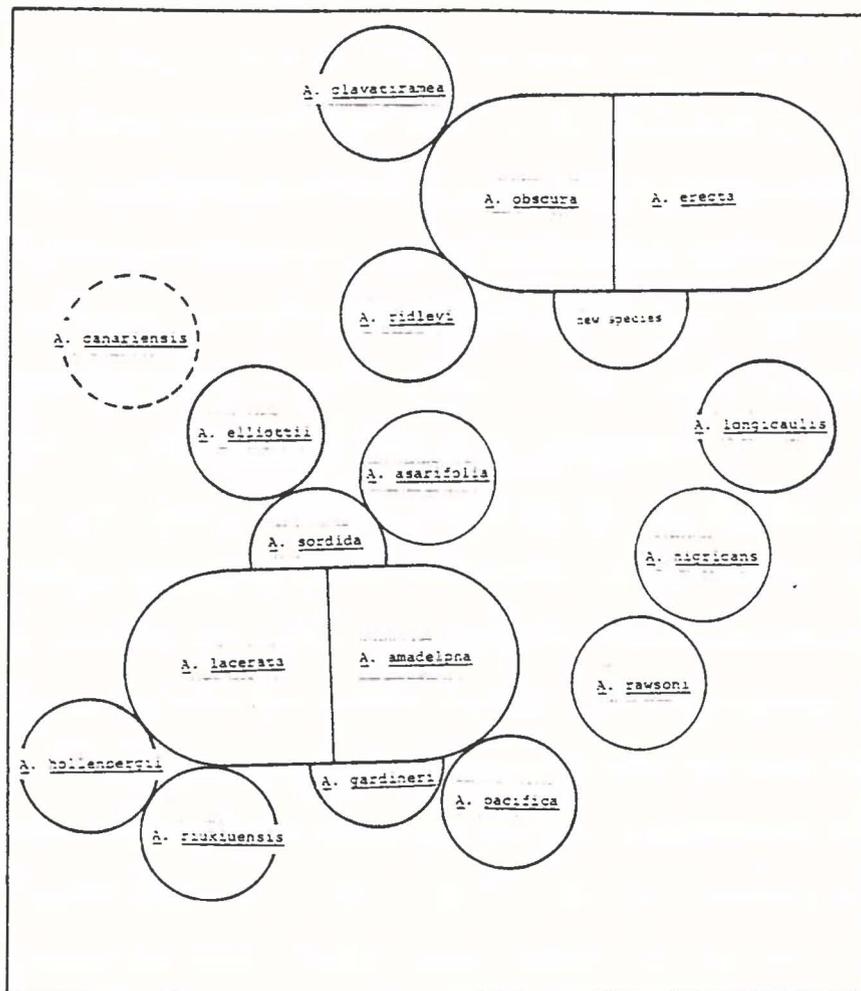


FIG. 2. Schematic representation of *Avrainvillea* alliances. The greater the intersection of circles, the closer the relationship.

two Avrainvillea species having the smallest average siphon size. Torulosity is present in some degree among all of the species, being most developed in A. amadelpa, A. pacifica, and A. gardineri. A. riukuensis, A. hollenbergii, and A. lacerata are the most tortuous and apically tapered. There is little surface ramification of the siphons and no pseudocortical development. A. amadelpa, A. gardineri, and A. pacifica are much more ramified, the former two sometimes developing a thin pseudocortex. Apices are rounded rather than tapered to points, and never less than 12  $\mu\text{m}$ . The apices of A. pacifica have a uniquely hooked character. Dichotomal constrictions are deep with the exception of A. hollenbergii and A. riukuensis.

The "sordida" group includes A. sordida, A. asarifolia, A. elliottii, and A. canariensis (?). The group is confined to the tropical Atlantic with the exception of A. sordida, whose distribution has been expanded to include the western Pacific. A. canariensis most likely falls within this group and is reported from the West African coast. In some respects the group may be loosely considered the geographic counterpart of the "lacerata" group. All members of the group have moderately thick, velutinous blades, short stipes, and more or less solitary habits. A. asarifolia is an exception. It may have a few blades and long stipes.

Siphon structure is predominantly cylindrical in the deeper layers becoming tapered and increasingly torulose near the surface. There is little or no surface ramification and no pseudocortical development. Siphon diameters do not exceed 38  $\mu\text{m}$  and average 20-30  $\mu\text{m}$ . They are often yellow to olive in color. Apices are often extremely tapered in A. asarifolia, becoming thread-like, whereas in A. sordida they are

tapered less, and in A. elliotii, subclavate to clavate. The apices of A. canariensis are reported to be rounded. The torulose character is most highly developed in A. asarifolia and least in A. sordida. Supradichotomal constrictions are deep with the exception of the surface siphons in A. sordida.

The "nigricans" group includes A. nigricans, A. rawsoni, and A. longicaulis. A. nigricans and A. longicaulis are pantropical and virtually identical in habit. A. rawsoni is the only member of the genus possessing a cespitose, nonflabellar habit. All three are dark brown-black and very spongy.

Siphon structure is predominantly moniliform and torulose with the exception of A. longicaulis which is almost exclusively cylindrical. The siphons are transparent to brown, isodiametric, nontapering, deeply constricted, and rounded apically. Siphon diameters are as great as 76  $\mu\text{m}$  but are most commonly in the 38-47  $\mu\text{m}$  range. A. nigricans may show some layering with cylindrical siphons in the deeper portions of the frond and some ramification near the surface. The moniliform character is very dominant in this group.

The "obscura" group includes A. obscura, A. claviramea, A. ridleyi, A. erecta, and Avrainvillea n. sp. This group is confined to the Indo-Pacific. All members of the group have a solitary habit. Short stipes are most typical with the exception of A. claviramea which has a very long stipe. The fronds are moderately thick, velutinous, and planar, except for A. obscura f. capituliformis and f. taylori. The holdfast is deep and embedded with sand.

Siphon structure is predominantly cylindrical and isodiametric with some irregular and patchy torulose character in A. obscura,

A. clavatiramea, and A. ridleyi. Torulosity is never seen in A. erecta and rarely in Avrainvillea n. sp. The siphons are transparent to olive. A. erecta has bright yellow siphons. Apices are rounded (exclusively in A. erecta) to distinctly clavate, the clavate character being most highly developed in A. clavatiramea. Siphon diameters range from 19-100  $\mu\text{m}$  in this group but more typically range from 28-47  $\mu\text{m}$ . Tapering of siphons near the surface is seen only in Avrainvillea n. sp. Supradichotomal constrictions are deep in all members with the exception of A. ridleyi.

#### Reproduction

There is little information on reproduction in Avrainvillea. Reports of "sporangia" by both Howe (1907) and the Gepps (1911) are the earliest known observations. They observed the presence of "protruding capitate or subclavate filaments" on the surface of the fronds of A. nigricans and later, A. erecta. The observations were made in January and October, respectively. Similar observations were made by Young (1977) in Panama during April of 1973 on A. longicaulis and A. rawsoni. Field observations of fertile plants have been made by this author in Guam during the months of January and February.

Avrainvillea leads a haplobiontic diplont life cycle. The production of gametes is a holocarpic process followed by the deterioration of the frond. Whether such production of gametangia is seasonal or continuous is not known. This, however, is not the only way in which Avrainvillea perpetuates itself.

Field observations confirm that standing crops of A. obscura remain fairly constant throughout the year (at least on Guam), yet individual

fronds have a life span of only 4-6 weeks, at which time they deteriorate and break off within 1 or 2 days. In most cases, however, new blades are already breaking the surface as the old ones die off.

The subterranean rhizome system is extraordinarily well developed in A. obscura, often many times larger than the photosynthetic portion. Excavation of the rhizome shows that the new plants often arise from already existing rhizomes. Interestingly, two plants have not been observed arising simultaneously from a single rhizome.

The possibility of cross breeding among closely allied species is not documented but this probably occurs. Communities of A. erecta and A. obscura often have members which appear to be intermediates of the two. Similar observations have been noted for A. nigricans and A. longicaulis.

On a nonbreeding level, some intermediates may be the result of closely growing juveniles whose thalli grow up fused together as a graft. This possibility was mentioned by the Gepps (1911) and one which this author believes possible. Resolution of such a point is best left to chemotaxonomists and laboratories equipped to conduct culture experiments. Such seemingly grafted plants have been examined by the author and cannot be totally disregarded.

SYSTEMATIC TREATMENT

Avrainvillea Decaisne 1842

Synonymy: Avrainvillea Decaisne, 1842, p. 108.

Fradelia Chauvin, 1842, p. 124.

Chloroplegma Zanardini, 1858, p. 290.

Avrainvillea, J. G. Agardh, 1887, p. 51; Murray and  
Boodle, 1889, p. 67; DeToni, 1889, p. 513; Wille,  
1890, p. 141; Howe, 1907, p. 508; Collins, 1909,  
p. 389; Wille, 1910, p. 128 (excluding Chlorodesmis);  
Gepp and Gepp, 1911, p. 19.

Type Species and Locality: Avrainvillea nigricans Decaisne, Bahama Is.,  
Caribbean Sea

Distribution: Pantropical plus southern Australia

Artificial Key to the species of Avrainvillea

- 1 - Thallus distinctly nonflabellar; cespitose habit...A. rawsoni
- 1 - Thallus distinctly flabellar; erect habit.....2
- 2 - Blades medium to thick, velutinous to spongy;  
stipitate; solitary or a few blades (1-4) per  
stipe.....3
- 2 - Blades thin and papery, often zonate and  
lacerate at the edges; branched stipes; one  
or two, to many (1-20) per stipe.....16

- 3 - Thallus with very long stipes in proportion to their blade size (Pl. IX, B).....4
- 3 - Thallus with short or stout, sessile stipes (Pl. VIII, A).....8
- 4 - Siphons predominantly cylindrical (sometimes slightly torulose).....5
- 4 - Siphons both cylindrical and torulose.....6
- 5 - Siphons with torulose character; apices rounded....A. longicaulis
- 5 - Siphons with some torulose character; apices distinctly clavate.....A. clavatiramea
- 6 - Siphons cylindrical in the interior, becoming increasingly ramified and torulose near the surface; apices tapered to sometimes threadlike.....A. asarifolia
- 6 - Siphons intensely torulose and moniliform throughout most of the blade; a few cylindrical siphons in the interior.....7
- 7 - Siphons ramified near the surface 19-28-(38-47)-66.A. nigricans
- 7 - Siphons less ramified, less moniliform; squat plant.....A. nigricans  
f. fulva
- 8 - Siphons predominantly cylindrical (occasionally torulose siphons may be seen but are definitely subordinate).....9
- 8 - Siphons markedly torulose and cylindrical.....13
- 9 - Siphons exclusively cylindrical, yellow; apices rounded.....A. erecta

- 9 - Siphons cylindrical with occasional torulose patches of nonyellow siphons; apices rounded and sometimes clavate.....10
- 10 - Siphons tapered towards the surface, apices rounded (12-9).....Avrainvillea n. sp.
- 10 - Siphons not tapered, apices clavate.....11
- 11 - Blades planar or multiply fused, tightly woven.....A. obscura  
f. proxima
- 11 - Blades open and unconsolidated to loosely woven.....12
- 12 - Blades loosely woven, particularly along the peripheral edges.....A. obscura  
f. taylori
- 12 - Blades sessile, capitular tuft of unwoven siphons.....A. obscura  
f. capituliformis
- 13 - Siphons tapered apically.....14
- 13 - Siphons rounded and sometimes clavate apically.....15
- 14 - Dichotomies weakly constricted, may be extremely tapered but not threadlike.....A. sordida
- 14 - Dichotomies strongly constricted, distinctly hooked apices.....A. pacifica
- 15 - Blades entire or split to the stipe forming lobes; single, supradichotomal swelling constricted; rounded to subclavate apices.....A. elliottii
- 15 - Blades narrow to eroded, sometimes gregarious in habit; single supradichotomal swellings absent; dichotomies weakly constricted; apices longly clavate.....A. ridleyi

- 16 - One to two blades per stipe.....17
- 16 - Three to twenty blades per stipe.....19
- 17 - Thallus large to 30 cm tall; siphons cylindrical becoming longly torulose near the surface, siphon diameters greater than 19  $\mu$ m, dichotomies moderately constricted.....A. gardineri
- 17 - Thallus very small, less than 10 cm tall; siphons evenly mixed (torulose and cylindrical), siphon diameters less than 19  $\mu$ m, dichotomies weakly constricted.....18
- 18 - Siphons of 4.5 - 6-(9-12)-19); sparsely tortuous; apices rounded.....A. riukuensis
- 18 - Siphons of 3-(6-12)-14; very tortuous; apices tapered; more torulose than above.....A. hollenbergii
- 19 - Apices tapered, tortuous, not ramified.....A. lacerata
- 19 - Apices rounded, not tortuous, ramified.....20
- 20 - Thallus large to 18 cm tall.....A. amadelpa  
f. submersa
- 20 - Thallus small and gregarious, 4-8 cm tall....A. amadelpa  
f. montagneana

Note: A. canariensis is not included in the key

Avrainvillea lacerata J. Agardh 1887

[Plates I. A, B, C; XII. A]

Synonymy: Udoëa lacerata Harvey, Exsicc. Friendly Is., 1855.

Avrainvillea lacerata J. Agardh, 1887, p. 54; Murray  
and Boodle, 1889, p. 71; DeToni, 1889, p. 515;  
Gepp and Gepp, 1911, p. 38; Nasr, 1947, p. 48;  
Taylor, 1950, p. 70; Trono, 1968, p. 175; Valet,  
1968, p. 50; Pham-hoang Hô, 1969, p. 511;  
Womersley and Bailey, 1970, p. 280.

Type Locality: Tonga, Polynesia

Type Deposited: British Museum

Distribution: Tropical Indo-Pacific including Malaysian and Indonesian  
Archipelagos, Philippines, Melanesia, and Polynesia [Plate XXII].

Specimens Examined: KAPINGAMARANGI, Newhouse 1109, 1027, 1213,  
July 1954 (DOTY). MARSHALL IS., Bikini Atoll, Smith 47-24,  
8 July 1947 (UC 1452277). LINE IS., Fanning Is., Wainwright,  
9 July 1963 (DOTY 20698); DeWreede 1255, 1217, Jan. 1970 (DOTY);  
Palmyra Atoll, Dawson 19408, 19473, 19580, 19541, 19456, 19440,  
19419, 19483, Oct. 1958 (UC M142094, MI42090, MI42091, MI42089,  
MI42112, MI42088, MI42087, MI42085). MARIANA IS., Anatahan,  
Tobias 4 and 8, 1 Jan. 1975 (GUAM). W. CAROLINE IS., Yap,  
Tsuda 4042, 30 Nov. 1970 (GUAM); Palau, Meñez, 22 Aug. 1960  
(US 49113, 49112, 49114 and DOTY 15984, 21675, 21164); Ogden  
N979, 1978 (OGDEN). TONGA, Harvey 86, 188? (BM - type);  
Moseley 1884 (BM). SOLOMON IS., New Georgia, Womersley and  
Bailey 496, 3 Sep. 1965 (UC M256401, US 48605); Gizo Is.,

Womersley and Bailey 513, 5 Sep. 1965 (UC M256400, US 48608); Florida Is., Bailey 123a, July 1965 (ADU). SOCIETY IS., Tahiti, Setchell and Parks 5200, 5110, June 1922 (UC 261226, 261225); Crossland 6663, May 1925 (UC 667654); TUAMOTU IS., Raroia Atoll, Doty 11882, 21 Aug. 1952 (DOTY). PHILIPPINES, E. Samar, Cordero, 12 June 1973 (PNH 112468); Zamboanga, Meñez T1051, 16 Sep. 1967 (DOTY); Palauan, anonymous 5726, 24 Apr. 1964 (UC M115148); anonymous 8-224, 7 Oct. 1928 (UC 699328). JAVA, Setchell 549c, May 1929 (UC 624593); Setchell 547, May 1929 (UC 624592). SINGAPORE, Cormer 23196, 1 Jan. 1930 (UC 417177). MALAYSIA, Penang, Burkill 3381, 21 Jan. 1964 (DOTY).

History: A. lacerata was originally collected by Harvey in Tonga. He listed the new alga in his *Algae Exsiccatae*, Friendly Islands (1855) under the name Udotea lacerata. No description accompanied the new species. It was not until 1887 that a formal diagnosis was published by J. Agardh in which he recognized the species as belonging to Avrainvillea. He included Udotea sordida and Chlorogplegma sordidum in this synonymy, an error which was unfortunately perpetuated by Murray and Boodle (1889). In 1911 the Gepps reexamined these specimens and excluded them from their synonymy. A detailed discussion of the early synonymy of A. lacerata is given by them.

Over the past sixty years the alga has been widely reported throughout the tropical Indo-Pacific.

Description: The plants are light green to olive, to 12 cm tall. The thallus is characterized by many small blades arising from a repeatedly branching stipe. The blades are papery in texture,

thin, and distally lacerate. In shape they are mostly cuneate, but occasionally obovate or orbicular, 2 cm wide by 2-3 cm tall, sometimes reaching 4-6 cm wide by 4-5 cm tall. The slender stipe is multiply and irregularly branched. The holdfast is a compact rhizomal tuft attaching to rubble as opposed to the deep sandy type found in the "obscura" group. Plants are often found in rocky, somewhat cryptic habitats.

The siphons of the interior are cylindrical, pale olive to colorless. In the deeper portions of the frond the siphons range from (19-28) becoming more slender and distinctly tapering near the surface (12-9)-6. The tapering characteristic is quite pronounced. The surface siphons may show a lightly and irregularly torulose character but this is not a dominant feature. Although the surface siphons may be moderately tortuous they are not so highly ramified and interwoven as in A. amadelpa. Dichotomies are deep and often longly constricted.

Discussion: The Gepps recognized two morphological forms of A. lacerata. Forma typica is described above. A second variety, robustior, refers to a habit identical with that of A. amadelpa f. montagneana though the siphon structure was supposedly identical to that of A. lacerata. This variety was found in the western distributional range of A. lacerata nearer the type locality of A. amadelpa. Examination of the Gepp's v. robustior suggests an eroded A. amadelpa, a possibility acknowledged by the Gepps. A. lacerata v. robustior is reclassified as A. amadelpa.

Examination of a large and wide variety of specimens, including the type, has established that A. lacerata is remarkably uniform throughout its range.

The Micronesian material fits the classical pattern of A. lacerata f. typica. Moving east and south into the Marshalls, Kapingamarangi, and the Line Islands, some of the materials begin to take on some "amadelpa" character, i.e., more heavily ramified, torulose, and less tapering surface siphons. This observation was also noted by Taylor (1950). However, the specimens may still be regarded as A. lacerata. Circling again to the west, the material once again takes on the classical A. lacerata character and, indeed, A. amadelpa is found there. Moving up through the Solomons and into the Philippines, the classic pattern once again dominates, as it does throughout Java, Malaysia, and Singapore.

A. lacerata has been reported in the literature from the Red Sea and eastern coast of Africa. Examination of some east African material reveals it to be A. amadelpa f. submersa. Red Sea material will most likely prove to be A. amadelpa as well.

Affinities: A. lacerata is a pivotal species around which several other species revolve, forming the "lacerata" group. Most closely allied are A. amadelpa and A. sordida, followed by A. hollenbergii and A. riukuensis, in approximately equal importance.

A. lacerata may be distinguished from A. amadelpa by its generally larger and slimmer habit, papery and lacerate fronds, and tapering (6  $\mu$ m), less torulose apices. A. lacerata never develops a pseudocortex, a characteristic which is sometimes found in A. amadelpa.

It differs drastically in habit from A. sordida. A. sordida is solitary and more squat. Internally, A. sordida's siphons are less tortuous and nonconstricted (or slightly so) at their dichotomies.

A. hollenbergii and A. riukuensis are distinguished from A. lacerata by their very small siphon diameters, which average 6-9  $\mu\text{m}$ , and may be cylindrical or quite torulose, both deep within the blade as well as superficially. Also, the siphons of these two species appear less tapered.

Floristic and Miscellaneous Listings: Dawson (1957, 1962a), Doty (1954), Kanda (1944), Segawa and Kamura (1960), Setchell (1926), Svedelius (1924), Tanaka (1960), Taylor (1966, 1977), Trono (1978), Trono and Tuason (1978), Tsuda and Belk (1972), Tsuda and Tobias (1977), Tsuda and Wray (1977).

Avrainvillea hollenbergii Trono 1971

[Plates III. A; XII. B]

Synonymy: Avrainvillea hollenbergii Trono, 1971, p. 52.

Type Locality: Ifaluk Is., Caroline Islands, Micronesia

Type Deposited: Private herbarium of M. S. Doty, Univ. Hawaii

Distribution: Known only from Ifaluk. [Plate XXII].

Specimens Examined: CAROLINE IS. Ifaluk, Meñez, 10 Aug. 1960

(DOTY 23123 - Type); Abbott 129a, Oct. 1953 (UC M107304).

History: Specimens of the new species were collected by Meñez in the Carolines in 1960. Trono (1968), while working on a floristics paper, encountered the specimen and recognized it as a new Avrainvillea species, which he described in 1971. Another specimen, collected by Abbott in 1953, and described by her (Abbott, 1961) as A. obscura has been found to be A. hollenbergii. Additional records are not known.

Description: Plants are olive, small, 3-8 cm tall, solitary or consisting of two to three blades arising from a single stalk. The

blades are cuneate, thin, and distinctly zonate, forming lobed or slightly lacerate edges. Secondary lobes may arise from a peripheral edge or from the flat middle portion of the blade. The stipe is narrow and from 1-3 cm in length. The holdfast consists of a thick rhizomal tuft from which the stipe arises.

Internally, the siphons are very narrow ranging from 3-(6-12)-14. These siphons and those of A. riukuensis, are the narrowest in the genus. The siphons are predominantly longly torulose to cylindrical throughout the blade, becoming increasingly tortuous near the surface. The dichotomies are weakly constricted, if at all, especially the surface siphons. Apices are rounded and those siphons of 3-6  $\mu\text{m}$  are tapered. The blade teases apart easily and shows no evidence of pseudocortical development.

Discussion: A. hollenbergii is another member of the "lacerata" group. Its small tightly interwoven siphons are its most distinctive characteristic. Trono (1971) states that there is a pseudocortex. I must disagree on this point.

Affinities: A. hollenbergii is most closely allied with A. lacerata and A. riukuensis. In habit, A. hollenbergii resembles A. lacerata with respect to its thin fronds. However, it does not have the many blades so typical of A. lacerata. Internally, A. hollenbergii may be distinguished from A. lacerata by its very small, torulose siphons. It differs from A. riukuensis by its torulose siphons. A. riukuensis is rarely torulose and has siphons of slightly larger average diameter.

