

**OCCASIONAL PAPERS**  
OF  
**BERNICE P. BISHOP MUSEUM**  
HONOLULU, HAWAII

Volume XXIII

August 31, 1962

Number 6

**Some *Liagora*-inhabiting species of *Acrochaetium*<sup>1</sup>**

By ISABELLA A. ABBOTT

HOPKINS MARINE STATION OF STANFORD UNIVERSITY

INTRODUCTION

The genus *Acrochaetium* (Rhodophyceae, Nemalionales) is known chiefly from floristic accounts, the most notable of which are those of Rosenvinge (1909),<sup>2</sup> Børgesen (1915-1920, 1927, and 1937), and Kylin (1944). Drew (1928) and Nakamura (1941, 1944) monographed the genus for limited geographical areas. Only Hamel (1927) studied the genus from various geographical areas, and his contribution provides an understanding of the species known up to his time. Papenfuss (1945, 1947), in reviewing the literature of the *Acrochaetium-Rhodochorton* complex, organized the species into convenient groups. Recently Feldmann (in press) pointed out the need for major revision, and he is now preparing a monograph on the group.

One of the difficulties facing any worker in this group is the large number of inadequately described species, most of which are known from only scanty material. Furthermore, the limits of variation in the majority of the species are unknown. It seems likely, as Baardseth (1941) suggests, that a species may be known under more than one name.

No one had studied *Acrochaetium* inhabiting a given genus until the recent rich collection of *Liagora*, a red alga belonging to the Nemalionales, from the Sulu Sea afforded me an opportunity to study the variation in *Acrochaetium* as it occurs in that genus. For comparative purposes, good collections of properly preserved *Liagora* from Bermuda, the Hawaiian Islands, and the Gulf of California were

<sup>1</sup> All of the algae from the Philippines discussed in this paper were collected by Donald P. Abbott on the 1957 Sulu Sea Expedition, jointly sponsored by Bishop Museum and the Philippine National Museum.

<sup>2</sup> Dates in parentheses refer to Literature Cited, p. 119.

utilized. This leaves only two large geographic areas known to contain many species of *Liagora* from which no collections have been obtained: the Caribbean and the Indian Oceans, especially the area around Mauritius. No mention has been made of Formosa, the Ryukyus, the Bonin Islands, and southern Japan because a cursory examination of the Philippine *Liagora* shows that the species of the two areas are largely similar.

The small filamentous plants which constitute the genus *Acrochaetium* are usually epiphytes on other algae and on other marine plants, but they may also be endophytic, epizooic, or endozooic. They are, for the most part, very simple in construction, a few species consisting of only a few cells in short filaments. Their reproduction is simple also. Many species produce only monospores; others, in addition to this mode of propagation, bear simple carpogonial branches, whose carpogonia produce only a few carpospores after fertilization. Spermatangia may occur on the same plant or on separate plants from the carpospore-bearing ones. A few species may also have tetrasporangia.

*Liagora* is widely distributed in the tropics, especially the subtropics. It is composed of forms which are multiaxial and have radiating assimilatory filaments. These filaments contain to a greater or lesser degree a coating of calcium carbonate which may or may not be accompanied by a mucosoid material. The plants average 8 to 16 cm. in height, varying greatly in size, shape, and branching and in development of reproductive structures. Although their external variations are great, there is remarkable uniformity in the internal vegetative structure. Few of the approximately 60 species are well known.

So far, the epiphytes under study have not been reported from all the localities where *Liagora* species are known, but my present studies indicate that it would be a rare *Liagora* which did not contain one or more species of *Acrochaetium*.

This study encompasses 23 species of *Acrochaetium*, four of which are being placed in synonymy and six of which are proposed as new. Sexual plants for eight species are described. Two new species are from the Philippines, three are from Hawaii, and one is from Bermuda.

The specimens cited will be deposited in the herbaria of Bernice P. Bishop Museum (BISHOP), the University of Michigan (MICH), the Philippine National Museum (PNM), the University of California, Berkeley (UC), the Cryptogamic herbarium of the University of Paris (PAR), and my own herbarium (IA).

Type and isotype materials of the new species are on microscope slides, accompanied by a specimen of *Liagora*. Other material is either on slides or on dried specimens of *Liagora*. I consider the slide specimens the critical ones.

#### ACKNOWLEDGMENTS

I wish to thank my husband, Donald P. Abbott of Stanford University, G. F. Papenfuss of the University of California, W. R. Taylor of the University of Michigan, M. S. Doty of the University of Hawaii, and P. C. Silva of the University of California for placing material of *Liagora* at my disposal. I also wish to thank Jean Feldmann of the University of Paris for allowing me to see his manuscript on *Acrochaetium*. I am greatly indebted to Donald P. Rogers of the University of Illinois for help with all the Latin diagnoses, except for that of *A. imitator* which was done by Hannah Croasdale of Dartmouth College.

My husband does not have field collecting numbers, or a collection of algae. Therefore, in citing specimens which he collected for me, I have used my own numbering system which will facilitate reference to the specimens, as they are deposited in various herbaria.

#### TAXONOMY OF ACROCHAETIACEAE

The family Acrochaetiaceae contains at least five genera which contain several hundred species. Following Papenfuss (1945, 1947), it includes *Acrochaetium* Naegeli, *Kylinia* Rosenvinge, *Audouinella* Bory, and *Rhodochorton* Naegeli. *Liagorophila* Yamada has since been added (Yamada, 1944). J. Feldmann, in a paper read at the Bangkok meetings of the Pacific Science Congress (1957), of which I have a manuscript copy, removed *Audouinella* and *Rhodochorton* to a new family, Audouinellaceae, in which he includes the genus *Grania* (Rosenvinge) Kylin. He adds to the Acrochaetiaceae *Balbiana* Sirodot and proposes a new genus, *Rhodothamniella* Feldmann.

Papenfuss (1945, 1947) attempted to bring order into the confusion of the many species and myriad variabilities in this complex. He proposed in 1945 that all forms with a parietal chromatophore be restricted to the genus *Acrochaetium*, and that those with a stellate chromatophore be restricted to *Chromastrum* Papenfuss. He also drew (1945) the limits for the genera *Rhodochorton* and *Audouinella* and removed *Chantransia* from the Acrochaetiaceae.

Kylin (1944), in a paper received by Papenfuss after the war, stated that *Kylinia rosulata* Rosenvinge (1909)—the type species of *Kylinia* Rosenvinge—had a stellate chromatophore. Therefore, Papenfuss (1947) placed his genus *Chromastrum* in synonymy with *Kylinia*. Feldmann (1958) now states that Kylin was mistaken in the identity of his plant, that *K. rosulata* has a parietal chromatophore, and that the genus contains only two species, *K. rosulata* and *K. australis* Levring (1953). The genus is further characterized by the following: stalked "spermatocysta" ("on hyaline androphore cells," Levring, 1953), and the undivided fertilized carpogonium producing carpospores directly. The latter is a character of prime distinction.

Feldmann proposes that the genus *Acrochaetium* contain only those species which have one chromatophore (parietal or stellate) in each cell, the "spermatocysta borne on vegetative undifferentiated cells, gonimoblast with sporogenous filaments bearing terminal carpospores; carpogonium transversely divided after fertilization." His reason for characterizing the genus so as to include both types of chromatophores is the fact that in his study of certain French species the chromatophores intergrade. I found, in the present studies, that only one species, *A. liagorae*, showed this character; but since so many of the species of *Acrochaetium* (*sensu latiore*) occur in the temperate waters around France, Britain, and Sweden, it would be wise to await the monograph by Feldmann before assessing this character. I have, therefore, chosen to use the name *Acrochaetium* in its widest sense. We have not come very far; Børgesen said the same thing 25 years ago (1937).

Because of the simplicity in reproduction shown by members of this family, Feldmann considers them to be lacking in a "true carpogonial branch," and on the strength of this belief he places the Acrochaetiaceae and Audouinellaceae in a separate order, the Acrochaetiales. I cannot agree with him on this point. The Nemalionales show great diversity in the form, the position, and the development of the carpogonial branch. The Helminthocladiaceae, which many consider "typical" of the Nemalionales, show special diversity, as has been demonstrated by Papenfuss (1946) in *Trichogloea*, by Yamada (1938 in *Liagora*; 1944 in *Liagoropsis*), by Desikachary (1956), and by Desikachary and Balakrishnan (1957) in certain species of *Liagora*. In some of these only the carpogonium participates in gonimoblast formation (*Liagoropsis*, Yamada 1944, Desikachary, 1957; *Liagora mucosa* Desikachary and Balakrishnan, 1957); in others the entire