Floristic and Miscellaneous Listings: Trono (1968), Tsuda and Wray (1977).

Avrainvillea riukuensis Yamada 1932

[Plates II. C, D; XII. C]

Synonymy: Avrainvillea riukuensis Yamada, 1932, p. 267.

Avrainvillea gracillima Børgesen, 1940, p. 52.

Type Locality: Naha, Okinawa, Japan

Type Deposited: Hokkaido University Herbarium, Japan

Distribution: Known certainly from the Ryukyu Islands and Mauritius

[Plate XXII].

Specimens Examined: OKINAWA, Yamada 12768b, June 1931 (SAP - cotype).

MAURITIUS, Børgesen 902, 15 Oct. 1929 (C).

History: The alga was first collected in 1931 and described the following year. In 1940, Børgesen described a new species, A. gracillima, from Mauritius. Examination of both type specimens suggests synonymy with A. riukuensis which takes priority as the older name.

Description: A. riukuensis is pale, brownish green, and solitary, 2-10 cm tall. The blade is thin distinctly zonate, and cuneate. The edges are smooth or slightly lacerate. The stipe is 2-3 cm long and very narrow, 0.5 cm. The holdfast is small and bulbous, reportedly attached to rocks and coral rubble.

Siphons range in diameter from (9-12)-19 deep within the blade but are mixed with siphons of (4.5-6) in diameter both in the interior and surface portions of the blade. These siphon diameters are among the smallest in the genus. The siphons tease apart easily and are mostly cylindrical becoming increasingly tortuous near the surface. Siphons may show some torulosity for a short distance, but this is

uncommon. Dichotomies are moderately to poorly constricted. Apices are not tapered into threads but delicately rounded. Unlike other Avrainvillea species, in which there is often a noticeable layering of larger siphons to the inside, A. riukuensis has a homogeneous mixture of all the sizes throughout the frond.

Discussion: Yamada's A. riukuensis and Børgesen's A. gracillima have identical microscopic structure. In habit they are similar though Børgesen's type plants are very small. Both workers report that their specimens were found growing on calcareous algal walls and rubble. This is fairly atypical for Avrainvillea.

Yamada reports his plants as growing as tall as 17 cm and the surface siphons being as wide as 20  $\mu\text{m}$ . My measurements suggest a smaller average range. Siphons of 20  $\mu\text{m}$  near the surface were rare. Børgesen reported siphon diameters of up to 30  $\mu\text{m}$ . These were not evident and, if present, are very rare and certainly not typical. In other respects I agree with Børgesen's and Yamada's descriptions.

The patchy distribution of the alga is undoubtedly artificial and will begin to fill in as more collecting is done.

Affinities: A. riukuensis is another member of the "lacerata" group. It is most closely allied with A. lacerata in terms of internal structure but its remarkably small siphon size quickly distinguishes this species. In habit it resembles A. gardineri and A. hollenbergii. These two are quite distinctive internally, the former having larger siphons which are quite torulose near the surface. The latter is quite torulose throughout, though its siphons are also very narrow.

Floristic and Miscellaneous Listings: Dawson (1962a), Segawa and Kamura (1960).

Avrainvillea amadelpha (Mont.) Gepp 1908

[Plates I. D; XII. D; A-IV. C]

Synonymy: Udotea amadelpha Montagne, 1857, p. 136.Chloroplegma sordidum Zanardini, 1858, p. 290.Avrainvillea lacerata Hieron., 1895, p. 24; Harvey-Gibson,  
1908, p. 77.Avrainvillea amadelpha, Gepp and Gepp, 1908, p. 42;

Gepp and Gepp, 1911, p. 42; Børgesen, 1940, p. 54;

Nasr, 1947, p. 48; Børgesen, 1948, p. 33.

Type Locality: Galega Is., Indian Ocean

Type Deposited: Paris Museum

Distribution: Red Sea, down the coast of E. Africa across the Indian  
Ocean, Polynesia, and eastern Micronesia [Plate XXI].Specimens Examined: SOCIETY IS., Tahiti, Crossland 7027, 25 Sep. 1928  
(UC 341210); Crossland 7066, 28 Sep. 1928 (UC 341172); Crossland  
7245, 7 Nov. 1929 (UC 791865); Crossland 7293, 9 Sep. 1929  
(UC 667852). FRENCH SOMALILAND, Papenfuss and Scagel PR-I-9,  
16 Sep. 1962 (UC 1451311). ZANZIBAR, Hildebrandt 184, Dec. 1875  
(UC 434145). KOSRAE, Best, June 1979 (GUAM).History: The original specimens were collected by Le Duc from  
Galega (Indian Ocean) and later described by Montagne as Udotea  
amadelpha. In the following year Zanardini described a new genus,  
Chloroplegma, from an interesting specimen collected from the Red  
Sea. In 1895 the specimens were recognized as belonging to the genus  
Avrainvillea. In 1908 E. S. Gepp redescribed the species as A.  
amadelpha.

Description: Plants of A. amadelpha f. montagneana (most common) are dark brown to olive, short, 4-8 cm in height, densely congregated, and arise from a multiply branched stipe. The blades are cuneate to spatula-like, 0.5-1 cm wide by 1-2 cm tall, thin but firmly interwoven. Peripheral edges of the blades are usually entire to quite eroded. The stipes are always branched, 2-3 cm long and 0.25 cm wide. The holdfast consists of a rhizomal mat which spreads laterally to accommodate the gregarious habit.

Plants of A. amadelpha f. submersa (deep-water form and probably less common) are tall, 12-18 cm in height, consisting of a few fronds, 3-10 in number, arising from a branched stipe. In habit this plant may easily be confused with A. lacerata.

The internal structure of both forms consists of two layers. The deeper areas of the frond are composed of predominantly cylindrical siphons (19-25) in diameter. Towards the surface, the siphons taper to an average diameter range of (19-15)-12. They are quite torulose and increasingly ramified. Dichotomal constrictions are moderate to deep. These surface ramuli may interweave to form a pseudocortex. Apices are rounded and do not taper to 6  $\mu$ m as in A. lacerata. The apices may be quite tortuous and intermittently swollen.

Discussion: The Gepps recognized two forms of A. amadelpha, a reef form, montagneana, and a deep-water form, submersa. The reef form is the most common and the one on which typical members of the species is based. There was no opportunity to examine the Gepps' f. submersa, but from their description, drawings, and some interesting specimens collected by Papenfuss and Scagel off the east coast of Africa, which I've had the opportunity to examine, this form is quite

distinctive. The habit of f. submersa is nearly identical to that of A. lacerata. Plants may be up to 18 cm tall, possessing several fronds arising from a branched stalk. Unlike A. lacerata, however, A. amadelpha f. submersa is not papery in texture or lacerated. Internally, both forms of A. amadelpha are identical.

The pseudocortex, which is the supposed earmark of the species, is not always well developed. Both the Gepps (1911) and Børgesen (1940) recognized this, and seem to stress its importance in their description. One should examine at least two areas of the blade to determine whether or not this feature is present. Pseudocortical development may be environmentally controlled and the lack of such development does not automatically rule out A. amadelpha. The structure of the apical ramuli is more important.

The close alliance of A. amadelpha with A. lacerata has resulted in another problem. Two forms of A. lacerata have been recognized historically (see A. lacerata discussion), one of which is an eroded form of A. amadelpha. Specimens of A. lacerata f. robustior are now reclassified as A. amadelpha.

The authenticated distribution of A. amadelpha is quite patchy. From its type locality in the Chagos Archipelago of the Indian Ocean, it is also reported from the Red Sea, and, somewhat unexpectedly, in the Tuamotus of Polynesia, and most recently, Kosrae in southeastern Micronesia. Obviously, this species is more widespread than initially believed.

Affinities: A. amadelpha is most closely allied with A. lacerata and A. gardineri. To a lesser extent it is also allied with A. ridleyi, A. pacifica, and A. asarifolia.

In habit, both A. amadelpa and A. lacerata are similar, but A. lacerata is generally larger, has a thinner blade, and is very lacerate. The internal siphon structure is also similar, both species having deeper cylindrical siphons of 19-25  $\mu\text{m}$  in diameter. A. lacerata, however, may be distinguished by its tapering (to 6  $\mu\text{m}$ ), less torulose surface siphons. Lack of a pseudocortex is not sufficient to rule out A. amadelpa.

A. gardineri has a large solitary habit and thin blade. As to internal structure, the two species are very difficult to distinguish. The siphons of A. gardineri are mostly longly torulose and tend to show little tapering between the deeper and more superficial siphons. A. gardineri may eventually prove to be synonymous with A. amadelpa in spite of their differences in habit.

A. amadelpa may be distinguished from A. ridleyi in that the latter's average siphon diameters are larger and there is a definite clavate character. Also, the torulose character is more highly developed in A. ridleyi.

A. pacifica has a thicker, generally solitary blade. The internal structure is similar but the ultimate ramuli of A. pacifica are extremely hooked and twisted at their apices. Moreover, A. pacifica is quite moniliform, even in the deeper layers.

Finally, it has been suggested that A. amadelpa and A. asarifolia are geographic counterparts (Gepp and Gepp, 1911), differing only in habit. I cannot agree with this interpretation. A. asarifolia has a solitary habit, more tapering, and more torulose apices. It is much closer to A. sordida.

Floristic and Miscellaneous Listings: Dawson (1962a), Lami (1932), Lipkin (1972), Newhouse (1969), Papenfuss (1968), Rayss (1959), Svedelius (1924), Tsuda and Wray (1977).

Avrainvillea gardineri Gepp & Gepp 1908

[Plates II. A; XIII. A]

Synonymy: Avrainvillea gardineri Gepp and Gepp, 1908, p. 179; Gepp and Gepp, 1909, p. 389; Gepp and Gepp, 1911, p. 36.

Type Locality: Cargados Carajos, Indian Ocean

Type Deposited: British Museum

Distribution: Known only from Cargados Carajos [Plate XXI].

Specimens Examined: Cargados Carajos, Gardiner, 1905 (BM - type).

History: Two specimens were collected by N. L. Gardiner from deep water (30-47 fathoms) off Cargados Carajos in 1905.

Description: The plants are pale olive, solitary, and distinctly stipitate to 30 cm tall. The blade is thin, zonate, and somewhat translucent when held up to the light. The blades are rhomboid to orbicular, 12-20 cm in diameter, and entire to quite lacerate at their peripheral margins. The stipe is narrow and well developed but short, 1-2 cm, in proportion to the large size of the blade. The holdfast is similar in size to the stipe, extending deeply into the substratum several centimeters.

Internally, the siphons are loosely interwoven but very difficult to tease apart. Some areas seemed to be pseudocortical. The siphons are cylindrical (19-28) in the deeper regions of the blade becoming increasingly torulose nearer the surface. Dichotomies are moderately constricted and wide angled. The degree of ramification near the

surface is variable. Older portions of the blade are more heavily woven. The apices are rounded and not tapered (12-15).

Discussion: In habit A. gardineri is suggestive of A. nigricans. Both are very large. A. gardineri's texture, however, is much thinner and less spongiöse than that of A. nigricans. Moreover, the holdfast of A. gardineri is not composed of a rhizomal mat, but a single deep continuation of the stipe, like that found in the "obscura" group.

The internal structure of A. gardineri is alarmingly similar to that of A. amadelpha, including what appears to be a lightly developed pseudocortex in the older portions of the plant. The torulose character in the type specimens of A. gardineri is less compact, being long and not so tapering. This difference, however, is hardly satisfactory in and of itself.

The possibility of A. gardineri's synonymy with A. amadelpha cannot be entirely ruled out. The type locality for both species is in the Chagos Archipelago. In addition, A. amadelpha f. submersa has a habit at least somewhat closer to that of A. gardineri but never reaches the extreme sizes reported for A. gardineri. Because of this extreme difference in habit and so little material on which to judge, A. gardineri remains a discrete species but closely allied with A. amadelpha.

Affinities: A. gardineri is most closely allied with A. amadelpha in terms of siphon structure. In habit they are conspicuously different and should be easily distinguishable. Other allies include A. pacifica and A. nigricans. The habit of A. pacifica is generally solitary (though two or three fronds are possible) and it is very thick. Internally, its siphons form uniquely hooked apices. A. gardineri might be

confused as A. nigricans in the field because of its large size, but in texture A. gardineri is very thin. Moreover, A. nigricans is quite moniliform in most specimens, and its siphons are larger in diameter. On these points the plants may be easily distinguished.

Floristic and Miscellaneous Listings: Svedelius (1924).

Avrainvillea pacifica Gepp & Gepp 1911

[Plates II. B; XIII. B; A-II. D]

Synonymy: Avrainvillea pacifica Gepp and Gepp, 1911, p. 37.

Type Locality: Faulopa, Ellice Islands, Pacific

Type Deposited: British Museum

Distribution: Ellice Islands, American Samoa [Plate XXI].

Specimens Examined: ELLICE IS., Faulopa, A-14, 16 Sep. 1898

(BM 292 - type). SAMOA, Randall, 9 May 1974 (GUAM).

History: The original specimens were collected during the Funafuti Expedition and were thought to be A. lacerata until examined by the Gepps.

Description: The plants are brownish green, stipitate, consisting of one or two fronds. Blades are spongy to velutinous, cuneate to reniform, and entire at their peripheral edges. Blades are 5-8 cm in width and 3-6 cm tall. The stipe is thick and relatively short, 1-2 cm, but the holdfast is bulbous.

The siphons are lightly torulose throughout the frond (19-28) and tapering to 9  $\mu$ m at the surface. The siphons become increasingly ramified near the surface and more intensely torulose to even moniliform. Apices are distinctly hooked and twisted at their apices, though there is no pseudocortex.

Affinities: A. pacifica is another member of the "lacerata" group. It is most closely allied with A. amadelpa in terms of siphon structure. It is uniquely different, however, in its hooked and pointed apices. This unique characteristic makes it quite easy to identify. In habit it is somewhat reminiscent of A. sordida but is easily distinguished from that species by the hooked apical character.

Floristic and Miscellaneous Listings: Chapman (1955), Dawson (1962a), Schmidt (1928), Svedelius (1924), Tsuda and Wray (1977).

Avrainvillea elliotii Gepp & Gepp 1911

[Plates IV. B, C, D; V. A, B; XIII. C; A-IV. B]

Synonymy: Avrainvillea sordida Murray and Boodle, 1889, p. 70 and 238; DeToni, 1889, p. 514.

Avrainvillea elliotii Gepp and Gepp, 1911, p. 35.

Avrainvillea geppii Børgesen, 1913, p. 87; Taylor, 1960, p. 161.

Avrainvillea elliotii, Taylor, 1960, p. 162.

Avrainvillea atlantica Joly et al., 1965, p. 159.

Avrainvillea elliotii, Dawes, 1974, p. 79.

Type Locality: Grenada, Caribbean Sea

Type Deposited: British Museum

Distribution: The species is widely distributed throughout the Caribbean, Gulf of Mexico, and the southern Atlantic coast of Brazil [Plate XIX].

Specimens Examined: GRENADA, Morne Rouge Bay, Elliott, May-June 1887 (BM 218 - type). W. FLORIDA, Dawes 7037, 30 June 1971 (USF 96776). BELIZE, Dawes 9014, 15 June 1978 (USF 135044). VIRGIN IS., St.

Croix, Ogden 631, 602, 597, July 1976 (OGDEN); St. Jan, Børgesen 2011, 17 Mar. 1906 (C - Børgesen's type for A. geppii). BRAZIL, São Paulo, Joly, 22 Jan. 1960 (SP - Joly and Yamaguishi's type for A. atlantica).

History: Original specimens were collected by Elliott in Grenada for Murray. They were included along with other specimens of A. sordida in Murray and Boodle's 1889 description. Some twenty years later, the Gepps recognized the error and ascribed the unique specimens to a new species. The species is a common one and apparently more widespread than previously believed. Examination of the type plants of Joly and Yamaguishi's A. atlantica and Børgesen's A. geppii revealed that they are members of the Gepps' A. elliottii.

Description: Plants are brownish olive, generally solitary, and lightly zonate, from 6-15 cm tall. The blades are typically thin but can be moderately thick, and soft. The blades may be obovate to longly, transversely reniform with a vertical split to the stipe. In this habit the plant might be described as lobed. The blades range from 2-5 cm tall by 6-10 cm in width. The peripheral margins may be entire, lobed, or slightly lacerate. The stipe is narrow, 2-5 cm in length. The holdfast is erect and deeply penetrating into the substratum.

The siphons of A. elliottii are irregularly cylindrical, becoming patchily and irregularly torulose near the surface, 15-(20)-38. Supradichotomal constrictions are deep and often characterized by a single swelling just above the fork. There is little ramification of the surface siphons and no tapering apically. Apices are rounded to slightly subclavate or clavate.

Discussion: An interesting aspect of A. elliotii's habit is a split-lobed configuration which is often present. This characteristic is not reliable by itself but may be helpful as a field aid. The supradichotomal swellings are not uniformly present but are another useful guide.

Examination of Børgesen's A. geppii suggests its synonymy with A. elliotii. Though the type of A. geppii does not have the split-lobed habit, its internal structure is identical with that of A. elliotii. In Børgesen's (1913) discussion of his plants, he relates a conversation with the Gepps in which they believed his plants to be A. sordida or A. asarifolia. He disagreed with them on grounds of differences in habit. He states that his plants were more closely allied with members of the "obscura" group because of their rounded to subclavate apices. Later, Mrs. Gepp examined a specimen of A. geppii and was of the opinion that it was probably A. elliotii. Again Børgesen disagreed, this time on the grounds of his plant's greater torulose character. I must disagree with Børgesen on all three of his arguments. Habit is not a solely reliable criterion in most cases. A. geppii is decidedly not a member of the "obscura" group, and finally, slight differences in torulose character based on only two specimens is probably not sufficient to distinguish it from A. elliotii. I have, therefore, placed A. geppii in synonymy with A. elliotii.

Joly et al. (1965) described a new Avrainvillea species, A. atlantica. Having been afforded an opportunity to examine their type, as well as other specimens, I believe it to be yet another example of A. elliotii. Joly and Yamaguishi state that they found no torulose character in their plants. I cannot agree with that. Clearly,

there are patchy torulose areas in the surface layers of the individuals I examined. They speculated on the alliance between their plants and A. canariensis, this point remains to be resolved at some future date.

Affinities: A. elliotii is yet another member of the "sordida" group. It is distinguished from A. sordida by its slightly thicker siphons, which are more uniform in diameter throughout the blade. Unlike A. sordida, there is no extreme apical tapering.

It may be distinguished from A. asarifolia by its considerably smaller habit, less torulose, nontapering, and nonramified apices. A. elliotii appears to align itself between A. sordida and A. asarifolia.

Floristic and Miscellaneous Listings: Collins (1909), Dawson (1962a), Diaz-Piferrer (1969a, 1969b), Schnetter (1978), Svedelius (1924).

Avrainvillea asarifolia Børgesen 1908

[Plates III. D; IV. A; XIII. D]

Synonymy: Avrainvillea asarifolia Børgesen, 1908, p. 34; Gepp and Gepp, 1911, p. 44; Børgesen, 1913, p. 89; Taylor, 1960, p. 161; Dawes, 1974, p. 78.

Type Locality: St. Thomas, Caribbean Sea

Type Deposited: University of Copenhagen (?)

Distribution: Gulf of Mexico, Caribbean, especially well-known from the Bahamas and Virgin Islands [Plate XIX].

Specimens Examined: DOMINICAN REPUBLIC, Santo Domingo, Rodriguez and Lopez 7162, Dec. 1974 (UC 1457482); Almodovar 7344, 26 Jan. 1976 (UC M260946); Randall 5093a, 12 Apr. 1965 (UC M110561). VIRGIN

IS., St. Croix, Ogden, Feb. 1979 (GUAM). BELIZE, Glover's Reef, Tsuda 4200, 3 Nov. 1971 (US 48096, and GUAM). FLORIDA, Humm, 25 June 1971 (USF 129738); Dawes 3511a, 23 Apr. 1966 (USF 77041).

History: Specimens were originally collected in the Virgin Islands by Børgesen and later described by him in 1908. Since that time the species has been widely reported throughout the Gulf of Mexico and the Caribbean Sea.

Description: The plants are dark olive, solitary, and zonate, to 20 cm tall. The blades are thin to medium thickness, tightly woven, and smooth-edged. They are orbicular to cordate-rotundate, 6-10 cm tall by 6-15 cm wide. The stipes are well developed, cylindrical, and narrow, 2-12 cm long. The holdfast is deeply penetrating to form a bulbous mass just below or on the surface of the substratum.

The siphons are predominantly cylindrical (20-30) in the deeper portions of the blade, becoming tapered and increasingly torulose, and ramified near the surface (8-13). The dichotomies are strongly constricted and the apices tapered, often to such an extent that the surface siphons appear threadlike.

Discussion: A. asarifolia has been referred to as the geographic counterpart of A. amadelpha. I cannot agree with this interpretation. The habit of A. amadelpha is fundamentally different, consisting of densely congregated fronds arising from a multiply branched stipe. The tapering character of the surface siphons is a reliable character, and is absent in A. amadelpha. A. asarifolia is a member of the "sordida" group rather than the "lacerata" group.

Affinities: A. asarifolia is most closely allied with A. sordida and A. elliottii. It differs from A. sordida in habit, being typically larger and less yellow in color. Internally, it is more torulose, ramified, and apically tapered than A. sordida. A. elliottii is easily distinguished by its slightly larger diameter siphons, lack of surface ramification, rounded, rather than tapered apices, and single supradichotomal swellings.

Floristic and Miscellaneous Listings: Dawson (1962a), Diaz-Piferrer (1969a), Phillips and Springer (1960), Schnetter (1978), Svedelius (1924), Taylor (1928, 1969a, 1969b), Tsuda and Dawes (1972).

Avrainvillea sordida Murray & Boodle 1889

[Plates III. B, C; XIV. A]

Synonymy: Rhipilia longicaulis Kützing, 1858, p. 13.

Avrainvillea sordida Crouan ex Mazé and Schramm, 1870-77,  
p. 89.

Avrainvillea sordida Murray and Boodle, 1889, p. 70 and  
238; DeToni, 1889, p. 514.

Avrainvillea levis Howe, 1905, p. 565; Collins, 1909, p. 390.

Avrainvillea sordida, Gepp and Gepp, 1911, p. 40.

Avrainvillea levis, Taylor, 1960, p. 162; Humm and Taylor,  
1961, p. 365.

Avrainvillea sordida, Gilbert and Doty, 1969, p. 124.

Avrainvillea levis, Dawes, 1974, p. 79.

Type Locality: Guadeloupe, Caribbean Sea

Type Deposited: British Museum

Distribution: Known throughout the Caribbean Sea, Gulf of Mexico, and  
the Philippines [Plate XVIII. A, B].

Specimens Examined: GUADELOUPE, Mazé 30, 1887 (BM - type). FLORIDA KEYS, Croley, 24 Nov. 1966 (USF 81494). BAHAMAS, Howe 3996, 19 Feb. 1905 (UC 77227, Howe's type of A. levis); Howe 1478, 15 Dec. 1907 (DOTY). BELIZE, Dawes 6997, 23 Oct. 1971 (USF 96857). PHILIPPINES, Velesquez 3503, May 1958 (PNH 34930); Gutierrez, 20 Apr. 1960 (PNH 41417).

History: Original specimens were collected by Crouan and designated as Avrainvillea sordida. Mazé and Schramm published the species without a description. A diagnosis was not supplied until 1889 when Murray and Boodle revised the genus. The type was Maze No. 30.

In 1905, Howe redescribed the species under the name A. levis. A new type (Howe 3996) was so designated.

In 1911, the Gepps considered A. levis to be a synonym of A. sordida and accordingly combined the two. Examination of both Maze's No. 30 and Howe's 3996 confirms the Gepps' conclusions. The two are conspecific.

The inclusion of Rhipilia longicaulis in the synonymy is correct in this author's opinion. It is excluded as the priority name for reasons discussed under A. longicaulis.

Description: Plants are olive to dirty yellow-brown, solitary or with two or three fronds, zonate, to 12 cm tall. The blades are thin, but soft and spongy, 3-8 cm wide. They are cuneate, obovate, or reniform. The edges of the blades are generally entire or somewhat lobed. The stipe is stout to moderately long, 1-4 cm. The holdfast is erect.

The siphons are transparent to yellow and mostly cylindrical, especially in the deeper areas of the blades. They range in diameter from (19-28)-37. Near the surface, the siphons may become lightly

torulose, tapered (12-9)-6, and tortuous. Apices are rounded to tapered but not so threadlike as in A. asarifolia. The surface siphons may be lightly interwoven. Dichotomal constrictions are deep in the larger siphons of the interior, becoming absent in the finer surface siphons.

Discussion: The "sordida" group may be considered the geographic counterpart of the "lacerata" group, though the former is found within the latter's domain. A. sordida is the pivotal species from which A. asarifolia and A. eliottii radiate. As expected, A. sordida shows sufficient variation in habit to make a field identification difficult.

Affinities: A. sordida often possess yellow siphons, a characteristic only regularly demonstrated by A. erecta. Its closest allies are A. asarifolia and A. eliottii. From A. asarifolia it differs by the presence of a less torulose character and less dramatically tapered apices. A. sordida differs from A. eliottii in that A. eliottii exhibits slightly thicker siphons, which are more uniform in diameter throughout the blade. Moreover, it does not exhibit the tapering, tortuous apices as does A. sordida.

Floristic and Miscellaneous Listings: Almodovar and Blomquist (1965), Britton and Millspaugh (1920), Dawson (1962a), Diaz-Piferrer (1969a), Howe (1907, 1918, 1920), Humm and Taylor (1961), Kim (1964), Svedelius (1924), Taylor (1969a, 1969b), Tsuda and Dawes (1972).

Avrainvillea nigricans Decaisne 1842

[Plate VI. A, B, C, D; XIV. B, C, D; A-I. B]

Synonymy: Avrainvillea nigricans Decaisne, 1842, p. 108.

Fradelia fuliginosa Chauvin, 1842, p. 124.

Avrainvillea sordida v. longipes Crouan ex Mazé and Schramm  
1870-77, p. 90.

Rhipilia longicaulis Dickie, 1874, p. 312.

Avrainvillea nigricans, J. Agardh, 1887, p. 53; Murray and  
Boodle, 1889, p. 70 and 238; DeToni, 1889, p. 513.

Avrainvillea longicaulis Murray and Boodle, 1889, p. 70  
and 238; DeToni, 1889, p. 514.

Avrainvillea nigricans, Howe, 1907, p. 508; Børgesen, 1908,  
p. 30; Vickers and Shaw, 1908, p. 23.

Avrainvillea longicaulis, Vickers and Shaw, 1908, p. 23.

Avrainvillea nigricans, Collins, 1909, p. 390; Gepp and Gepp,  
1911, p. 23; Børgesen, 1913, p. 84; Britton, 1918,  
p. 501; Taylor, 1950, p. 69; Taylor, 1960, p. 160;  
Tanaka, 1964, p. 77; Trono, 1968, p. 175; Dawes, 1974,  
p. 79.

Type Locality: Guadeloupe, Caribbean Sea

Type Deposited: Paris National Museum

Distribution: Widely distributed throughout the tropical Atlantic,  
Gulf of Mexico, and Caribbean Sea. Also distributed throughout  
Micronesia, the Philippines, and the east African coast.

Unauthenticated report from Fiji [Plate XVIII. A, B].

Specimens Examined: FLORIDA KEYS, Dawes 3912, 25 June 1966 (USF);  
Dawes 8805, Apr. 1978 (USF 135005); Dawes 5912, Dec. 1967 (USF);  
Taylor, 30 June 1926 (UC 315150); Howe 2963, 31 Mar. 1904 (UC  
77233). BERMUDA, Bernatowicz 51-787, 27 Jan. 1951 (UC 948383);  
Taylor and Bernatowicz 49-264, 14 Mar. 1949 (UC 948384);  
Bernatowicz 50-10, 7 Nov. 1950 (UC 948385); Bernatowicz 50-310,

24 Nov. 1950 (UC 948386); Bernatowicz 50-459; 18 Dec. 1950 (UC 948387); Bernatowicz 53-400. 8 June 1953 (DOTY); Bernatowicz 53-492, 23 July 1953 (DOTY). BAHAMAS, Howe 1480, 22 Dec. 1907 (DOTY); Howe 4052, 21 Feb. 1905 (UC 77231). CUBA, Dawson 7595, 10 May 1949 (UC 1404993). VIRGIN IS., Ogden N1131, 20 Mar. 1979 (GUAM); Welch, Mar. 1961 (GUAM). JAMAICA, Taylor 56-548a, 26 Apr. 1956 (UC M105396). MARTINIQUE, Hamel 15, Apr. 1930 (UC 687741). VENEZUELA, Diaz-Piferrer 20525a, 6 Mar. 1966 (UC 1403864); Diaz-Piferrer 20525b, 6 Mar. 1966 (UC 1403870). MARSHALL IS., Rongerik Atoll, Smith 47-222, 21 Aug. 1947 (UC 1452276); Bikini Atoll, Taylor 46-275, 14 May 1946 (UC 791705). MARIANA IS., Guam, Lassuy, 3 Feb. 1977 (GUAM). CAROLINE IS., Mokil, Meñez, 29 June 1960 (UC 1457275); Meñez, 29 June 1960 (DOTY 21380, 21317, 21343, 23096, 15973); Ifaluk, Meñez, 10 Aug. 1960 (DOTY 23110); Ulul, Meñez, 6 Aug. 1960 (DOTY 15860); Puluwat, Meñez, 7 Aug. 1960 (DOTY 23072). MOZAMBIQUE, Papenfuss and Scagel 1099, 15 Nov. 1962 (UC 1451284).

History: A. nigricans is the species on which the genus was originally described by Decaisne in 1842. The plants are easily recognized in both habit and siphon structure. Only A. longicaulis, whose habit is virtually identical, has been confused with A. nigricans. This accounts for the "teeter-totter" synonymy.

Though the species was first described from the Caribbean, it is also widely recognized in the tropical Indo-Pacific.

Description: A. nigricans is generally characterized as a dark brown to black plant, nonzonate, solitary, growing scattered or gregariously. Plants are typically large at maturity, up to 25 cm tall, but may be shorter. The blades are very thick, spongy, felt-like, and

sometimes hairy, cuneate to obovate, or rhomboid. Edges of the fronds are smooth to sometimes lightly lacerate. The blades are 3-25 cm in width and 3-20 cm tall, arising singly (occasionally more) from rounded to flattened stipes, which are 2-16 cm long. The holdfast is well developed, penetrating deeply into the substratum, or horizontally along the surface.

The siphons are predominantly moniliform 19-28-(38-47)-66, though in some specimens the deeper siphons may be more cylindrical. The siphons are not tapering but may become increasingly ramified near the surface, thus becoming smaller in diameter. Dichotomal constrictions are deep and the apices rounded. Tortuousness is not characteristic.

A. nigricans f. fulva Howe is described by him as a thicker, more squat plant, having poorly differentiated stipes and fronds. The siphons are coarser, 50-60  $\mu$ m, tapering (?), and less moniliform.

Discussion: A. nigricans is a most striking representative of the genus. As pointed out by Howe, Børgesen, the Gepps, Taylor, and others, the plant's habit can be quite variable, yet having once seen it in situ, an investigator usually recognizes it. A. nigricans is typified by its moniliform character, dark color, and large size. It must be emphasized, however, that these criteria also apply in varying degrees to A. rawsoni and A. longicaulis. Moreover, moniliform and torulose characters are not unique to just a few Avrainvillea species. It is seen in at least half of the species though seldom so conspicuously as in A. nigricans and A. rawsoni. The absence of moniliform character rules out A. nigricans, but its presence certainly does not rule it in.

Though many specimens of A. nigricans possess very large blades, blade size is not reliable by itself. Juvenile plants, in particular,

have to be taken into consideration, especially in scattered patches where mature plants may be scarce. Siphon size is not correlated with frond size. The average size ranges from 38-47  $\mu\text{m}$  but can go as high as 66  $\mu\text{m}$  and down to 19  $\mu\text{m}$ . The latter extreme applies to surface ramuli only, a character which is not always well developed.

Børgesen (1908) distinguished his plants by holding them up to the light. Because of the relatively loose texture, the plants are said to be translucent. Fresh specimens from the Virgin and Mariana Islands groups have not demonstrated this character.

Having examined specimens from throughout the range of A. nigricans I find them quite variable in habit, but reasonably consistent as to internal structure. This is contrary to most early workers' findings. Most described extreme variability at both levels. The Gepps (1911, p. 25) state that "they are so perplexing in their variability, that it seems quite impossible to separate them into satisfactory groups..." Howe (1905) went so far as to publish his A. nigricans f. fulva. This variant was described by him as having a, "more cuneate flabellum, flatter, broader, less differentiated stipes, and in the firmer-walled, usually coarser though often more tapering filaments, which are less regularly moniliform, often more tortuous..." Examination of A. nigricans f. fulva (Bernatowicz No. 50-459 and Howe No. 1480) agrees well with Howe's description except for the tapering. I must disagree on this point. Tapering was not apparent and is a characteristic I do not consider consistent with A. nigricans. A. nigricans f. fulva does show less of the moniliform character and may possibly be an intermediate of A. longicaulis and A. nigricans, a possibility suggested by the Gepps and Børgesen.

Comparisons between Atlantic and Indo-Pacific materials showed no major differences. A. nigricans consists of two groups. The first is the classic A. nigricans of predominantly moniliform character. There is little evidence of layering between deeper siphons and those of the surface and there is a minimum amount of ramification. The second group is more like that of Howe's f. fulva excluding his references to tapering. They are less moniliform to the inside and quite ramified at the surface, the surface siphons being more moniliform. Several of Taylor's specimens from the Marshall Islands fit this category.

The holdfast is quite well developed either horizontal or deeply penetrating. In sandy or muddy habitats, where water motion is moderately strong, erosion may result in the more horizontal appearance of the holdfast.

Affinities: A. nigricans is most closely allied with A. longicaulis and A. rawsoni. The siphons of A. longicaulis are cylindrical and not moniliform, despite nearly identical habits and well-established community alliances. A. rawsoni has a nonflabellar, cespitose habit and less deeply constricted, torulose siphons.

Floristic and Miscellaneous Listings: Almodovar and Pagan (1967), Britton and Millspaugh (1920), Collins and Hervey (1917), Dawson (1956), Diaz-Piferrer (1964b, 1969a, 1970), Gilmartin (1960), Howe (1918, 1920), Kapraun and Bowden (1978), Kim (1964), Mathieson and Dawes (1975), Phillips and Springer (1960), Svedelius (1924), Taylor (1969a, 1969b, 1972), Tsuda and Wray (1977), Vickers (1905).

Avrainvillea rawsoni (Dickie) Howe 1907

[Plates V. C, D; XV. A]

Synonymy: Rhipilia rawsoni Dickie, 1874, p. 151.Avrainvillea nigricans, Mazé and Schramm, 1870-77, p. 89;

Murray and Boodle, 1889, p. 70; DeToni, 1889, p. 513.

Avrainvillea rawsoni Howe, 1907, p. 510; Collins, 1909,

p. 390; Gepp and Gepp, 1911, p. 22; Taylor, 1960, p. 159.

Type Locality: Barbados, Caribbean Sea

Type Deposited: British Museum

Distribution: Common throughout the southern Atlantic, Gulf of Mexico  
and Caribbean Sea [Plate XIX].Specimens Examined: BERMUDA, Castle Is., Taylor and Bernatowicz 49-525,  
25 Mar. 1949 (UC 948419). BAHAMAS, Howe 5211, 30 Nov. 1907 (MO  
in UC 207254, UC 867512); Dawes 2772, 10 Aug. 1965 (USF 69017);  
Howe 1481, 8 Dec. 1907 (DOTY, BM). HAITI, Bartlett 17993, 23  
June 1941 (UC 677036); Bartlett 17828, 1 May 1941 (UC 677064).  
DOMINICAN REPUBLIC, Santo Domingo, Almodovar 7343, 26 June 1976  
(UC M260945). PUERTO RICO, Guayanilla, Almodovar 7033, 10 Aug.  
1974 (UC 1456557); Guardarrayo, Almodovar 5105, 4 Sep. 1965 (UC  
M155277); Isla Mona, Almodovar 7193, 22 Mar. 1975 (UC 1457507);  
Culebra, Almodovar 4050, 26 Mar. 1961 (UC M206713); Howe 4276,  
5 Mar. 1906 (UC 207528); Cabo Rojo, Almodovar 4570, 15 May 1962  
(UC M271026); Aguirre, Almodovar 4648, 11 Oct. 1962 (UC M109975);  
Caja de Muertos, Almodovar 7283, 14 July 1975 (UC 1457494); Cayo  
Santiago, Almodovar 4738, 7 Jan. 1963 (UC M109924). VIRGIN IS.,  
St. Croix, Ogden "B", Mar. 1979 (GUAM). FLORIDA KEYS, Dawes  
5954, 10 Dec. 1974 (USF); Dawes 3754, 23 Apr. 1966 (USF).

MARTINIQUE, Hamel 366, 18 Apr. 1930 (UC 751107). BARBADOS, Rawson and Watts, 188? (BM - type). JAMAICA, Taylor 56-426, 7 Apr. 1956 (UC M105341); Taylor 56-522, 24 Apr. 1956 (UC M105384). E. PANAMA, Taylor 39-236, 4 Apr. 1939 (UC 690597).

History: Specimens of A. rawsoni were originally placed with A. nigricans. It was not until 1907 that Howe recognized the specimens as a new species.

Description: Plants are dark green to brown, nonstipitate, forming a unique nonflabellar, cespitose mass of siphons which may project upwards as rotundate, finger-like projections, 4-10 cm tall. These may or may not be anastomosing. The texture is distinctly spongiose, similar to that found in A. nigricans.

The siphons are quite large, ranging from 38-(47-56)-76, though there is rarely more than a 15-unit range within a given specimen, e.g., 38-50  $\mu\text{m}$  or 60-76  $\mu\text{m}$ , etc. The siphons are very torulose to moniliform and isodiametric throughout the plant. The dichotomies are deeply constricted, apices rounded and sometimes tortuous. The tortuous character seems to be related to the amount of sand entrapped in the thallus.

Discussion: Having been afforded the opportunity to examine a wide range of plants, including fresh specimens from the Virgin Islands, it was found that A. rawsoni is remarkably consistent throughout its range. Its affinities with A. nigricans are most apparent though its lack of flabella is most unique.

Affinities: A. rawsoni is most closely allied with A. nigricans. However, A. rawsoni exhibits such a unique habit that even aberrant forms of A. nigricans are seldom misidentified. A. rawsoni is the only

member of the genus exhibiting a consistently nonflabellar habit. Internally, A. rawsoni, could be confused with A. nigricans, though the latter is usually more variable in terms of siphon size, which may show quite a large difference between deeper and surface layers, and, the degree of moniliformness. Moniliform character is much less consistent in A. nigricans. A. longicaulis is not moniliform and is thus differentiated from A. nigricans and A. rawsoni without difficulty.

Floristic and Miscellaneous Listings: Almodovar (1964), Almodovar and Pagan (1967), Britton and Millspaugh (1920), Dawson (1962b), Diaz-Piferrer (1964a, 1964b, 1969a), Earle (1972), Svedelius (1924), Taylor (1969a, 1969b, 1972), Tsuda and Dawes (1972), Young (1977).

Avrainvillea longicaulis (Kütz.) Murray & Boodle 1889

[Plates VII. A, B; XI. C; XV. B; A-I. A]

Synonymy: Rhipilia longicaulis Kützing, 1858, p. 13. (as to name only)

Avrainvillea sordida v. longipes Crouan ex Mazé and Schramm, 1870-77, p. 90.

Avrainvillea longicaulis Murray and Boodle, 1889, p. 70.

Avrainvillea mazei Murray and Boodle, 1889, p. 70.

Avrainvillea longicaulis, Howe, 1907, p. 509.

Avrainvillea mazei, Børgesen, 1908, p. 32.

Avrainvillea longicaulis, Collins, 1909, p. 391.

Avrainvillea mazei, Gepp and Gepp, 1911, p. 27; Børgesen, 1913, p. 85.

Avrainvillea longicaulis, Britton and Millspaugh, 1920, p. 611; Taylor, 1960, p. 60.

Type Locality: Guadeloupe, Caribbean Sea

Type Deposited: British Museum (=A. mazei, Mazé No. 65)

Distribution: Tropical Atlantic, Caribbean, Gulf of Mexico, and  
Micronesia [Plate XVIII. A, B].

Specimens Examined: NORTH CAROLINA, Searles 20478, 30 June 1972 (UC 1455050). BERMUDA, Wadsworth 68, Mar. 1890 (UC 97300); Taylor and Bernatowicz 49-1717, 11 May 1949 (UC 948409); Bernatowicz 49-1987, 7 June 1949 (UC 948407); Bernatowicz 50-47, 9 Nov. 1950 (UC 948408). FLORIDA KEYS & WEST COAST, Dawson 7409, 23 May 1949 (UC 1404966); Dawes 3913, 25 June 1966 (USF 77817); Killip 41781, 18 Jan. 1952 (UC M056077); Dawes 1723, 23 Aug. 1964 (USF 69005). BAHAMAS, Dawes 2872, 8 Aug. 1965 (USF 69007); Howe 5173, 28 Nov. 1907 (UC 207064); Howe 1479, 11 Dec. 1907 (DOTY). PUERTO RICO, Almodovar 6139, 26 Feb. 1970 (UC 1408142). VIRGIN IS., Ogden N1130, 2 Mar. 1979 (GUAM). JAMAICA, Taylor 56-568, 6 May 1956 (UC M105408); Pease and Butler 770, June 1900 (UC 111744). GUADELOUPE, Mazé 65, 1887, (BM - Murray and Boodle's type for A. mazei). GUAM, Stojkovich, 3 Feb. 1979 (GUAM).

History: Avrainvillea longicaulis was newly described by Murray and Boodle in 1889. In the same paper they also described another new species, Avrainvillea mazei. The synonymy of A. longicaulis included Rhipilia longicaulis Kützing 1858, and A. sordida v. longipes Crouan. There was no synonymy attached to their A. mazei.

Several years later it was recognized by Howe and other workers that some of Murray and Boodle's specimens, which they had labeled A. longicaulis, were really A. nigricans. Howe (1907), who had seen many specimens of A. longicaulis, recognized A. longicaulis (Kütz.) Murray

and Boodle, but considered their A. mazei a synonym for A. longicaulis. He retained the epithet longicaulis because he considered Rhipilia longicaulis to be the true type. He believed it more judicious to disregard Murray and Boodle's error and retain A. longicaulis.

Børgesen (1908, p. 32) disagreed with Howe's interpretation. He considered Rhipilia longicaulis to be a synonym of A. mazei, which he recognized as a good species. As far as he was concerned, A. longicaulis did not exist. Børgesen states that, "had Howe now called this species [R. longicaulis] A. longicaulis Howe, I might perhaps agree with him..." Børgesen goes on to say:

In my opinion, the confusion which Murray and Boodle have brought into the Avrainvillea by this [the retention of the epithet longicaulis] is made much more hopeless. It seems to me that neither the diagnosis of Kützing nor his figure may be said to give any particularly good characteristic of A. longicaulis in the sense of Howe. As on the other hand we have in the diagnosis of Murray and Boodle's new species A. mazei a comparatively good description, in which they point out the chief characteristic for this species. . . it seems to me the only correct course to use their name [A. mazei] of this species.

The Gepps (1911) recognized A. mazei and not A. longicaulis. They disagreed with Howe's lumping of A. longicaulis and A. mazei along with Rhipilia longicaulis. Essentially, Howe chose to keep A. longicaulis on the assumption that Rhipilia longicaulis was a good synonym. The Gepps raised this question and believed that Rhipilia longicaulis was a synonym of A. sordida (a conclusion with which I am in agreement), and, therefore, the A. longicaulis of Murray and Boodle and Howe were really other species. They concluded that Murray and Boodle knew "what they meant" by A. longicaulis and A. mazei, i.e., their A. longicaulis was really A. nigricans, and their A. mazei was actually A. longicaulis (in the sense of Howe but excluding Rhipilia longicaulis).

Examination of Mazé's type for A. mazei, and many fresh and preserved specimens of A. longicaulis, reveals that they are identical. The problem arises with the acceptance or rejection of Murray and Boodle's Rhipilia longicaulis in their synonymy. According to the rules of nomenclature the following would occur.