carpogonial branch becomes involved (*Trichogloea*, some species of *Liagora* as studied by Desikachary and Balakrishnan, 1957) in the formation of the cystocarp. In some, therefore, the carpogonium, placed terminally on a special branch, may be thought to be just as sessile as if it were produced directly on a vegetative filament, as it is in *Acrochaetium papenfussii*, *A. dotyi*, *A. liagorae*, *A. imitator*, and (at times) *A. rongelapense*. Because the lower vegetative cells bearing the carpogonium are not involved in gonimoblast formation in some specimens of *A. trichogloea* and of *A. tuticorinense*, they have been designated as "stalks" in this paper. However, in the loosely defined term "carpogonial branch," as currently understood, they would also qualify as part of the branch. In order to avoid the awkward use of the term "carpogonial branch one-celled," I have used the term "sessile carpogonium" and for the condition arising when more than one cell is involved, the term "carpogonium on a one-celled stalk." Neither usage is meant to imply that these female reproductive structures are different from the more elaborate ones in, for example, the Dumontiaceae, or the more fixed ones in the Rhodomelaceae.

In *Kylinia* as circumscribed by Feldmann (1958), the carpogonium is a simple flask-shaped structure with a trichogyne. Carpospores are produced directly from it after fertilization, the carpogonium proper apparently not dividing but "budding off" carpospores. Except for one transverse division in the carpogonium after fertilization, *Acrochaetium imitator* shows the same type of carpospore development in this study. The transverse division is similar to genera in the Helminthocladiaceae (*Nemalion*, *Liagora*, *Helminthora*), although none of these produce carpospores in the same way as does *Kylinia*.

To judge from Feldmann's description and illustrations of the androphore or spermatocystophore of *Kylinia* (1958), these stalk-like structures bearing the spermatangia are homologous to the stalks which bear spermatangia in some species of *Acrochaetium* (*A. papenfussii*, *A. rongelapense*). Stalks of this kind are commonly found in genera of the Helminthocladiaceae (*Nemalion*, *Liagora*, and *Helminthora*). Of the four kinds of spermatangial plants found in the *Acrochaetium* species in this study, only one, *A. imitator*, would qualify under Feldmann's characterization of the genus: "spermatocysta borne on vegetative undifferentiated cells." The other seven species showing male plants have spermatangia borne on specialized cells. The species showing spermatangial plants may be grouped as follows:

Spermatangia in terminal corymbose or nearly corymbose clusters; stalked: *A. rongelapense*, *A. trichogloae*, *A. papenfussii*, *A. tuticorinense*.

Spermatangia in lateral circinnately formed clusters: *A. dotyi*.

Spermatangia in small panicles, the spermatangial mother cells producing spermatangia on all surfaces: *A. liagorae*.

Spermatangia in terminal groups of one to three, formed from an ordinary vegetative cell: *A. imitator*.

These comparisons are not meant to detract from the characters shown by *Kylinia* as a genus separate from *Acrochaetium*, but to show that *Acrochaetium* has species within it which demonstrate a wide range of variations in almost any character selected for comparison. In my opinion, the more constant of these characters—those associated with sexual reproduction—are directly comparable with those of the Nemalionales. Because of these phylogenetic relationships, I strongly recommend the continued inclusion of the Acrochaetiaceae in the Nemalionales.

#### DESCRIPTIONS OF SPECIES

The species of *Acrochaetium* reported as growing on *Liagora*, including those reported here, may be placed in four comparatively natural groups. (The only one not discussed in this paper is *A. daviesii*.)

1. Growth from a persistent basal cell representing the spore, the original spore aseptate or becoming septate, chromatophore parietal, plant mostly epiphytic.