Assuming that the Gepps were correct in their conclusion that Rhipilia longicaulis is really a synonym of A. sordida, then A. sordida (=Howe's A. levis) would be renamed A. longicaulis. A. longicaulis Murray and Boodle would become A. nigricans, and A. mazei (which Howe equated with A. longicaulis Murray and Boodle) would become A. sordida (recall that Murray and Boodle included A. sordida v. longipes in their synonymy of A. longicaulis).

In the sixty or so years that have intervened since this problem was last tackled, A. longicaulis has been widely reported in the literature (that which is synonymous with Mazé No. 65, Murray and Boodle's type for A. mazei). Likewise, A. sordida (=Howe's A. levis) is a well recognized plant. To quite literally reverse the names in the interest of a nomenclatural technicality, hardly seems judicious, especially in view of their recognized status. The only other option is to disregard all synonymies involving Rhipilia longicaulis and accept Murray and Boodle's A. mazei. Specimens that have been called A. longicaulis would be changed to A. mazei. Although this would be an effective way to "clean the slate," it seems even less judicious than a name reversal. It is the opinion of this author that A. longicaulis (Kütz.) Murray and Boodle be retained, as to name only, and that A. mazei be included as a synonym.

Description: The plants are dark brown to nearly black, to 25 cm tall. Blades are solitary, cuneate to obovate, nonzonate, thick and spongy, and nonlacerate, 6-10 cm wide by 6-8 cm tall. The stipes vary from 3-12 cm in length and are tightly woven, though still soft like the blade. The holdfast consists of a rhizomatous mat from which additional individuals may sprout to give the appearance of a more gregarious habit.

The siphons are light brown, uniformly cylindrical, and definitely not tapering, 28-(38-47)-65. There is no evidence of moniliform character. Dichotomal constrictions are deep and a very faint torulose character may rarely be seen.

Discussion: The habits of A. longicaulis and A. nigricans are virtually identical. Moreover, they are often found growing next to one another in the same community. Fortunately, microscopic examination of the siphon structure readily differentiates the two. Interestingly, both the Gepps (1911, p. 27) and Howe (1907, p. 510) commented on individuals they had seen which appeared to be grafts of A. longicaulis and A. nigricans. "The specimen contains intrusive torulose filaments of another species, A. nigricans." Examination of Howe's A. nigricans f. fulva is somewhat suggestive of A. longicaulis intermediates. The implications of these observations are reviewed under the generic discussion and are mentioned here as a point of added emphasis regarding the likeness of the two species.

A. longicaulis is now recognized from the Pacific. Specimens from Micronesia fit the type material well and are fairly common.

Affinities: A. longicaulis is most closely allied with A. nigricans. It is easily distinguished from A. nigricans by its lack of moniliform siphons. Though A. nigricans can be variable on this point, A. longicaulis is not.

Floristic and Miscellaneous Listings: Almodovar (1964), Britton (1918), Collins (1909), Collins and Hervey (1917), Dawson (1962b), Diaz-Piferrer (1964a, 1969b), Howe (1920), Schnetter (1978), Svedelius (1924), Taylor (1969a, 1969b, 1972), Valet (1968), Vickers and Shaw (1908), Young (1977).

Avrainvillea obscura (C. Agardh) J. Agardh 1887

[Plates X. A, B, C, D; XI. A, B, D; XV. C, D;

XVI. A; B-I. A, B, C, D; B-II]

Synonymy: Anadynomene obscura C. Agardh, 1823, p. 401.

Avrainvillea obscura J. Agardh, 1887, p. 53; Murray and Boodle, 1889, p. 71; DeToni, 1889, p. 515; Gepp and Gepp, 1911, p. 32; Taylor, 1950, p. 67; Tanaka and Itono, 1969, p. 1.

Avrainvillea capituliformis Tanaka, 1967, p. 14; Tanaka and Itono, 1969, p. 4.

Type Locality: Guam, Mariana Is., Pacific

Type Deposited: Lund University Herbarium

Distribution: Malaysian archipelago extending from Singapore to Bali, eastward across the Philippines, and northward toward southern Japan. Range continues across Micronesia with the Marshall Islands its easternmost boundary. The species has not been reported from Polynesia to date [Plate XX].

Specimens Examined: GUAM, Tumon Bay, Stojkovich T-1 through T-23, Jan.-Feb. 1979 (GUAM); Tumon Bay, Taylor 5070, 23 Mar. 1964 (GUAM); Pago Bay, Stojkovich P-1 through P-50, Feb.-Mar. 1979 (GUAM); Bangi Islets, Stojkovich B-1 through B-6, Mar. 1979 (GUAM); Cocos Lagoon, Stojkovich C-1 through C-16, Mar. 1979 (GUAM). SAIPAN, Susupe, Rechebei, 15 Apr. 1973 (GUAM); Chalan Kanoa, Tsuda 1938, 23 Feb. 1968 (GUAM). YAP, Colonia, Tsuda 5226, 4 Mar. 1977 (GUAM). PALAU, Kayangel, Tsuda 5201, 17 Jan. 1976 (GUAM); Urukthapel, Ogden N978, Sep. 1978 (OGDEN). TRUK, Dublon, Stojkovich 73, Mar. 1977 (GUAM). MARSHALL IS., Uorikku Is., Bikini, Smith 47-122a, July-Aug. 1947 (MICH, UC 1452273); Smith 47-122b, July-Aug. 1947 (MICH, UC 1452274); Smith 47-122c, July-Aug. 1947 (MICH and UC 1452272); Rongerik, Smith 47-215, July-Aug. 1947 (MICH, UC 1452275). PHILIPPINES, Catanduanes Prov., Doty and Valesquez 16657, 21 May 58 (DOTY); Camiguin, Tanaka 19671, 19 Nov. 1964 (PNH 109316). SOUTHERN JAPAN, Yoron Is., Tanaka 2, 25 Oct. 1967 (KAG). SINGAPORE, Singapore, Burkill 2712, 8 May 1961 (DOTY). SOLOMON IS., Guadalcanal, Womersley and Bailey 620, 24 Sep. 1965 (ADU, A36648).

History: The type specimen was collected from Guam (then referred to as the Ladronez Is.) by Gaudichaud in the early 1800's. The specimen was originally placed in the genus Anadynomene by C. Agardh. J. Agardh later recognized the plant as belonging to the genus Avrainvillea. Recent collections of the species in the Indo-Pacific have created some confusion with respect to the species' autonomy from A. erecta. See discussion section.

Description: A. obscura proxima (most common) consists of a stout, solitary plant possessing a well developed holdfast and stipe which pass into a substantial blade. The blade is olivaceous to dark green in situ. A deep orange-brown band may be seen along the peripheral margin of some plants. The blades are faintly zonate (evident in fresh specimens only), spongy to subvelutinous in texture, moderately thick, and usually quite firm (except for the growing edge, which tends to be only loosely woven to free). Blade shape is variable from single, planar, cuneiform-obovate, reniform, or somewhat rotundate. Blades from two or more crowded plants may grow together to form multiply fused fronds above the substratum. Excavation of the holdfast region, however, reveals discreet rhizomes. Growing edges may be smooth or lightly digitate. Blades range from 3-6 cm wide by 3-5 cm tall.

The stipe is continuous with the blade and of the same color and texture as the blade. They range from 1-5 cm long and 3-8 mm in diameter.

The holdfast of A. obscura is extremely large, often several times the size of the combined blade and stipe portions of the plant. The sandy rhizomatous holdfast is very long, ranging from 4-20 cm into the substratum, and bending 90 degrees to form a complex subterranean network. Unfortunately, this portion of the plant is rarely collected and is, therefore, of limited taxonomic value.

A. obscura forma (Taylor, 1950) is generally solitary, having a well developed holdfast but poorly developed stipe, resulting in a nearly sessile habit. The alga is here on referred to as f. taylori. The blade is olivaceous and unconsolidated, forming a soft, loosely woven flabellum (not a tuft) up to 8 cm in length by 4-6 cm broad. Peripheral siphons may be loosely woven but are predominantly free.

The stipe is poorly developed at 1 cm long and 1-2 cm in diameter (similar to that of A. erecta).

The holdfast is similar to that described under A. obscura proxima.

A. obscura f. capituliformis (new form) is a short solitary plant, olivaceous in situ. The blade and stipe are completely reduced to an open capitular tuft of nonwoven siphons which pass directly into the typically massive holdfast. The globular tuft ranges up to 4.5 cm in diameter by 4 cm tall. This is a more extreme ecomorph of Taylor's A. obscura forma.

Microscopic examination of the siphons shows an identical pattern for all three ecomorphs with the exception of average siphon diameter. A. obscura is characterized by olive (occasionally light brown) to transparent siphons ranging in size from 28-(38-47)-56 in proxima, (56-88)-125 in f. taylori and (38-47)-70-100 in f. capituliformis. Structurally, the siphons are cylindrical in the deeper portions of the blade, isodiametric, and nontapering apically. Near the surface the diameter may increase or decrease slightly but the siphons may still be characterized as nontapering. Apices are rounded or clavate. At least 25 percent of the apices should show the clavate character. Clavate apices average 56  $\mu\text{m}$  but may go as high as 125  $\mu\text{m}$  in A. obscura f. taylori. In general, the freer the peripheral frond filaments, the greater their diameters, and the more pronounced their clavate character. Surface filaments may additionally show an intermittent torulose character, but this is not widespread and varies considerably between individuals as well as within individuals. Identification of this characteristic is not so important in the identification of A. obscura as it is in ruling out A. erecta. In A. obscura it is particularly important to

examine at least two different parts of the frond to determine this point. Tortuous siphons are not seen. Dichotomies are deeply constricted in the upper portions of the plant. The angle of dichotomy is generally acute (of the rabbit-ear variety) though this point can be more difficult to determine in dried material.

Discussion: Although there was no opportunity to examine the type, Guam is the type locality and fresh specimens are readily available. Examination of fresh specimens agree well with Agardh's original description and with the Gepp's drawings, which were drawn for them by Dr. Nordstedt at the Lund Herbarium. As mentioned by both the Gepps (1911) and Taylor (1950), there is a torulose character present in most specimens, but it is definitely subordinate to the otherwise dominant cylindrical character of the siphons.

Examination of specimens throughout the biogeographical range of A. obscura, coupled with some in situ experiments confirm its morphologic plasticity. Specimens from the Marianas and Carolines fit the classical pattern of A. obscura proxima, while material from the Marshalls tends towards wider average siphon diameters, and, in the case of A. obscura forma, an extreme increase. Plants of the f. taylori variety have been collected from Guam, but siphon diameters have never exceeded 80  $\mu\text{m}$  unless experimentally manipulated.

Moving westward towards the Philippines the habit of A. obscura often becomes more like that of A. erecta, though the slight torulose character persists, thus distinguishing it from A. erecta. Toward the northern Philippines and Okinawa, A. obscura f. capituliformis is found. In habit this variety is sufficiently different to have

been misdescribed as a new Avrainvillea species by Tanaka (1967). Examination of the type (both liquid preserved and dried) as well as additional examples from both the Philippines and Yoron Island show that Tanaka's A. capituliformis is yet another ecomorph of A. obscura. Open tuft, capitular thalli are not uncommon in A. obscura. Indeed, such capitular forms are seen on Guam and can be experimentally induced.

Affinities: A. obscura is most closely allied with A. erecta, A. clavatiramea, and Avrainvillea n. sp. To a lesser extent it may be confused with A. longicaulis (at least in the microscopic comparisons of A. obscura f. taylori and f. capituliformis). The principal difference between A. obscura and A. erecta is that the former possesses generally larger and more variable siphon diameters, an olive color, intermittently clavate apices, and sparsely (here and there) torulose surface siphons. Also, the habit of A. obscura is more variable. The siphons of A. erecta are nearly always yellow-orange, never torulose, never clavate, and impressionally more rectilinear at the dichotomies. Tanaka and Itono (1969) pointed out the similarity of f. capituliformis to A. erecta based on associative habitat and slight yellow color. However, because of the atypical habit of f. capituliformis, they described it as a separate species. Again, cross comparisons of A. capituliformis, A. erecta, and A. obscura show that Tanaka's A. capituliformis is an A. obscura ecomorph for reasons already stated.

Taylor's A. obscura f. taylori may be confused with A. longicaulis microscopically, though in habit and holdfast type, the two species are so different that it is unlikely that these two could ever be confused.

A. obscura is also closely allied with A. clavatiramea. The two may be distinguished by A. clavatiramea's more conspicuously clavate apices, higher percentage of them, and more consistent (though again light) torulosity in the supradichotomal siphons. In addition, A. clavatiramea has a more longly stipitate habit and is known only from southern Australia.

Finally, there are specimens which clearly fall somewhere in between A. obscura and A. erecta, and, to a lesser extent A. ridleyi. These variants are routinely found in the Philippines and the Western Caroline Islands. These specimens are newly described in this paper. A. obscura may be differentiated from the new species by the latter's siphon character, which is closer to that of A. erecta, i.e., habit, yellow color (deep areas only) and rounded apices. It is distinguished from A. obscura and A. erecta on the basis of its combination of both rounded and tapered apices, and distinctive layering, i.e., a noticeable difference in the diameter of the deeper siphons in comparison to those of the surface. Tortuousness is never seen in A. erecta or A. obscura but it is common in the new species.

Floristic and Miscellaneous Listings: Abbott (1961), Bryan (1975), Gloud (1959), Gilbert and Doty (1969), Schmidt (1928), Svedelius (1924), Taylor (1966), Tokida (1939), Tsuda and Wray (1977).

Avrainvillea clavatiramea Gepp & Gepp 1911

[Plates IX. A, B; XVI. B]

Synonymy: Avrainvillea clavatiramea Gepp and Gepp, 1911, p. 33.

Type Locality: Port Phillip, Corio Bay, Victoria, South Australia

Type Deposited: British Museum

Distribution: Known only from southern Australia [Plate XX].

Specimens Examined: AUSTRALIA, Port Phillip, Victoria, J. B. Wilson, 10 Dec. 1887 and 9 Jan. 1888 (BM - type); Waldegrave, Sheperd A47193, 23 Oct. 70 (UC 1452434).

History: Plants collected by J. Bracebridge Wilson from southern Australia were originally labeled "A. obscura proxima" by Wilson. In 1911, the Gepps examined these specimens and cautiously placed them in a new species, A. clavatiramea. At the time of their description they had not had the opportunity to examine specimens of A. obscura though they did have sketches and other anatomic data. They did not consider their specimens to be A. obscura because of the wide range of siphon diameters, reduced torulosity, and less conspicuous clavate apices. In addition, they felt that the geographic separation was sufficient to preclude its being A. obscura.

Description: The plants are solitary to 12 cm tall, dark olive to brown, possessing long and narrow stipes to 5 cm in length. Holdfasts are small and not well developed or encrusted with sand grains as in A. obscura. Blades are cuneate to obovate, fairly thick becoming very thin at the upper margins. Peripheral edges are smooth to distinctly lacerate. The transition of the stipe into the blade is continuous rather than abrupt.

Siphons tease apart easily even in dried specimens. The siphons are cylindrical deeper within the blade, becoming increasingly torulose near the surface. Torulosity is very irregular along a given siphon, becoming intermittently cylindrical for a short distance, and then torulose again. Siphon diameters range from 19-(38)-57. Dichotomal constrictions are deep. At least 50 percent of the apices show the

clavate character. Others are rounded. The clavate character is more highly developed in A. clavatiramea than in A. obscura.

Discussion: Examination of three specimens including the type clearly shows that A. clavatiramea is different from A. obscura, though they are obviously closely allied. Naturally it would be desirable to examine many more individuals of A. clavatiramea to insure that the higher degree of clavate apices is indeed always so pronounced. The reliability of this taxonomic character is not really known. If the character is not reliable then A. clavatiramea would be placed in synonymy with A. obscura.

Affinities: A. clavatiramea is most closely allied with A. obscura and can be distinguished from that species by its more consistent, though irregular torulosity, and abundantly clavate apices. To a less reliable extent they differ in habit, A. clavatiramea being a somewhat slimmer plant with a long narrow stipe and less well developed rhizome.

Floristic and Miscellaneous Listings: Dawson (1962a), Svedelius (1924).

Avrainvillea ridleyi Gepp & Gepp 1911

[Plates IX. C, D; XVI. C]

Synonymy: Avrainvillea lacerata Gepp and Gepp, 1905, p. 339.

Avrainvillea ridleyi Gepp and Gepp, 1911, p. 33.

Type Locality: Christmas Island, Indian Ocean

Type Deposited: British Museum

Distribution: Known from Christmas Island and extending southeast into New Caledonia and Tahiti [Plate XXI].

Specimens Examined: CHRISTMAS IS., Ridley 243 and 244, Oct. 1904  
(BM - type). NEW CALEDONIA, Bay of Prony, Tsuda 5291, 31 Mar.  
1977 (GUAM). TAHITI, Crossland 7246, 7 Dec. 1929 (UC 791864).

History: The original specimens were collected by Ridley in 1904 on a collecting trip to Christmas Island. Because of their peculiar habit the Gepps erroneously believed them to be specimens of A. lacerata. Only later did they realize their error and assign the unusual plants to a new species.

Description: Plants are dark olive-brown to 5 cm tall, squat and tufted, consisting of a short, branched stipe which widens distally to form congregate narrow, spatula-like blades. The blade and stipe are not readily distinguishable, approaching a nonflabellar habit suggestive of A. rawsoni or A. amadelpa. The thallus is moderately thick and somewhat spongy, and easily teased apart. The holdfast is less well developed forming a surface rhizomal mat rather than the single deep, sand embedded type.

Microscopically, the deeper siphons are cylindrical 19-(28-38)-47 becoming lightly and supradichotomally torulose near the surface. Approximately 50 percent of the supradichotomal siphons show the light torulose character for at least a short distance. Dichotomies are weakly constricted and apices are not tapered but either rounded or longly clavate (38-47).

Discussion: A. ridleyi has broad affinities with both the "lacerata" and "obscura" groups. Described originally from Christmas Island, its range has now been expanded to include New Caledonia and Tahiti.

Affinities: A. ridleyi is most closely allied with A. clavatiramea. From A. clavatiramea it differs conspicuously in its habit, lack of deeply constricted dichotomies, and smaller average siphon diameter. On a more impressional basis, A. ridleyi is consistently more torulose than A. clavatiramea. In habit, A. ridleyi might be confused with A. amadelpha, A. rawsoni, or rarely A. lacerata. Microscopic examination quickly rules out A. lacerata and A. rawsoni, but A. amadelpha might be confused.

Floristic and Miscellaneous Listings: Dawson (1962a), Svedelius (1924).

Avrainvillea erecta (Berk.) Gepp & Gepp 1911

[Plates VIII. A, B, C, D; XVI. D; A-II. B; A-III. A]

Synonymy: Dichonema erectum Berkeley, 1842, p. 157.

Udotea sordida Montagne, 1844, p. 659.

Chloroplegma papuanum Zanardini, 1878, p. 37.

Chlorodesmis pachypus Kjellman, 1879-1880, p. 117.

Rhipilia andersonni Murray, 1886, p. 225.

Rhipidonema erectum Saccardo, 1888, p. 689.

Avrainvillea papuana Murray and Boodle, 1889, p. 71;

DeToni, 1889, p. 514; Heydrich, 1907, p. 101.

Avrainvillea erecta Gepp and Gepp, 1911, p. 29;

Børgesen, 1940, p. 53; Trono, 1968, p. 174;

Valet, 1968, p. 50; Pham-hoang Hô, 1969, p. 509;

Gilbert and Doty, 1969, p. 123; Womersley and

Bailey, 1970, p. 279.

Type Locality: Philippines

Type Deposited: British Museum

Distribution: Indo-Pacific from East African coast to the Philippines and western Micronesia. Also reported from the Solomon Islands [Plate XX].

Specimens Examined: PHILIPPINES, Cuming 2234, no date (BM - type); E. Samar, Cordero, 30 Nov. 1977 (PNH 124723); Kilay Is., Gilbert 699, Jan. 1941 (MICH); E. Samar, Cordero, 16 June 1978 (PNH 125490); Nagumbuaya, Doty, 20 May 1958 (DOTY 16799); Hundred Is., Moreland 777, 11 Mar. 1973 (DOTY). PALAU, Urukthapel, Ogden N894, 1978 (OGDEN). SOLOMON IS., Florida Is., Bailey 123b, 14 July 1965 (ADU A36647). VIETNAM, Truong Dong, Dawson 11162, 30 Jan. 1953 (MICH); Nhatrang, Dawson 11404, 27 Feb. 1953 (UC M098878). MALAYSIA, Gaya Is., Cleland, 5 Feb. 1965 (MICH); no author, 27 Nov. 1927 (MICH 341517). THAILAND, in Thai script, 15 May 1976 (GUAM 1 and 2). MADAGASCAR, Papenfuss and Scagel R-LXXII-4, 8 Sep. 1962 (UC 1451308, US 50380). ZANZIBAR, Papenfuss and Scagel PR-XIV-I, 17 Oct. 1962 (UC 1451309). MOZAMBIQUE, Papenfuss and Scagel PR-XXVII-10), 14 Nov. 1962 (UC 1451310, US 50379).

History: A. erecta has a long and confusing history which is extensively reviewed by the Gepps (1911). Mistakes in geography, incorrect herbarium numbers, and a lack of information about other species all contributed to the confusion reflected by the early synonymy. The Gepps discuss the resolution of these problems which led to the new combination A. erecta.

Description: A. erecta is a short, stout plant, 2-6 cm tall, bearing a planar, solitary blade, 2-6 cm tall, and up to 10 cm wide. The blade is typically reniform to subcuneate and olive to yellow-brown. The plant may be shortly stipitate or sessile. The blade is lightly zonate, thin, tightly woven, and difficult to tease apart. The peripheral growing edges may be loosely woven, entire, or slightly lacerated. The holdfast is very stout and embedded with sand, up to 10 cm long.

Siphons of the interior are exclusively cylindrical and isodiametric throughout, (28-47)-66. They are usually bright yellow to a little orange toward the interior. Torulose and tortuous characters are never present. Color and lack of torulosity are the two most constant features. Dichotomies are acute, deeply constricted, and are somewhat more rectilinear than those of A. obscura. Apices are rounded (never clavate or tapered). Siphon diameter is remarkably uniform throughout the plant.

Discussion: Examination of Cuming's type plant revealed a small, shortly stipitate blade of 2 cm in height. Siphons exhibited the classic yellow color, deeply constricted dichotomies, and diameters averaging 19-(28-38). Apices are rounded, nontapering, nonclavate, and never torulose.

On all specimens examined the siphon diameters fell within the Gepp's range of 30-60  $\mu\text{m}$ , though Gilbert and Doty's (1969) range 25-40  $\mu\text{m}$  fits more closely with the overall pattern. African, Thai, and Philippine materials averaged (28-38)-47, while Vietnamese, Malaysian, and Solomon Island materials average 28-(38-47), i.e., slightly larger. Some of

Dawson's Vietnamese material had peripheral siphon diameters as high as 66  $\mu\text{m}$ . However, the blades were loosely woven.

The close alliance between A. erecta and A. obscura has created no small amount of confusion (Gepp & Gepp, 1911; Gilbert and Doty, 1969; Womersley and Bailey, 1970). Specimens from the western portions of the distribution of A. erecta are readily distinguishable from A. obscura specimens from the eastern part of its respective distribution. The problem area occurs in the overlap zone of the two species, which is the Philippine area, Palau, and New Guinea. Plants showing a predominantly "erecta" habit but with internal features in alliance with A. obscura and A. ridleyi are fairly common. This group is newly described as a new Avrainvillea species.

Affinities: A. erecta is most closely allied with A. obscura and the newly described species. From the former it is distinguished principally by its yellow, nontorulose, nonclavate siphons and, to a lesser extent, erect, sessile habit. From the latter it is distinguished by its lack of tapering and somewhat tortuous apices. The new species is not yellow and may rarely show some torulosity and layering of wider, deeper siphons with narrower ones near the surface.

Floristic and Miscellaneous Listings: Chuang (1961), Dawson (1954), Diaz-Piferrer (1969a), Gilbert (1946), Jaasund (1976), Kanda (1940, 1944), Papenfuss (1968), Reinbold (1901), Schmidt (1928), Segawa and Kamura (1960), Svedelius (1924), Tanaka (1956), Taylor (1966, 1977), Tokida (1939), Tsuda and Wray (1977), Velesquez and Lewmanomont (1975), Weber van Bosse (1913), Yamada (1926).

Avrainvillea n. sp.

[Plates VII. C, D; XVII]

Type Locality: Yap, Western Caroline Islands, Pacific

Type Deposited: University of Guam

Distribution: Certainly known from the Western Caroline Islands and the Philippines. Wider distribution into the New Guinea area probable [Plate XX].

Specimens Examined: PHILIPPINES, Pangasinan, Moreland and Villena, 11 Mar. 1973 (DOTY). W. CAROLINE IS., Yap, Tsuda 4015a 4015b, 29 Nov. 1970 (GUAM).

Description: Plantae colore a claro olivaceo in lutosum luteum vergente 3-6 cm altae a brevi stipite 0.5-1 cm longo natae; frondibus solitariis tenuibus forma ab obovata ad orbiculatam tendente, nonautem zonata; filamentis cylindricis apice tenuioribus; filamentis interioribus circa (18-28)-38; facie exteriori 9-(12-18). Apices rotundi sed raro clavati, aliquando torulosi.

Plants pale olive to dirty yellow, 3-6 cm tall, arising from a short stipe 0.5-1 cm in length. Blades solitary, thin, obovate to orbicular, and nonzonate. Peripheral edges may be lightly lacerate. The holdfast is bulbous and sand encrusted, extending several centimeters into the substratum. Internally, the siphons are cylindrical often becoming tapered apically. The deeper siphons of the blade are cylindrical averaging (18-28)-38. Some of these may be deep orange or yellow. Surface siphons are generally transparent to olive and of a noticeably smaller diameter (12-18) often tapering further to (12-9). This layering character is not pseudocortical as in A. amadelpa.

Apices, though they may be tapering, never show the thread-like character of A. sordida or A. lacerata. Apices are rounded rarely clavate. A torulose character is occasionally seen, suggestive of A. obscura. Apical siphons which show the tapered character are often very tortuous.

Discussion: In habit this new species looks very similar to A. erecta and will regularly be confused with it in the field. These plants appear to be variants of both A. obscura and A. erecta simultaneously in terms of their siphon structure. A. erecta is suggested in terms of yellow color, and cylindrical nature (particularly in the deeper portions of the blade). In relationship to A. obscura, its surface siphons are pale olive and show a very slight torulose character. The clavate character is rarely present. The most striking difference which places these individuals in a new species is the tapering of the siphons apically. This character is never present in either A. erecta or A. obscura.

If one recognizes these variants as mere aberrant forms, the question that immediately suggests itself is whether or not A. obscura, A. erecta, and possibly, A. clavatirnea should all be lumped into a "catch all" species. The answer is "No" because A. obscura and A. erecta are clearly discreet from one another except in their overlap zone. Even in this zone pure specimens of A. obscura and A. erecta can be found. In addition, the new species shows the tapering character which is not evident in either A. obscura or A. erecta.

This species is named in honor of Dr. Roy T. Tsuda of the University of Guam.

## Species of Undetermined Taxonomy

Avrainvillea canariensis Gepp & Gepp 1911

Synonymy: Udotea tomentosa Vickers, 1896, p. 300.

Type Locality: Canary Islands

Type Deposited: ?

Distribution: Known only from the Canary Islands

Discussion: The author was not able to locate specimens of this species. From descriptions and figures given by the Gepps (1911, p. 36), it appears to be a member of the "sordida" group. Their description is quoted below:

Plant brownish-green, about 12 cm high, solitary, stipitate; stipes 5-6 cm long, simple, compressed, expanding cuneately into the frond; frond rotundate, large, 6-9 cm long by 7-11 cm wide, very obscurely zonate, thin, margin subentire to fimbriate or slightly lacerate; frond filaments cylindrical, here and there torulose, not tapering nor clavate, green to fulvous-brown, often collapsed and colorless when dry, coloured filaments usually 30-40  $\mu$ m diameter.

Floristic and Miscellaneous Listings: Børgesen (1925), Dawson (1962a), Lawson and Price (1969), Svedelius (1924).

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## PLATE I

- A. Avrainvillea lacerata, BM, type, Tonga.
- B. Avrainvillea lacerata, DOTY 21164, Palau.
- C. Avrainvillea lacerata, UC 417177, Singapore.
- D. Avrainvillea amadelpa f. montagneana, UC 791865, Tahiti.



## PLATE II

- A. Avrainvillea gardineri, BM, type, Caragados Carajos,  
Indian Ocean.
- B. Avrainvillea pacifica, BM, type, Fualopa Is.
- C. Avrainvillea riukuensis, SAP, type, Okinawa.
- D. Avrainvillea riukuensis, C. Børgesen 902, Mauritius Is.



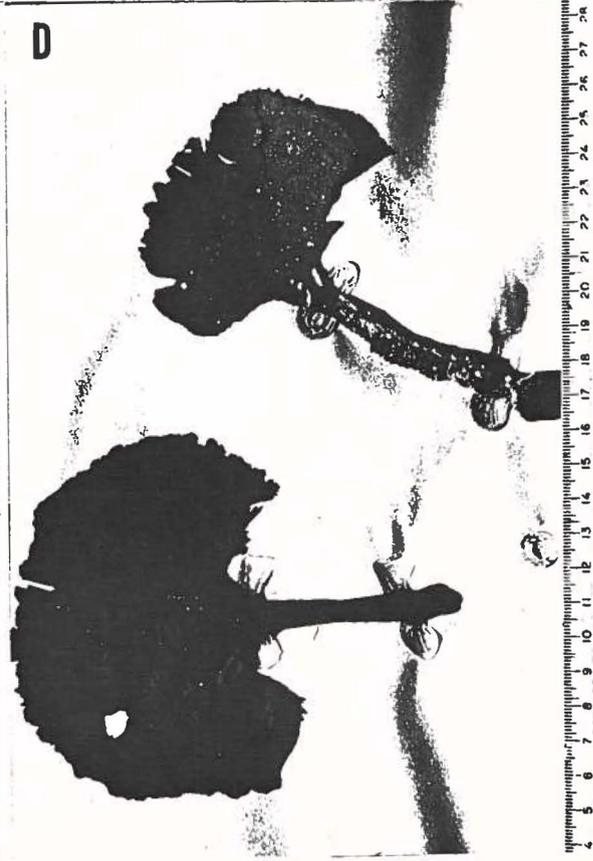
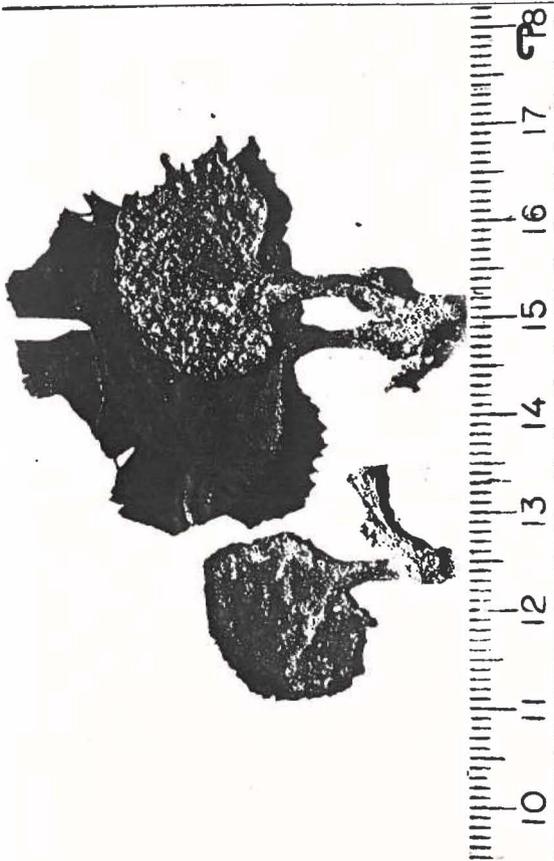
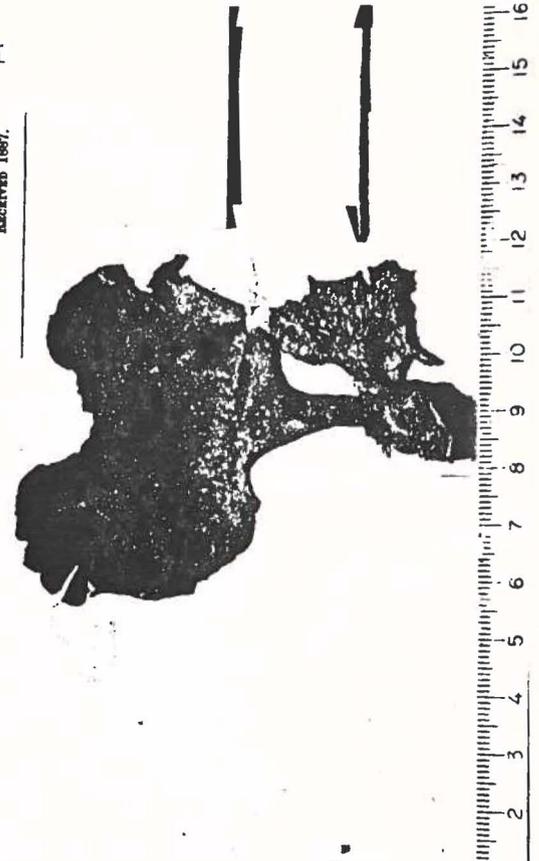
## PLATE III

- A. Avrainvillea hollenbergii, DOTY, type, Ifaluk.
- B. Avrainvillea sordida, BM, type, Guadeloupe.
- C. Avrainvillea sordida, UC 77227, Bahamas (Howe's type for  
    A. levis).
- D. Avrainvillea asarifolia, USF 77041, Florida.

PLATE III



MAZÉ: GUADELOUPE.  
RECOVERED 1887.



## PLATE IV

- A. Avrainvillea asarifolia, GUAM, St. Croix, Virgin Is.
- B. Avrainvillea elliottii, BM, type, Grenada.
- C. Avrainvillea elliottii, USF 135044, Belize.
- D. Avrainvillea elliottii, C, Børgesen 2011, St. Jan.

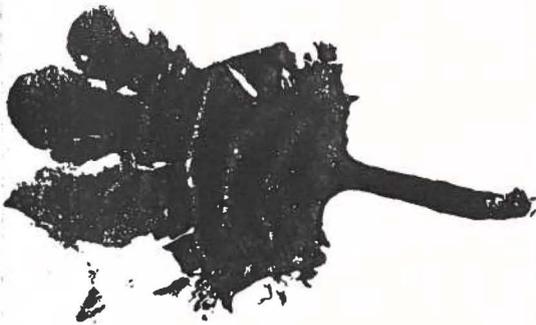
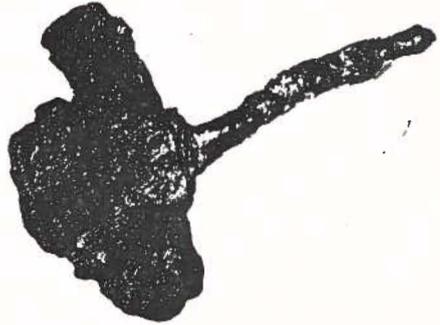
PLATE IV



A



B



C



D



## PLATE V

- A. Avrainvillea elliotii, SP 522, Brazil (Joly and Yamaguishi's type for A. atlantica).
- B. Avrainvillea elliotii, OGDEN 631, 602, 597, St. Croix, Virgin Is.
- C. Avrainvillea rawsoni, BM, type, Barbados.
- D. Avrainvillea rawsoni, GUAM, St. Croix, Virgin Is.

PLATE V

A. B. Johns.



1946  
This is the specimen that was  
found in the same locality as the  
specimen in the collection of  
the University of California, Berkeley.

*Alipha* (N.S.)  
Clemens, n. sp.  
Ancheta -  
Lower Devon  
9. In the collection of the University of  
California, Berkeley.

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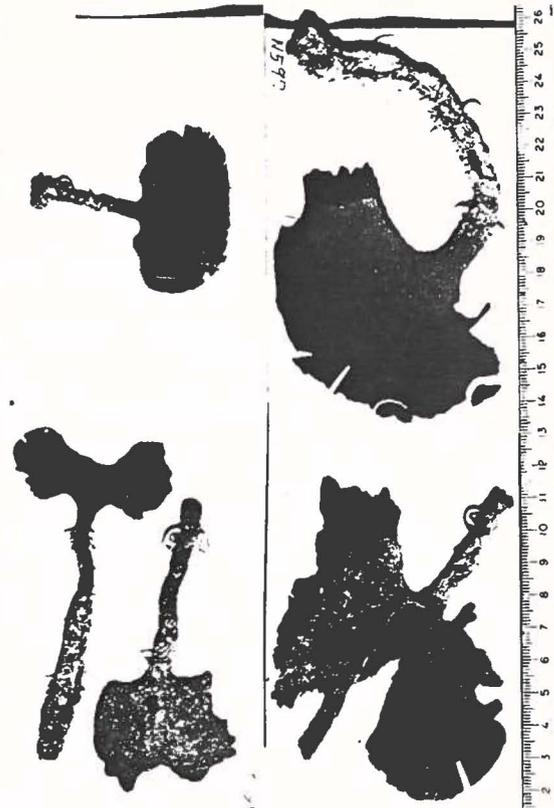
BARRETT  
General Purpose & Size 1/2 in.

*Alipha* (N.S.)  
Clemens, n. sp.  
Ancheta -  
Lower Devon  
9. In the collection of the University of  
California, Berkeley.

= *Alipha* (N.S.)  
Clemens, n. sp.  
Ancheta -  
Lower Devon  
9. In the collection of the University of  
California, Berkeley.

C

B



D



2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26

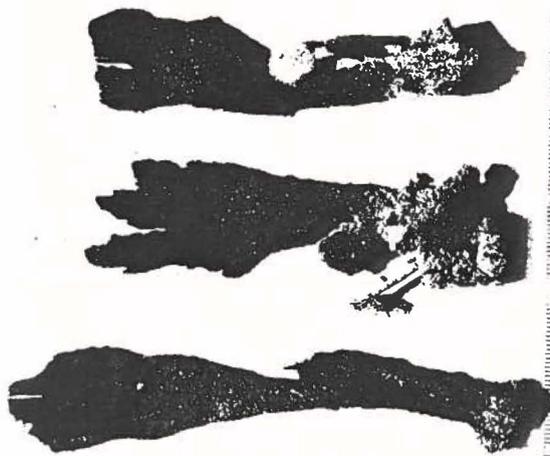
## PLATE VI

- A. Avrainvillea nigricans, UC 1457275, Urak Is.
- B. Avrainvillea nigricans, UC 77233, Florida Keys.
- C. Avrainvillea nigricans, UC 1452276, Rongerik,  
Marshall Is.
- D. Avrainvillea nigricans f. fulva, UC 948386, Bermuda.

PLATE VI



C D



## PLATE VII

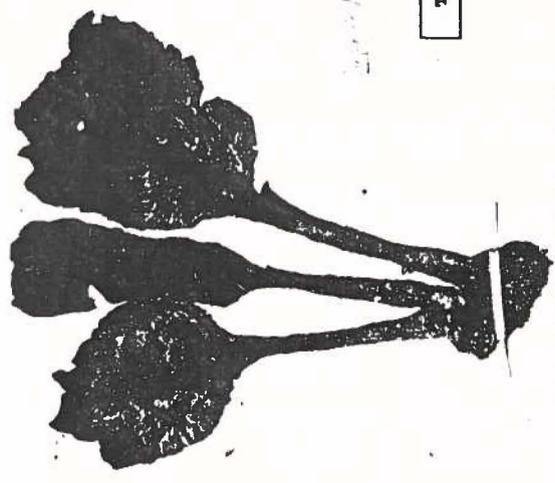
- A. Avrainvillea longicaulis, BM, type, Guadeloupe  
(original type for A. mazei).
- B. Avrainvillea longicaulis, UC 1408142, Puerto Rico.
- C. Avrainvillea n. sp., GUAM 4015a, type, Yap.
- D. Avrainvillea n. sp., GUAM 4015b, Yap.

W.A. 4010/10/10  
March 1902

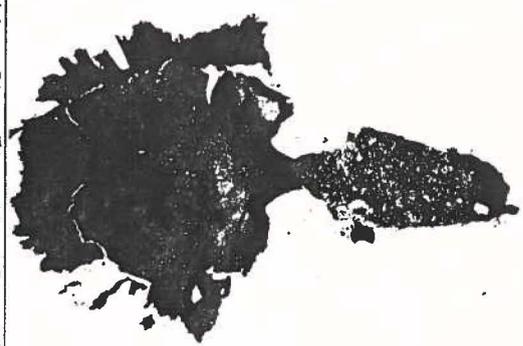
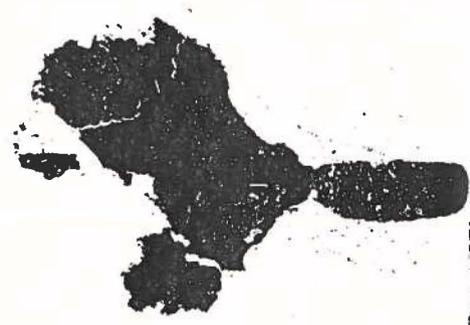
*Handwritten notes*

PLATE VII

Type Specimen



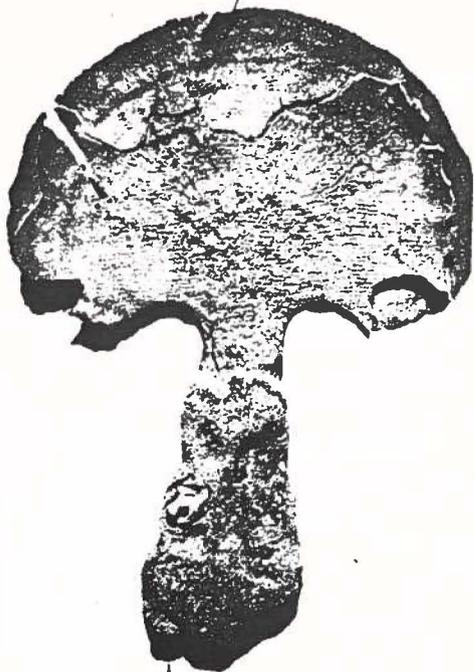
6139



## PLATE VIII

- A. Avrainvillea erecta, GUAM, western Thailand.
- B. Avrainvillea erecta, BM, type, Philippines.
- C. Avrainvillea erecta, DOTY 16799, Philippines.
- D. Avrainvillea erecta, UC 1451310, Mozambique.

PLATE VIII



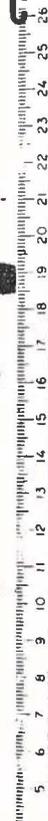
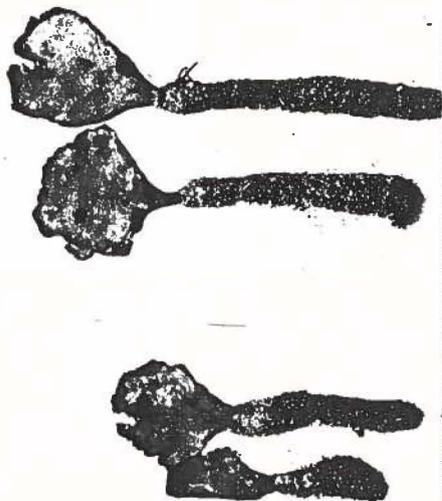
*Handwritten text, possibly a name or date, partially obscured by a stamp.*

2234

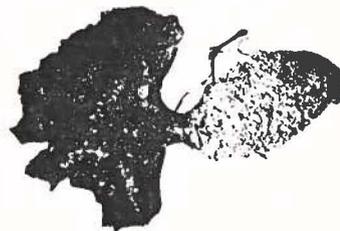
A



C



D



## PLATE IX

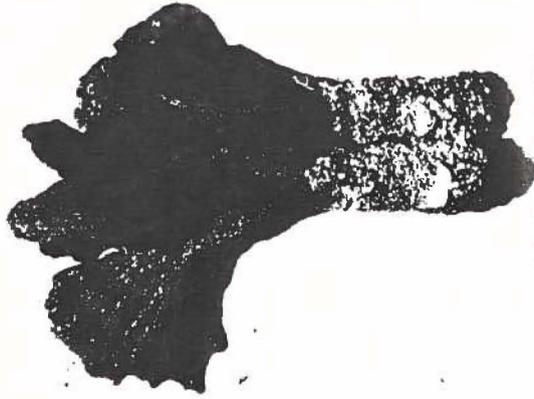
- A. Avrainvillea clavatiramea, BM, type, southern Australia.
- B. Avrainvillea clavatiramea, US 49864, southern Australia.
- C. Avrainvillea ridleyi, BM, type, Christmas Is., Indian  
Ocean.
- D. Avrainvillea ridleyi, BM, type, Christmas Is., Indian  
Ocean.