*Acrochaetium* *barbadense* (Vickers) Børgesen

*occidentale* Børgesen

*comptum* Børgesen

*angustum* (Drew) Papenfuss

*rongelapense* Abbott IN Taylor

*dotyi* Abbott, new species

*liagoraefilum* Børgesen

*nemalionis* (De Notaris) Bornet

*catenatum* Howe

2. Growth from a persistent septate spore, plant partly to wholly endophytic.

Chromatophore parietal:

*A. trichogloae* Børgesen

*nitidulum* Abbott, new species

Chromatophore stellate:

*A. papenfussii* Abbott, new species

3. Growth from an aseptate spore, soon pulled out of shape (non-persistent), plants partly to wholly endophytic.

Chromatophore parietal:

*A. laxum* Abbott, new species

*liagorae* Børgesen

*liagoroides* Børgesen

*imitator* Abbott, new species

Chromatophore stellate:

- A. *liagorae* Børgesen
- liagoroides* Børgesen
- actinocladium* Abbott, new species

4. Germination not known, or kinds other than those listed above.

Germination unknown:

- A. *vanbosseae* Papenfuss

Only the bases, which are multicellular, embedded in *Liagora*:

- A. *seriatum* Børgesen
- tuticorinense* Børgesen
- gracile* Børgesen
- daviesii* (Dillwyn) Naegeli (Børgesen)

#### GROUP I

Growth from a persistent basal cell representing spore, original spore aseptate or becoming septate, chromatophore parietal, plant mostly epiphytic.

1. ***Acrochaetium barbadense*** (Vickers) Børgesen, Dansk. Bot. Arkiv. 3 (1): 43, 1915 (figs. 1, *a-h*; 2, *a*).

*Chantransia barbadensis* Vickers, Ann. Sci. Nat. Bot. IX, 1: 60, 1905.

*Acrochaetium barbadense* (Vickers) Børgesen *sensu* Hamel, Recherches *Acrochaetium* 70, 1927.

*Acrochaetium occidentale* Børgesen, Dansk. Bot. Arkiv. 3 (1): 44, 1915.

*Acrochaetium occidentale* var. *caespitosa* Børgesen, Kgl. Danske Vidensk. Selskab., Biol. Meddel. 6 (6): 28-32, 1927.

*Acrochaetium angustum* (Drew) Papenfuss, Univ. Calif. Pub. Bot. 18 (14): 312, 1945.

*Rhodochorton angustum* Drew, Univ. Calif. Pub. Bot. 14(5): 185, 1928.

Plants epiphytic with endophytic system of branches, 1 to 5 mm. in height (mostly 1 to 2 mm.), arising from a single, large, globular persistent spore usually 12  $\mu$  in diameter, with thickened walls, spore sometimes septate; erect filaments branching directly above spore or some distance from it, branching subdichotomous, irregular, favoring upper portions; terminal filaments hairlike and tapering. Monosporangia borne usually to one side, sessile or pedicellate. Lower penetrating portions of plant below spore developing a linear rhizoidlike attachment, or this filament sending up secondary erect branches, some of which reach highest level of originally erect branches and bear monosporangia. Lower portions may develop massively thickened lateral walls (fig. 1, *d*), and cross walls becoming obscure. Cells of penetrating portion usually colorless, especially in lowest cells.

Type locality: Barbados.

Geographical distribution: Virgin Islands (Børgesen), Canary Islands (Børgesen), Channel Islands, California (Drew).

New records: Guadalupe Island, Pacific Mexico; Oahu, Hawaiian Islands; Bermuda.

Bermuda: in *Liagora farinosa*, west side of causeway between Hamilton Island and St. George's Island, April 16, 1949, *A. J. Bernatowicz, W. R. Taylor 48-801* (MICH, UC, PAR, IA); in *Liagora mucosa*, along Hamilton to St. George's Causeway, west side of Castle