## PLATE X

- A. Avrainvillea obscura proxima, GUAM, Guam. (Note fused blades)
- B. Avrainvillea obscura proxima, GUAM, Guam.
- C. Avrainvillea obscura f. taylori, UC 1452272, Bikini.
- D. Avrainvillea obscura f. capituliformis, KAG, Yoron Is.

PLATE X



A



B

C

D

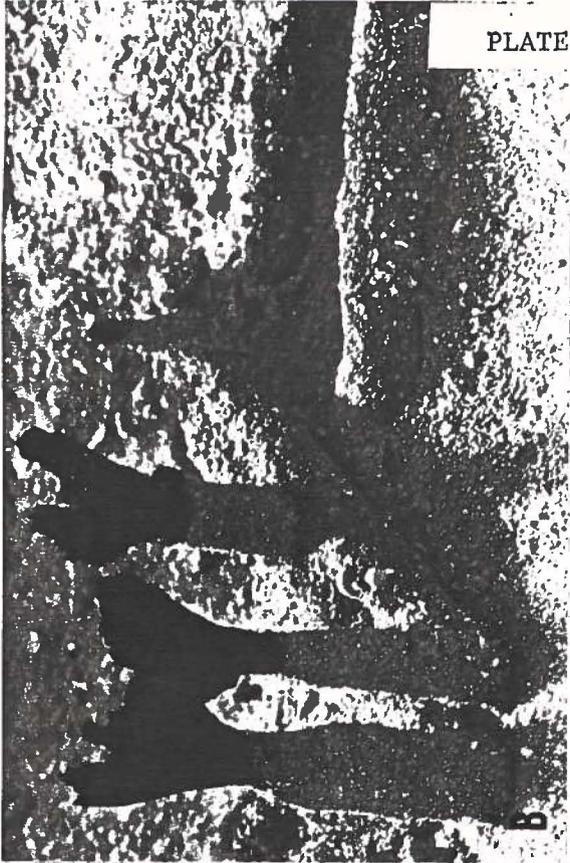
E



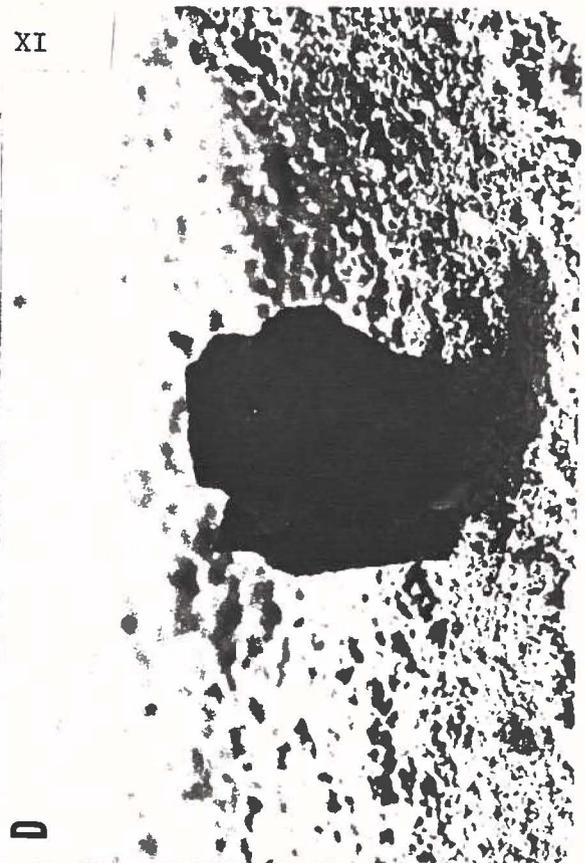
## PLATE XI

- A. Avrainvillea obscura f. capituliformis in its natural habitat.
- B. Avrainvillea obscura showing partial excavation of the rhizome system.
- C. A large population of Avrainvillea longicaulis in a reef flat hole on Guam.
- D. Avrainvillea obscura in its natural habitat.

PLATE XI



A



B



C



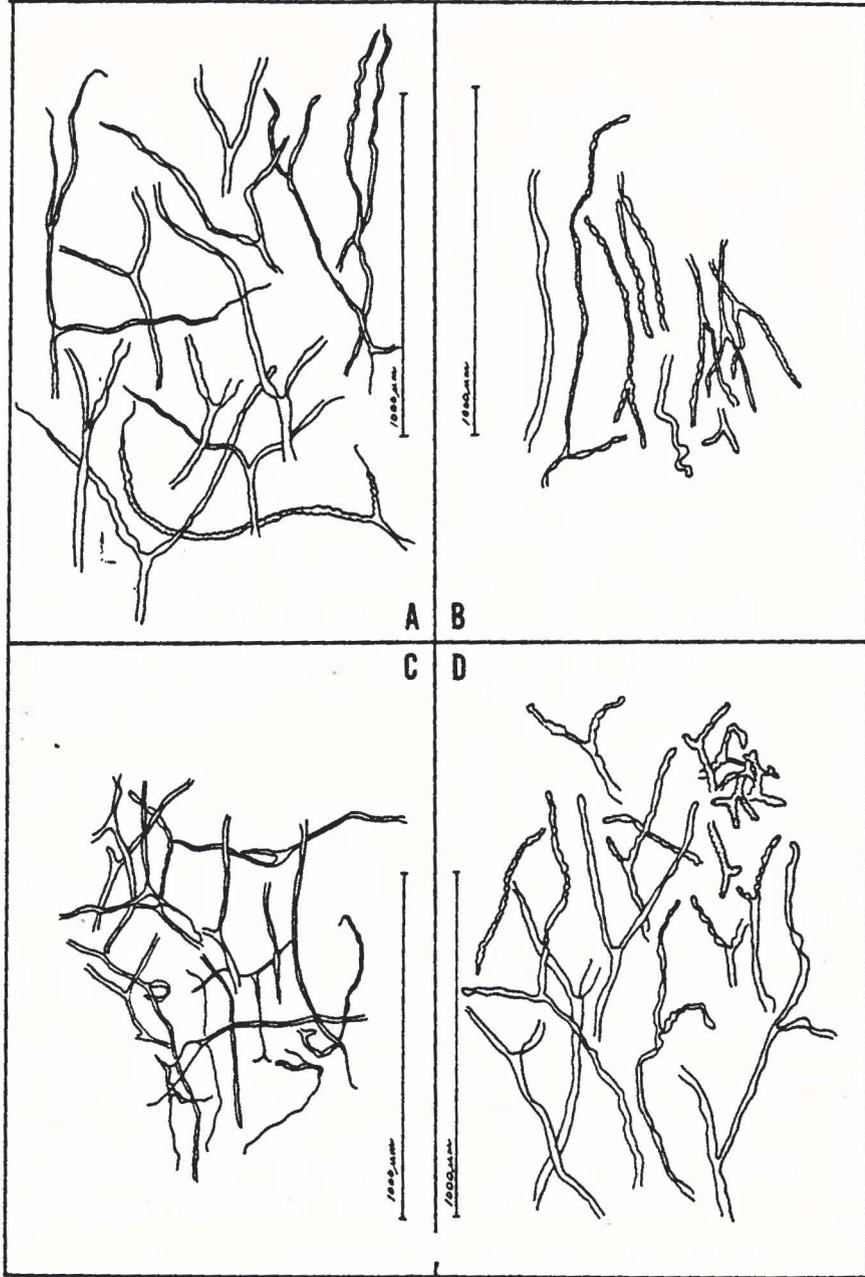
D

## PLATE XII

## Siphons

- A. Avrainvillea lacerata.
- B. Avrainvillea hollenbergii.
- C. Avrainvillea riukuensis.
- D. Avrainvillea amadelpa.

PLATE XII

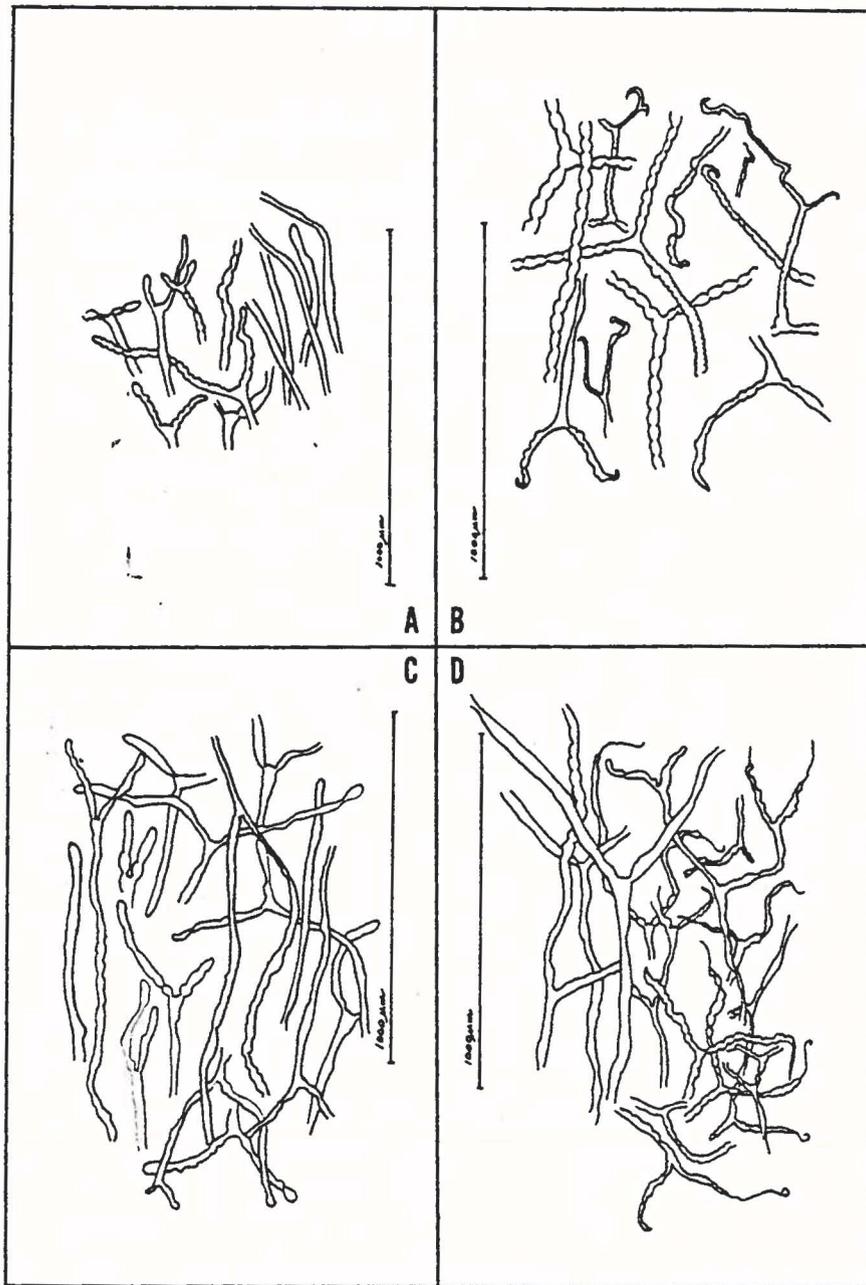


## PLATE XIII

## Siphons

- A. Avrainvillea gardineri.
- B. Avrainvillea pacifica.
- C. Avrainvillea elliottii.
- D. Avrainvillea asarifolia.

PLATE XIII

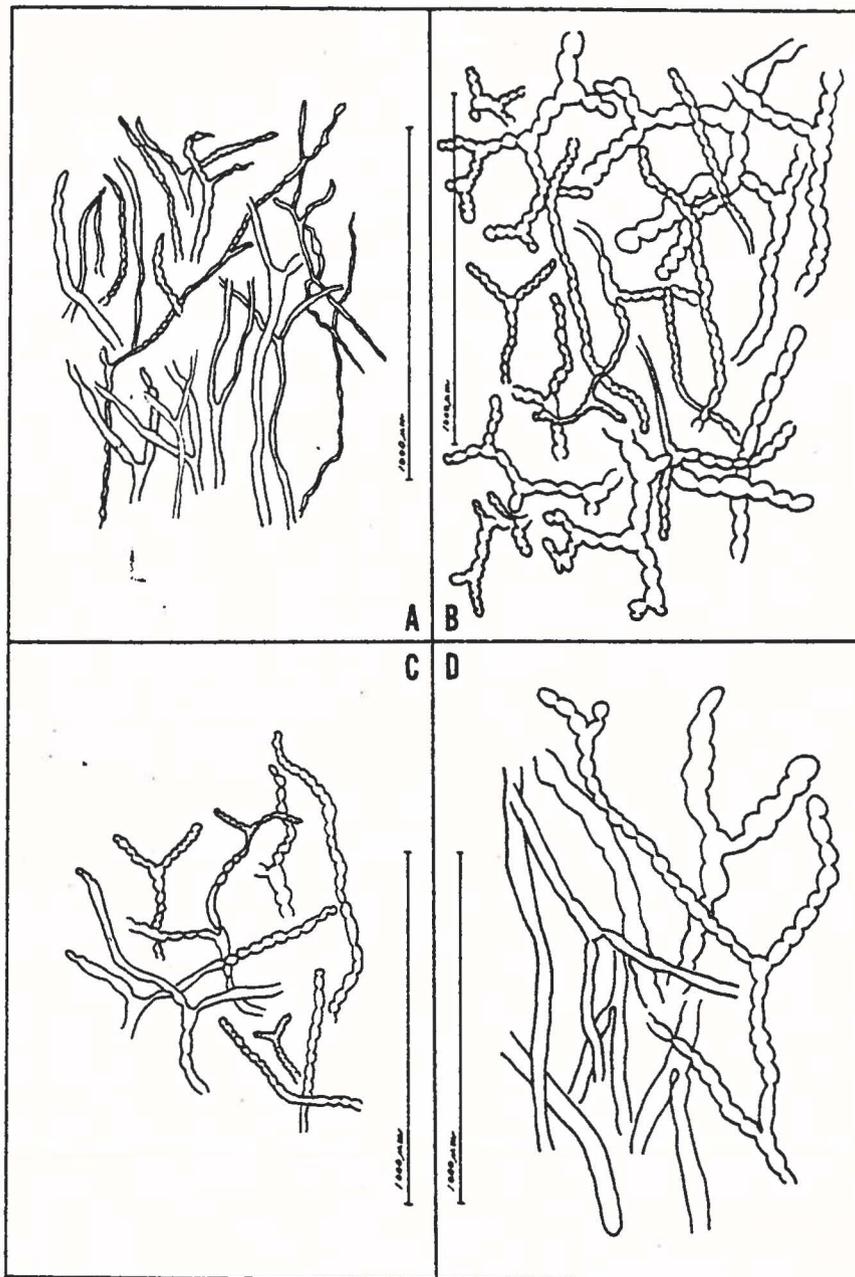


## PLATE XIV

## Siphons

- A. Avrainvillea sordida.
- B. Avrainvillea nigricans.
- C. Avrainvillea nigricans (Marshall Is.)
- D. Avrainvillea nigricans f. fulva.

PLATE XIV

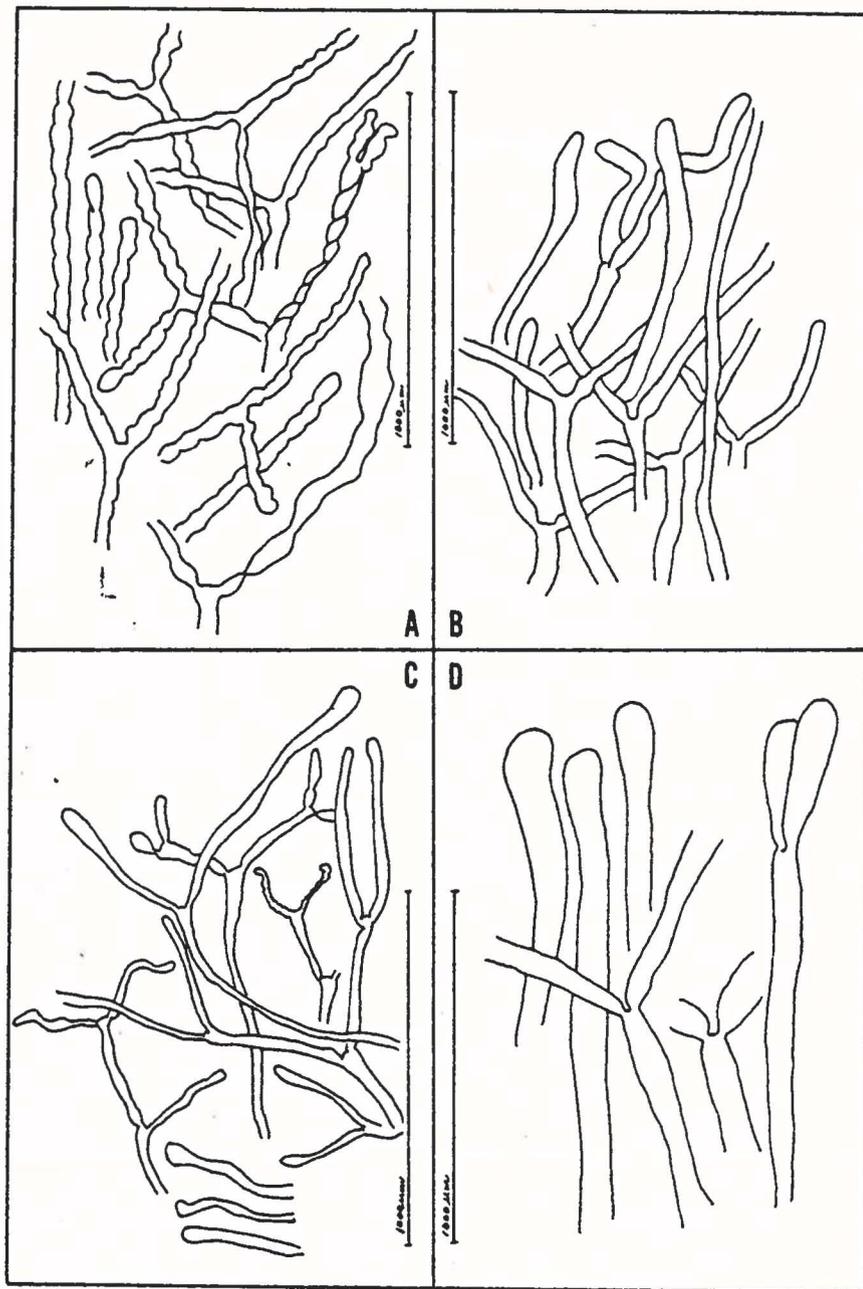


## PLATE XV

## Siphons

- A. Avrainvillea rawsoni.
- B. Avrainvillea longicaulis.
- C. Avrainvillea obscura proxima.
- D. Avrainvillea obscura f. taylori.

PLATE XV

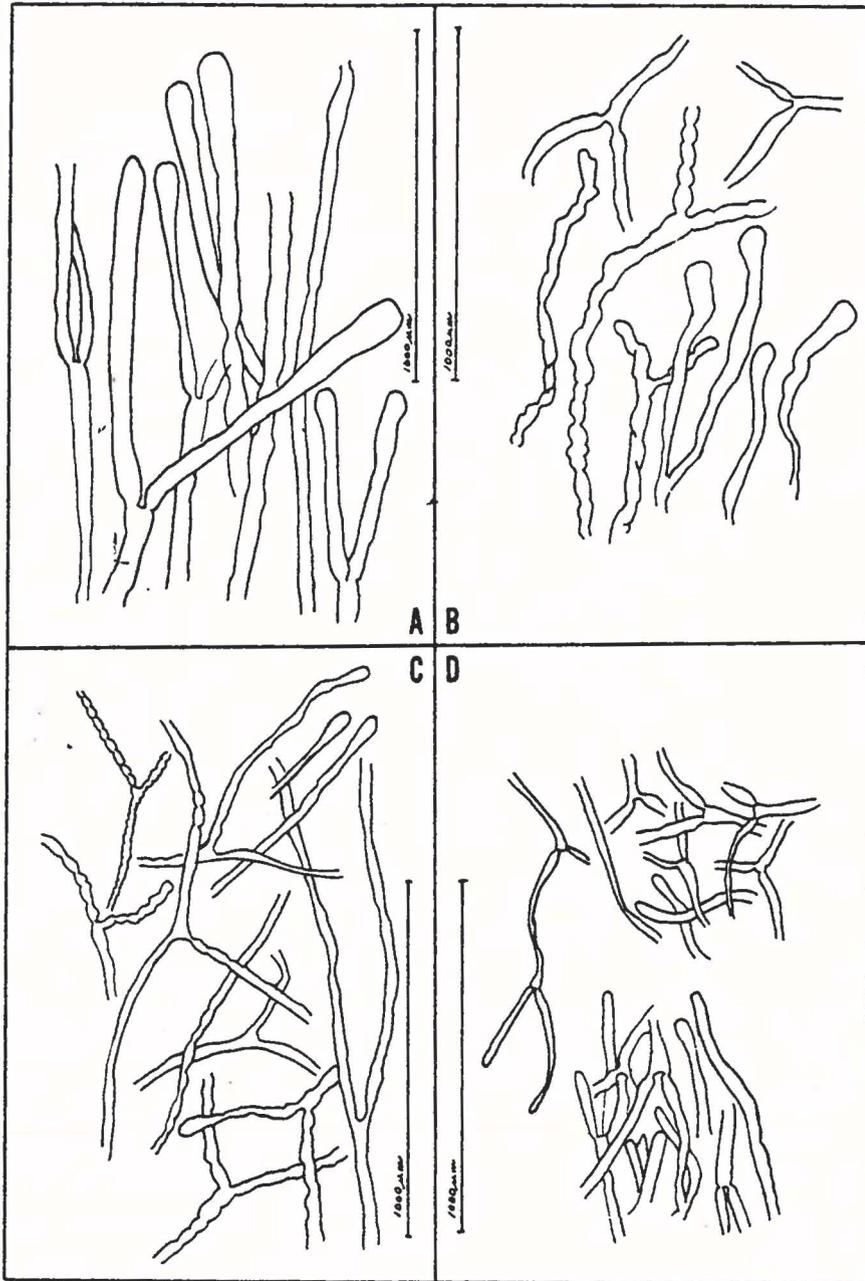


## PLATE XVI

## Siphons

- A. Avrainvillea obscura f. capituliformis.
- B. Avrainvillea clavatiramea.
- C. Avrainvillea ridleyi.
- D. Avrainvillea erecta.

PLATE XVI

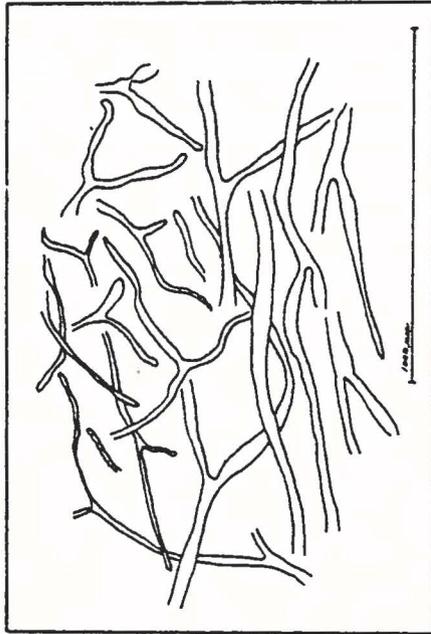


## PLATE XVII

## Siphons

Avrainvillea n. sp.

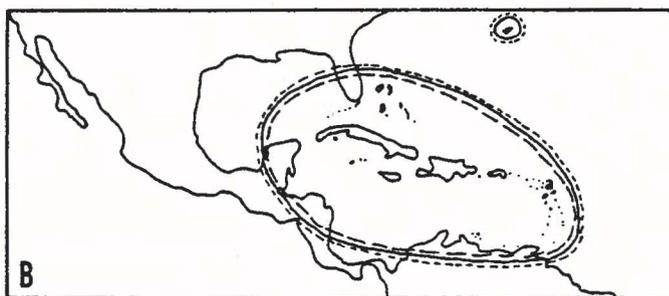
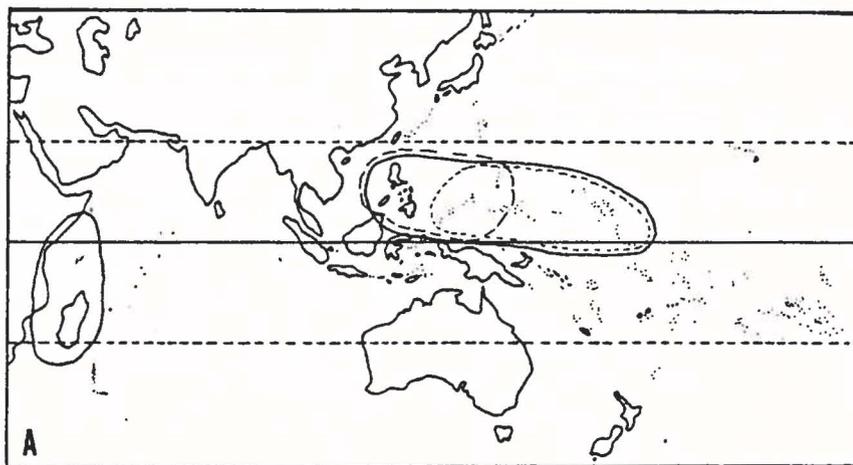
PLATE XVII



## PLATE XVIII

A and B. Authenticated biogeographic distribution of those Avrainvillea species occurring in both the Atlantic and Indo-Pacific provinces. Symbols are as follows: solid line, A. nigricans; dotted line, A. longicaulis; broken line, A. sordida. "a," represents the type locality for all three species (Guadeloupe).

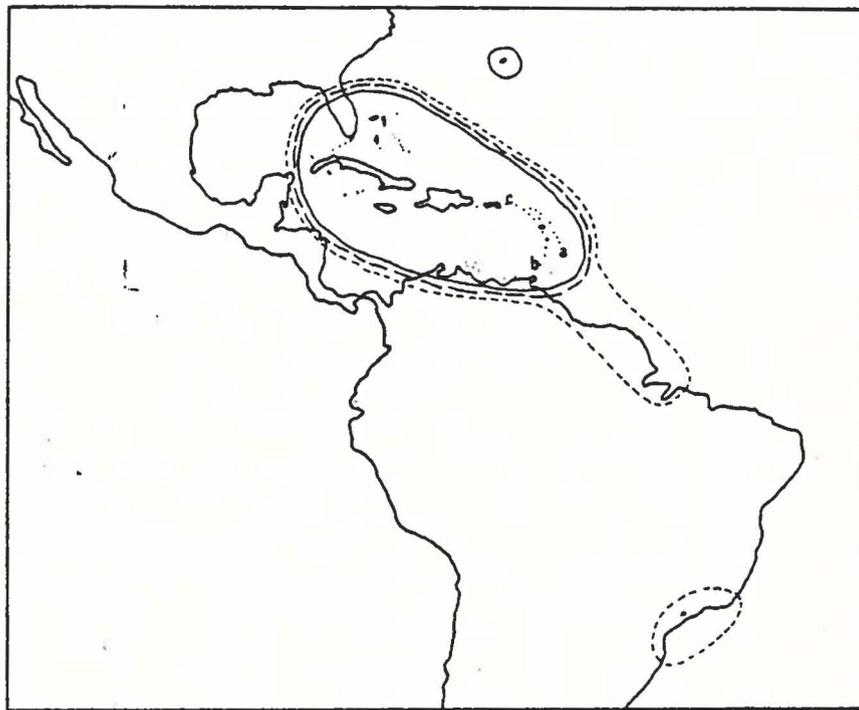
## PLATE XVIII



## PLATE XIX

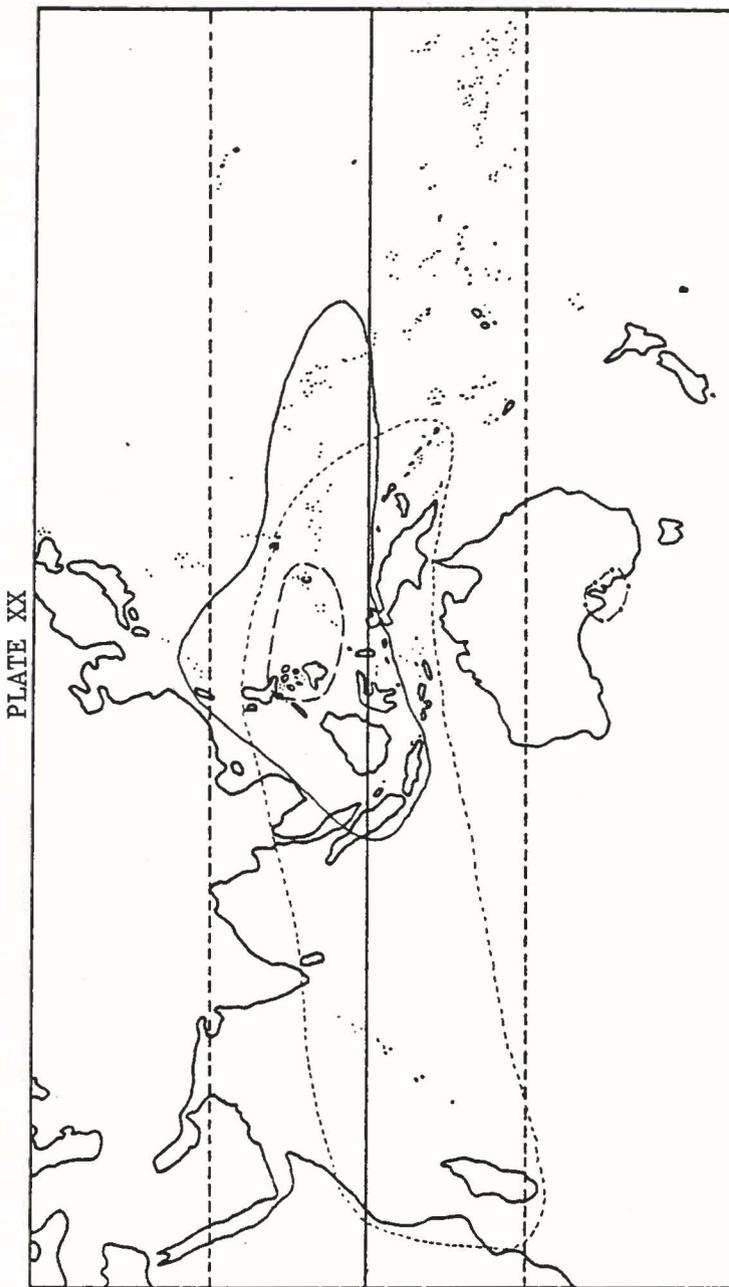
Authenticated biogeographic distribution of Avrainvillea rawsoni, Avrainvillea elliottii, and Avrainvillea asarifolia. Symbols are as follows: solid line, A. rawsoni; dotted line, A. elliottii; broken line, A. asarifolia. The type localities for each species are as follows: "a", A. rawsoni; "b", A. elliottii; "c", A. asarifolia.

PLATE XIX



## PLATE XX

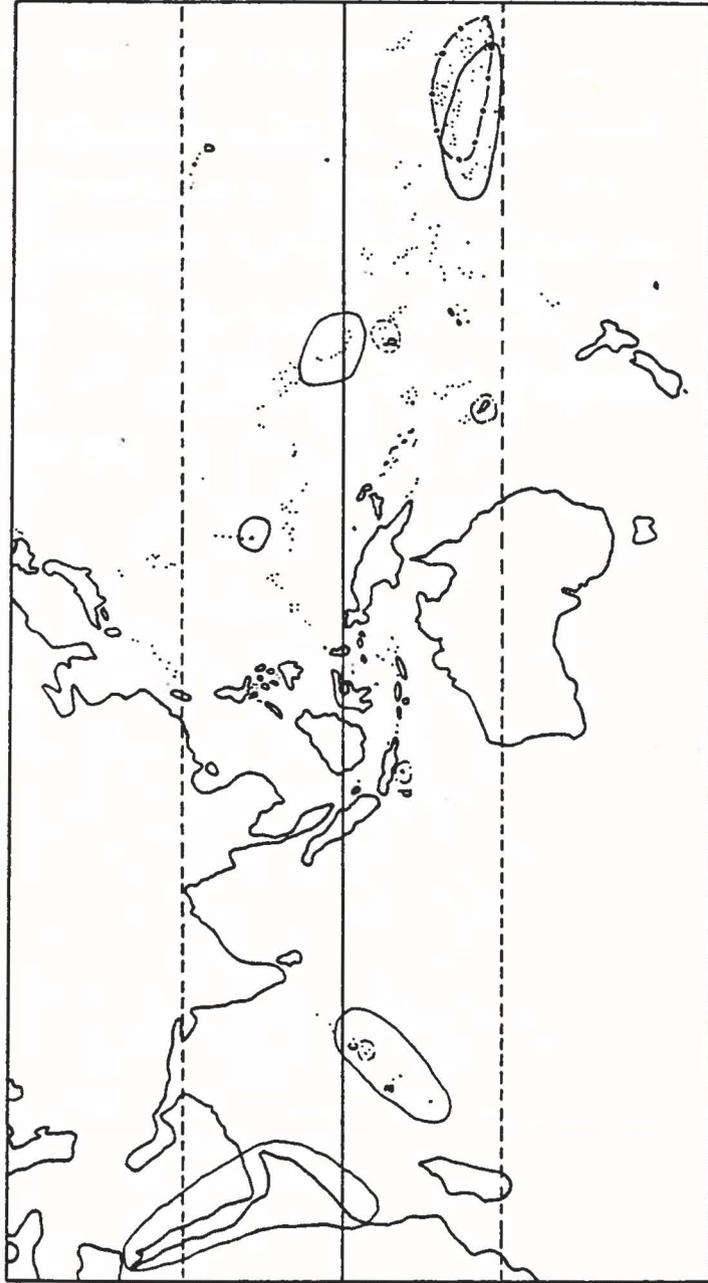
Authenticated biogeographic distribution of Avrainvillea  
obscura, Avrainvillea erecta, Avrainvillea n. sp., and  
Avrainvillea clavatiramea. Symbols are as follows:  
solid line, A. obscura; dotted line, A. erecta; broken  
line, Avrainvillea n. sp., dots and lines, A. clavatiramea.  
The type localities for each species are as follows: "a",  
A. obscura; "b", A. erecta; "c", Avrainvillea n. sp.; "d",  
A. clavatiramea.



## PLATE XXI

Authenticated biogeographic distribution of Avrainvillea amadelpa, Avrainvillea pacifica, Avrainvillea gardineri, and Avrainvillea ridleyi. Symbols are as follows: solid line, A. amadelpa; dotted line, A. pacifica; broken line, A. gardineri; dots and lines, A. ridleyi. The type localities for each species are as follows: "a", A. amadelpa; "b", A. pacifica; "c", A. gardineri; "d", A. ridleyi.

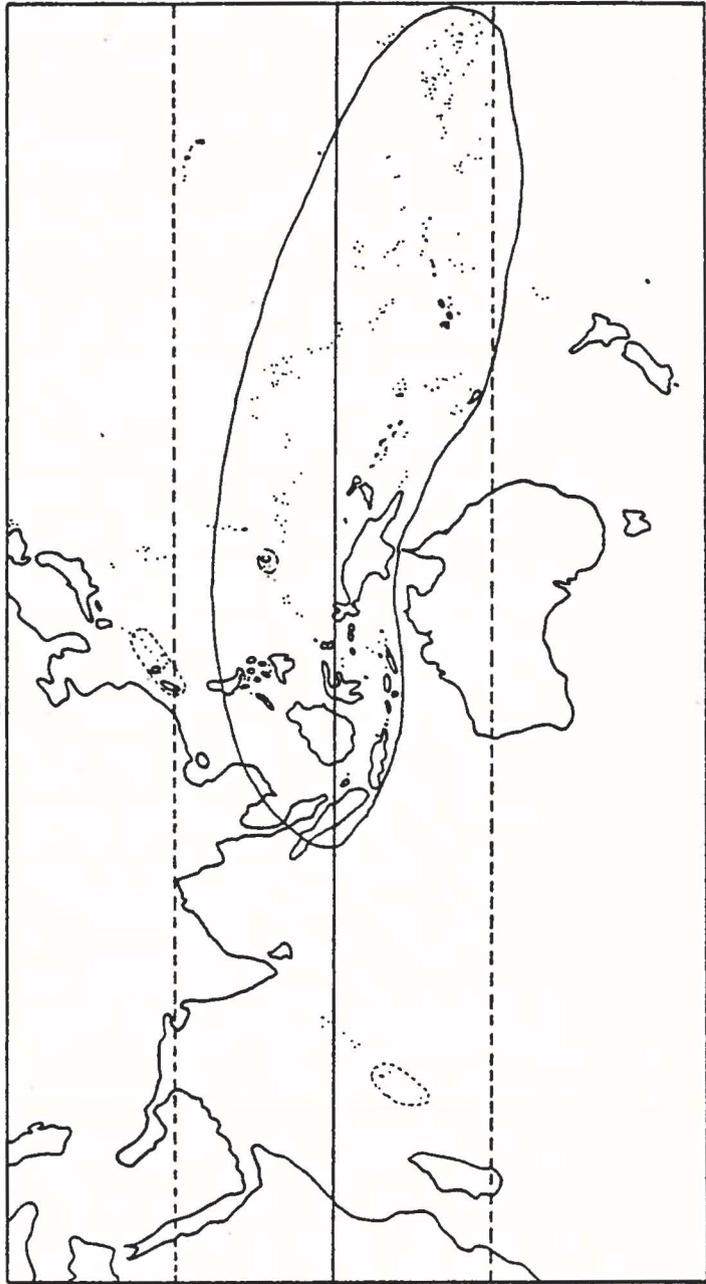
PLATE XXI



## PLATE XXII

Authenticated biogeographic distribution of Avrainvillea lacerata, Avrainvillea riukuensis, and Avrainvillea hollenbergii. Symbols are as follows: solid line, A. lacerata; dotted line, A. riukuensis; broken line, A. hollenbergii. The type localities for each species are as follows: "a", A. lacerata; "b", A. riukuensis; "c", A. hollenbergii.

PLATE XXII



APPENDIX A

GLOSSARY

## Glossary

- apices: terminal ends of siphons; clavate: swollen and bulb-like (Pl. A-II. C); hooked: curled and pointed (Pl. A-II. D); rounded: isodiametric and curved (Pl. A-II. B); tapered: pointed but sometimes rounded distally (Pl. A-II. A).
- attenuated: siphons becoming thinner, usually towards the surface, may or may not be ramified. See ramified. (Pl. A-I. D; A-II. D).
- capitular: rounded, spherical, rotundate tufts, nonplanar, e.g., A. obscura f. capituliformis.
- cespitose: plants growing in tufts, forming mats, e.g., A. rawsoni.
- clavate: see apices.
- coenocytic: united protoplasts forming one large cell.
- complanate: in one plane.
- constrictions: narrow supradichotomal portion of a siphon. Such constrictions may be very deep, shallow, or long. (Pl. A-III. A, B, C, D; A-IV. B).
- cordate-rotundate: inverted heart shape with a rounded point.
- cuneate: wedge shaped, like an inverted triangle.
- cuneiform-obovate: wedge shaped but with rounded edges.
- cylindrical: tube-like (Pl. A-I. A).
- dichotomous: repeated forkings distally along a siphon.
- elliptic: oval.
- flabellum: blade portion of the plant.
- gregarious: plants growing in clusters very close together, e.g., A. amadelpa. See solitary.
- isodiametric: tubular siphons in which the diameter remains constant over distance.
- moniliform: siphons having a series of alternating swellings and constrictions, like a string of beads, symmetrical. Note that this term is largely reserved for A. rawsoni and A. nigricans. It is a special case of torulose character. See torulose. (Pl. A-I. B; A-III. D).
- obovate: egg-shaped having the large end up.

planar: in one plane, flat, leaf-like.

pseudocortex: the ramification of siphons near the surface in which they interweave to the extent of appearing to be a thin skin-like covering, sometimes peeling away from the less consolidated inner layers of the blade.

ramification: presence of smaller, repeatedly branched, dichotomous branchlets, seen near the surface, most prominent in pseudocortical development. (Pl. A-IV. C).

rotundate: see capitular.

solitary: plants growing singly, not close together in a congested manner. See gregarious.

suborbicular: elliptical but very close to circular.

subrhomboid: blade having two parallel sides with opposite sides unequal, i.e., an irregularly shaped blade that does not conform to standard references.

tortuous: siphons having a twisted, spiral, zig-zag, kink near the surface. (Pl. A-I. C; A-IV. A).

torulose: cylindrical siphons with swellings at irregular intervals, asymmetric; longly torulose: swellings oval to very long with constrictions "longly" and unevenly spaced; lightly torulose: constrictions not deep; irregularly/patchily torulose: intermittently torulose and cylindrical for short distances. (Pl. A-I. C, D; A-III. B).

velutinous: velvet-like texture.

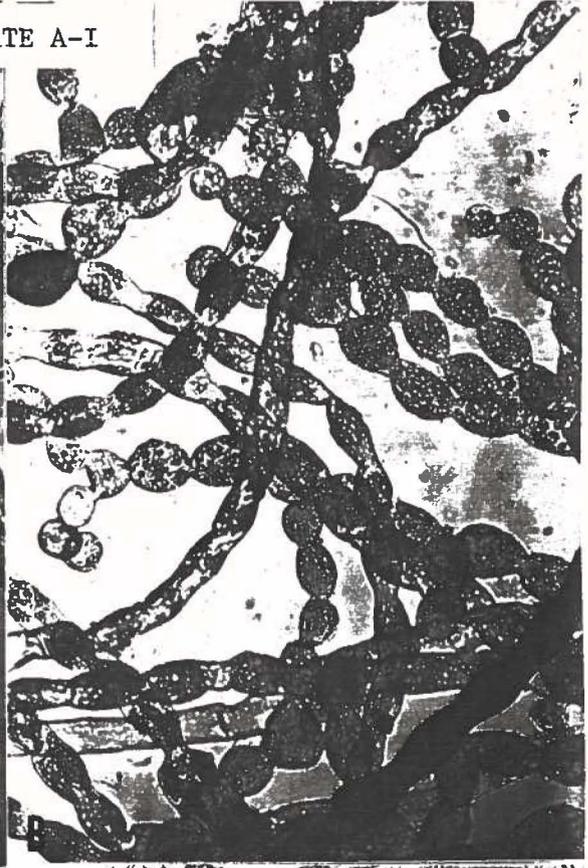
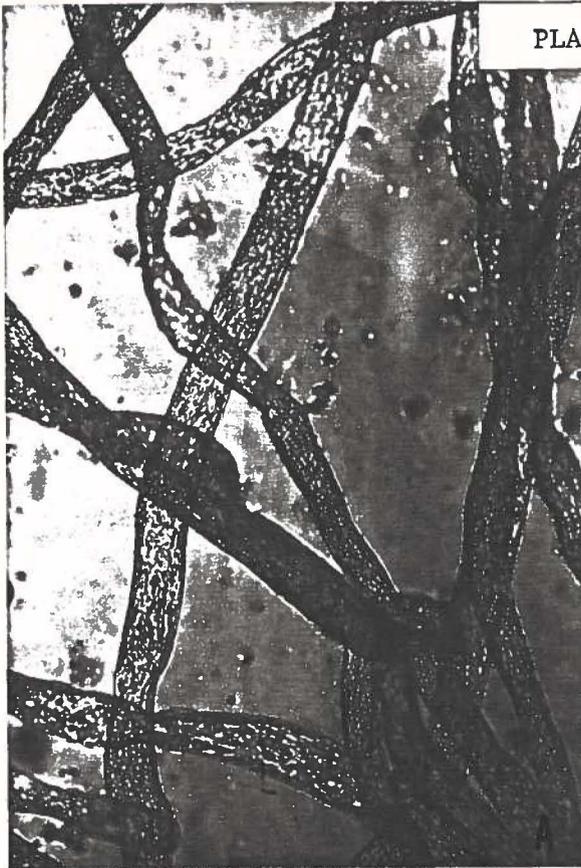
zonate: concentric pigmented rings radiating towards the leading edge of the blade.

## PLATE A-I

[Note: Magnifications are not uniform]

- A. Cylindrical siphons.
- B. Moniliform siphons.
- C. Mixed irregularly torulose and tortuous siphons.
- D. Mixed torulose and cylindrical siphons.

PLATE A-I



## PLATE A-II

[Note: Magnifications are not uniform]

- A. Tapered apex.
- B. Rounded apex.
- C. Clavate apex.
- D. Hooked apices. Note the larger cylindrical and torulose  
siphons in the background. Only found in A. pacifica.