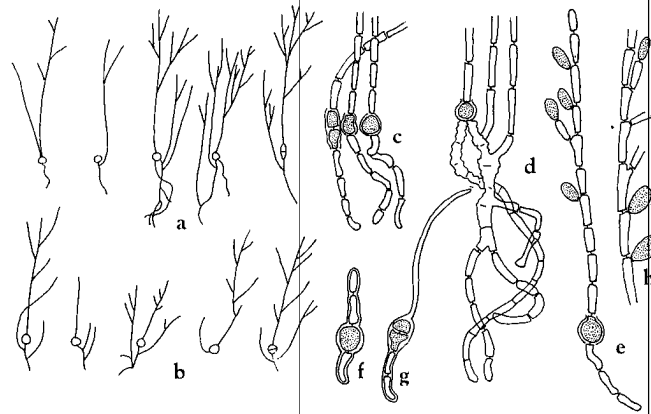


FIGURE 1.—*Acrochaetium barbadense*: **a**, habit diagrams, showing relationship of upper and decumbent branching to persistent basal spore (Bermuda, *Taylor 48-801* in *Liagora farinosa*); **b**, similar diagrams of specimens from Guadalupe Island (*Silva* in *Liagora californica*); **c**, basal spores, showing septate and nonseptate conditions in adjacent plants (Bermuda, *Taylor 48-801* in *Liagora farinosa*); **d**, basal portion, showing lateral thickening of decumbent filaments (Bermuda, *Taylor 49-515* in *Liagora mucosa*); **e**, young plant showing both stalked and sessile monosporangia and undivided basal spore (Guadalupe Island, *Silva* in *Liagora californica*); **f**, **g**, germinating spores (Guadalupe Island, *Silva* in *Liagora californica*); **h**, portion of mature plant, showing both stalked and sessile monosporangia (Bermuda, *Taylor 48-801* in *Liagora farinosa*).

Harbor, March 31, 1949, *Bernatowicz, Taylor 49-575* (MICH, US, IA); in *Liagora ceranoides*, St. George's Island, Whalebone Bay, April 19, 1956, *Taylor 56-708* (MICH, UC, IA).

Hawaiian Islands: in *Liagora farinosa*, Oahu, Laie Bay, May 30, 1946, *Abbott 1475* (BISHOP, MICH, UC, IA).

California: in *Liagora californica*, Catalina Island, Avalon, June, *Gardner 4921* (UC 294547). Type of *Rhodochorton angustum*.



Pacific Mexico: Guadalupe Island, February 1, 1950, *P. C. Silva* (PCS, UC, PAR, IA).

The species placed in synonymy have in common a persistent basal spore, from whose free surface erect filaments are produced (these constituting the main part of the plant) and from whose lower surface are produced rhizoidlike filaments that may bear erect branches. They differ from each other mainly in their method of branching in the erect portions.

When Børgesen described *A. occidentale* (1915) he suggested that his new species was perhaps the same as *A. barbadense*, but that *A. barbadense* had sexual organs which his plants lacked and that the sporangia were badly described in regard to position, shape, and size. In 1927 Hamel figured and described *A. barbadense* in some detail, presumably from Vickers' *exicattae* of Barbados algae, since a filament of *Liagora farinosa* appears in Hamel's figure. While no sexual plants of *A. occidentale* (*sensu stricto*) have yet been found, my studies show that such plants in other species are not as rare as one might think. However, they add little to the systematics of the genus at the species level. Inasmuch as Hamel's figures show the persistent basal spore in *A. barbadense* to be similar to that of *A. occidentale*, and inasmuch as the ramification of the erect branches, the sessile sporangia, and the measurements of cells and spores all fall within the variations of plants examined in this study, I have placed *A. occidentale* and its variety *caespitosa* in synonymy with *A. barbadense*.

*A. comptum*, also from the Virgin Islands, is distinguished from *A. occidentale* by two main characteristics: the divided nature of the persistent basal spore and the pedicellate nature of the sporangia. Germinating spores growing side by side in *Liagora farinosa*, the same species upon which *A. occidentale* was first described as growing, show that they can be undivided or divided on germination (fig. 1, *c*). Figure 1, *h* shows the pedicellate and sessile sporangia from a plant with an undivided basal spore (also growing on *Liagora farinosa*). I believe, therefore, that these characters cannot be used to separate two closely related species and feel that, since other characteristics shown by both species (branching, height of plant, relation of erect branches to the basal spore) intergrade, *Acrochaetium comptum* must be placed in synonymy with *A. occidentale* (*A. barbadense*). (See figure 1, *a*.)