PLATE A-II



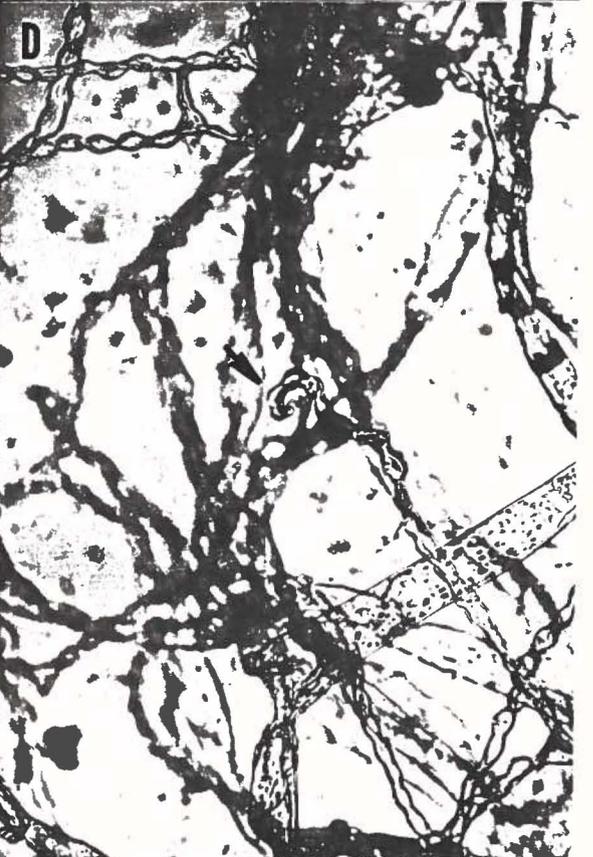
A



B



C



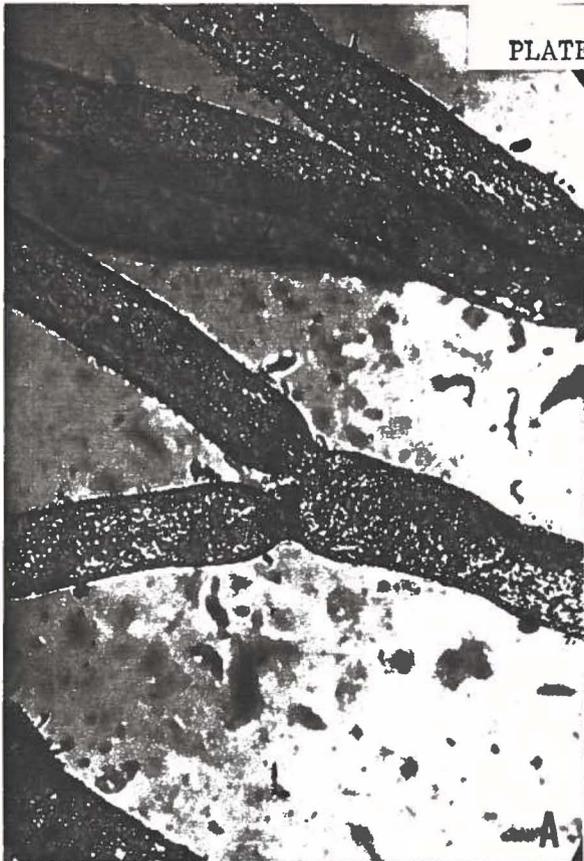
D

## PLATE A-III

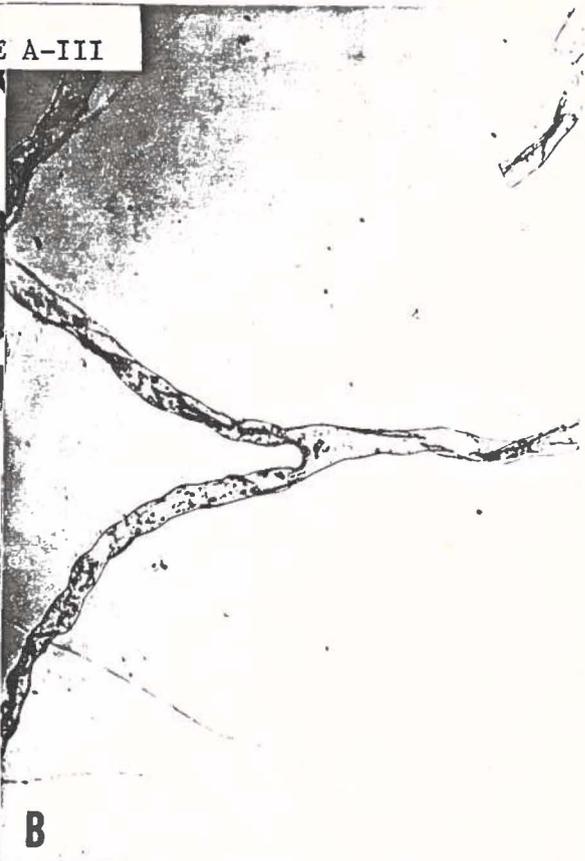
[Note: Magnifications are not uniform]

- A. Deeply constricted siphons.
- B. Weakly constricted siphons.
- C. Longly constricted siphons.
- D. Typically deep constrictions found in moniliform siphons.

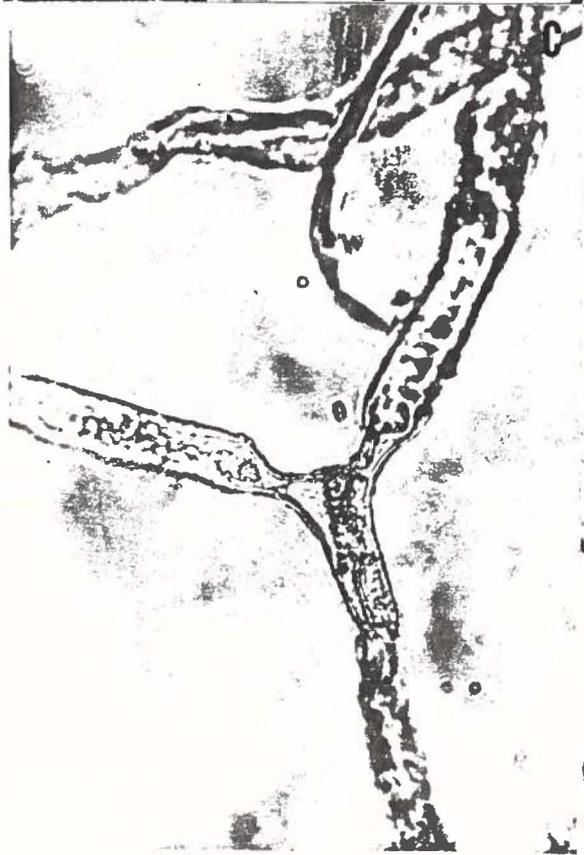
PLATE A-III



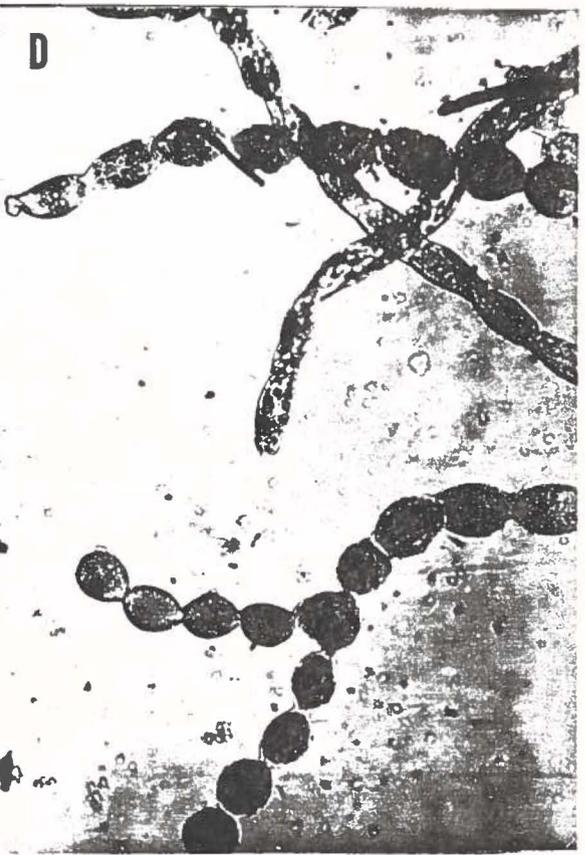
A



B



C



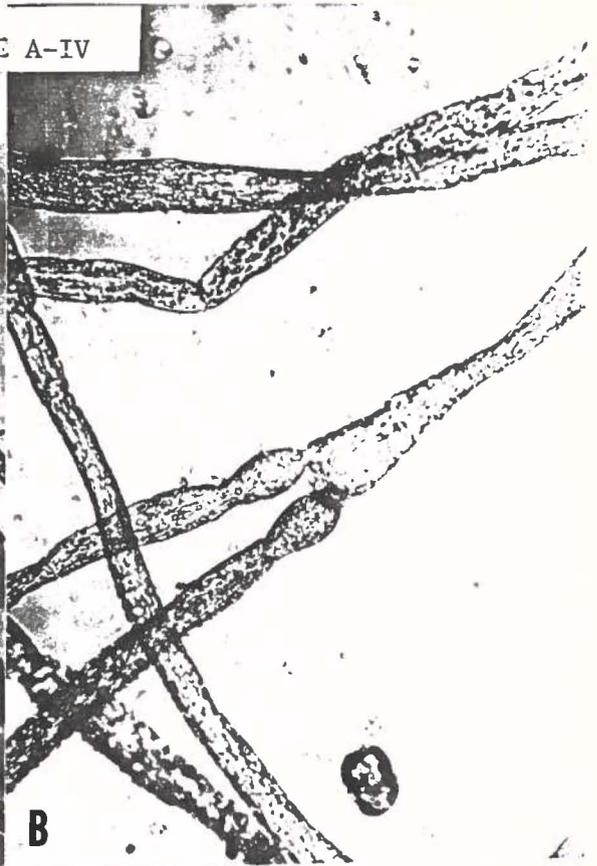
D

## PLATE A-IV

[Note: Magnifications are not uniform]

- A. Tortuous siphons.
- B. Single supradichotomal constriction, e.g., A. elliotii.
- C. Pseudocortical development composed of ramified, torulose siphons, e.g., A. amadelpa.

PLATE A-IV



APPENDIX B  
EFFECTS OF IN SITU SHADING AND REDUCED  
WATER MOTION ON THE MORPHOLOGY OF  
AVRAINVILLEA OBSCURA

Effects of In Situ Shading and Reduced  
Water Motion on the Morphology of  
Avrainvillea obscura

Introduction

Plasticity of habit is often found in Avrainvillea. Internal morphology is a more reliable taxonomic character, but even this is open to suspicion. The extent to which the environmental factors of reduced light and water motion affect morphology are of interest. How these two factors might affect overall habit configuration, siphon diameters, and torulose character were studied.

Materials and Methods

A. obscura (C. Ag.) J. Ag. was chosen as the species for experiments because of its availability and because of the presence of both isodiametric and torulose siphons. Two series of experiments were carried out near the University of Guam Marine Laboratory in Pago Bay.

The Pago Bay habitat may be characterized as a shallow (less than 1 m) sandy inner reef flat with large stands of the seagrass Enhalus acoroides (L. F.) Royle. A moderate longshore current flows through this area, often removing 5-6 cm of substratum from unprotected corridors between the seagrass patches. Sand spurs form at the downstream ends of the seagrass patches and it is in these areas that A. obscura is found.

The first set of experiments consisted of determining the relative effects of lit vs. shaded conditions as well as the effects of water motion on overall thallus morphology, both macro- and microscopic. Light shades were cut from 0.75-cm opaque plastic. This had a shading (approximately 55-65% transmittance) rather than a black-out effect.

The 30-cm<sup>2</sup> plates were held in place by four rebar legs which could be pounded into the substratum quite easily. Rubber washers cut from surgical tubing held the plates in place and allowed for any necessary vertical adjustments. Plates were adjusted to within 15-20 cm above the sand (Pl. B-I. B, D).

Modifications of the current were created by placing a small pile of rocks, broken coral, etc. around the test patch plants. This was a horseshoe-shaped wall approximately 20 cm high. In this way, water motion was reduced but not eliminated.

The following experimental treatments were performed with four replicates per run. Four shaded patches, four modified current patches, four shaded and modified current patches, and four unshaded and unmodified current patches (controls) were established. The number of plants per patch varied from one to seven or eight. Changes in individual plants were monitored weekly for five weeks. Qualitative field impressions were recorded photographically. At the end of the experimental run, all plants were collected and examined in the laboratory.

A second series of experiments involved wounding the blade in various ways. Portions of the blade were clipped with scissors. Vertical, horizontal, diagonal, and wedge shaped cuts were made. The treatments were performed on both juvenile and mature plants. The fate of each individual was then followed for the next two to three weeks.

All experimntal plants were tagged in situ with Dymo labels sewn through the upper portion of the holdfast with heavy thread. This did not seem to injure the plants in any way.

## Results

Juvenile plants which had just broken the surface showed an average growth rate of  $1.6 \pm .53$  cm during the first week,  $1.3 \pm .38$  during the second week,  $1.2 \pm .85$  cm during the third, and less than .1 cm thereafter. Weekly field observations over a 4-month period revealed that for A. obscura, a typical thallus life span may be on the order of 4-5 weeks maximum. By the end of the fourth week, the thallus was turning brown and visibly showing signs of degeneration. Within 1-2 days thereafter, a typical thallus withered away and broke off just above the hold-fast. Usually, however, a new thallus had just broken the surface next to or near the old one. Because of this, standing crops remained constant within a given population though the turnover rate for thalli was surprisingly rapid. These observations agree well with those of Young (1977), who observed a similar pattern in A. rawsoni (Dickie) Howe and A. longicaulis (Kütz.) Murray & Boodle in Panama.

In situ experimental combinations involving the relative effects of shade and water movement showed that water movement is more important than shade as an environmental factor influencing blade morphology for A. obscura. Under shaded conditions, fronds remained closely felted together throughout the experiment regardless of age class at the start. Under unshaded and reduced water motion conditions, there was a definite increase towards unconsolidated, fluffy fronds (Pl. B-I. A, C; B-II. A) and a concomitant increase in the peripheral siphon diameters (Fig. B-1). This effect was not conspicuous in juvenile plants for subsequent development resulted in essentially rotundate, unconsolidated fronds. In more mature plants, this fluffy morphology was exhibited in the new growth on the blade similar to that found on

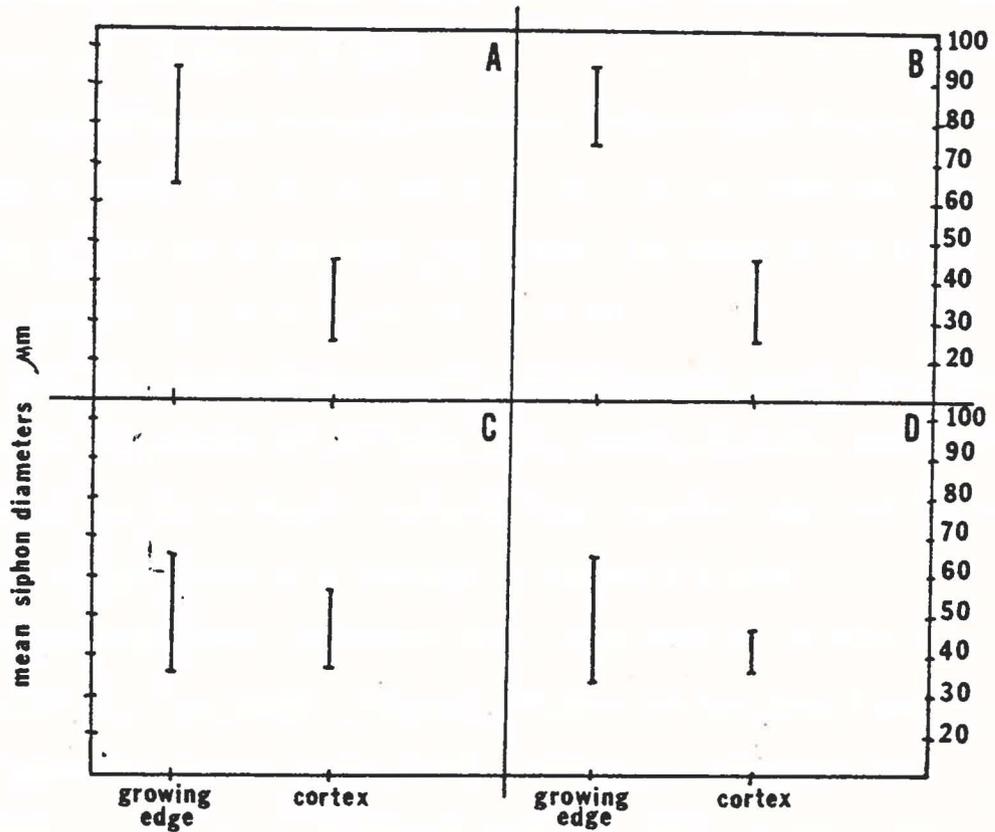


FIG. B-1. Average range of siphon diameters for four environmental treatments on individuals of *Avrainvillea obscura* after three weeks. Initial siphon diameters never exceeded 57  $\mu\text{m}$ . Symbols are as follows: A, shaded and decreased current flow; B, reduced current flow; C, shaded; D, control.

some of the clipped plants. The chi-square statistic for a 2 x 2 contingency table which compared blade type under normal and reduced current conditions was significant ( $\chi^2 = 6.36$ ,  $p < 0.025$ ). The chi-square statistic for blade type under shaded and unshaded conditions was not significant ( $\chi^2 = 0.020$ ,  $p < 0.001$ ).

Under conditions of combined shade and reduced water motion, the results were similar to those found with decreased water motion alone. The amount of new growth was less, which would be expected under the slightly reduced light conditions (Pl. B-I. C).

Although the torulose character of A. obscura is poorly developed in comparison to "members of the "nigricans" group, torulose character was not affected in the deeper portions of the blade. Only the leading, peripheral growing edges were subject to extensive change.

Clipping experiments on mature plants were not very successful. Less than 50% survived, and of these, little or no new growth was observed along the clipped edges. Of 39 plants, 11 showed no new growth, while 7 developed new growth averaging  $.85 \pm .24$  cm in one week. The remaining 21 plants died. Death was most likely imminent due to natural senescence rather than the clipping.

Clipping experiments on juvenile plants revealed considerable new growth. Among 26 plants, 18 showed new growth along the wounded edge averaging  $1.1 \pm .53$  cm after one week. The remaining 8 plants died, probably due to the clipping trauma in this case. In all cases the new filaments did not readily assume the normal thallus configuration. Rather the new siphons were usually 20-50  $\mu\text{m}$  larger in diameter than in similar peripheral siphons of nonwounded plants, i.e., 38-47  $\mu\text{m}$  vs. 66-95  $\mu\text{m}$ .

## Discussion and Conclusions

The results of these experiments suggest several things, perhaps the most important of which is the environmental influence of water motion on morphology as well as siphon diameter. This is now documented for at least one species and probably holds to varying degrees for other Avrainvillea species. Reduced water motion is definitely an important factor in the alteration of frond morphology. This is in contrast to Peterson's (1972) findings for Caulerpa racemosa in which light proved the more critical factor.

Information on growth rate proved useful not only as a tool for observing frond changes, but also in establishing the life span. First, differential growth rates between juvenile and mature, or nearly mature, plants results in variable responses with respect to the degree of morphologic responsiveness to the two treatments. Mature plants typically exhibited less significant changes than did juvenile plants. Second, the potential number of individuals that may sequentially arise from a single rhizome is unknown. Production of new individuals from the rhizome is certainly dominant over sexual reproduction during most of the year. Certainly, semi-weekly monitoring for a one-year period could put this matter in perspective. Finally, torulosity appears to be a constant character, altered only along the peripheral growing edge of an immature frond.

From the taxonomic perspective, three points are learned. First, siphonal diameters along the outer peripheral edge are definitely not reliable. Second, torulosity appears to be fundamentally less affected, except along the outermost edge. Finally, blade morphology is definitely subject to local environmental conditions.

## Literature Cited

- Peterson, R. D. 1972. Effects of light intensity on the morphology and productivity of Caulerpa racemosa (Forsskal) J. Agardh. *Micronesica* 8:63-86.
- Young, J. R. 1977. Ecological observations on the reproduction of the tropical marine alga Avrainvillea from Panama (Siphonales, Codiaceae). Unpublished paper presented at Int'l Seaweed Symposium, 1977, Santa Barbara.

## PLATE B-I

- A. Close-up of shaded and reduced current plants, final.

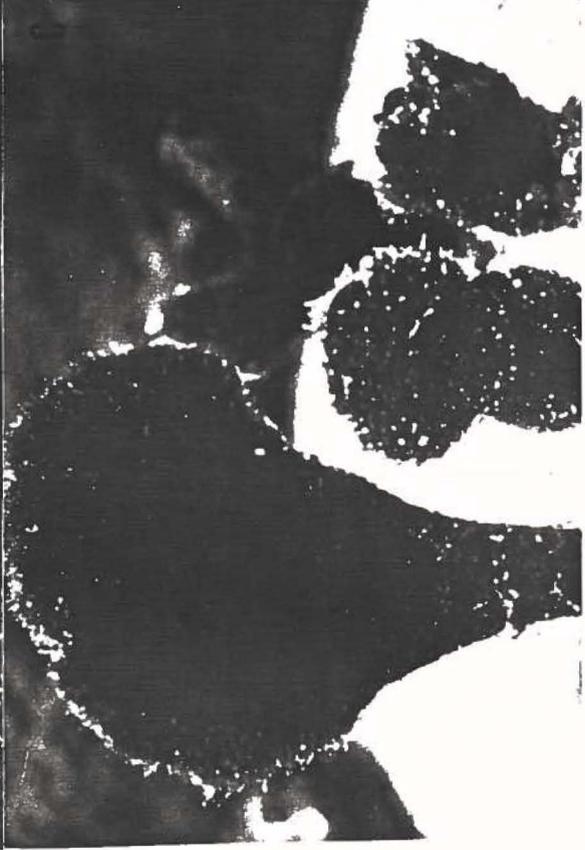
Note the loosely to nonwoven siphons of the  
peripheral edges.

- B. Pago Bay study site showing shade in place over test  
plants.

- C. "Fluffy" plants in reduced current habitat.

- D. Close-up of shaded and reduced current plants, initial.

PLATE B-I



## PLATE B-II

A "fluffy" individual from a reduced current habitat.

Protruding siphons are empty gametangia.

PLATE B-II