*A. angustum* (fig. 1, *b*) represents shorter plants (0.5 to 1.5 mm.), with slightly broader filaments than in either *A. occidentale* or *A.*

*comptum*. The internal portions below the spore are said by Drew (1928) to show a more horizontal nature than the vertical condition shown for *A. occidentale* by Børgesen (1915, his fig. 42, *c*). The sporangia in *A. angustum* are reported by Drew to be pedicellate whereas Børgesen says they are sessile in *A. occidentale*. I find that *A. angustum* most commonly has vertical (linear) lower filaments and has sessile as well as pedicellate sporangia (figs. 1, *e*; 2, *a*). The same is true of *A. occidentale*. The germinating spore in both entities may be single or septate (figs. 1, *c, f, g*; 2, *a*). In old plants of *A. angustum*, as in *A. occidentale*, many terminal laterals show a lightly staining protoplast and an apparent conversion to hairlike appendages to as much as half the diameter of the filaments giving rise to the laterals (fig. 2, *a*). All things considered, *A. angustum* may be nothing more than a more robust *A. occidentale*. Its occurrence in an isolated, well-marked species of *Liagora* might well account for the differences which, in my opinion, are minor. I believe the two species to be conspecific (fig. 1, *a, b*). As reconstituted here, *Acrochaetium barbadense* is distinguished by its persistent basal spore, from whose free surface is produced a tuft of erect branches terminating in hairlike filaments. The lower surface of the basal spore produces rhizoids.

The largest of these plants (to 5 mm.) is *A. occidentale*, a plant first described from the Virgin Islands. It is characterized by a single undivided persistent basal spore, from which arise, directly or indirectly, the soft, flexible, tufted erect branches (fig. 1, *a*). The cells of these branches are 5 to 12  $\mu$  wide by 24 to 72  $\mu$  long in the middle portions of the plant. They taper upward into hairlike filaments. Monosporangia are borne in small numbers usually to the adaxial side of these erect branches. They are usually sessile, 7.0 to 12  $\mu$  wide by 17 to 21  $\mu$  long.

*Acrochaetium nemalionis*, reported by Vickers to be in *Liagora farinosa* from the Canary Islands, is similar according to Rosenvinge (1909, p. 126, figs. 53-54); but according to Bornet (1904), the germinating (original) spore becomes indistinct. Rosenvinge could not see the germinating spore. I was able to find it, though the much-entwined basal portions with many rhizoids are certainly not of *A. barbadense* as understood here. Therefore, I feel that *A. nemalionis* cannot be included in this species.

*A. corymbiferum* (Thuret) Batters (*A. bornetii* Papenfuss) is the first species of *Acrochaetium* in which sexual organs were described (Thuret, 1863). It grows on *Helminthocladia purpurea*, a temperate-

water species with the "spring-brunnen-typus" organization of *Liagora*. Hamel (1927, pp. 27-29, fig. 26, *b*) was the first to discover that it develops from a persistent basal spore which may produce erect branches from the lower endophytic filaments. From Hamel's figure 25 (1927) it appears that some relationship might be found if a critical examination were made of *A. corymbiferum* and the *A. barbadense* complex. According to Hamel (1927, p. 70) the female reproductive structures of *A. barbadense* resemble those of *A. corymbiferum*. This comparison should certainly be made. Lacking properly preserved material of *A. corymbiferum* and female plants of *A. barbadense* for comparative studies, I am unable to pursue this problem.

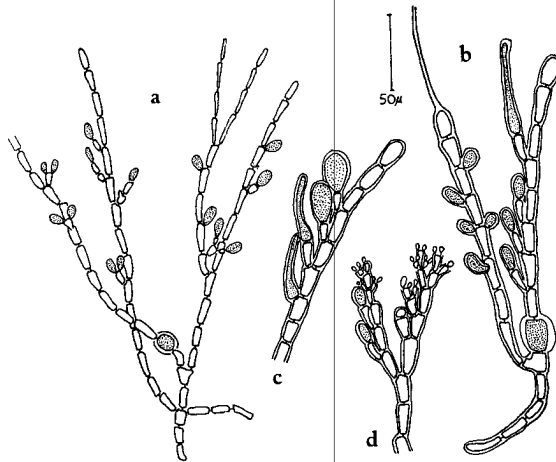


FIGURE 2.—*a*, habit of mature plant of type of *Rhodochorton angustum* (California, Gardner 4921 in *Liagora californica*). *b-d*, *Acrochaetium rongelapense*: *b*, habit, showing nature of monosporangia and carpogonium (stippled) of type specimen (Marshall Islands, Taylor 46-609 in *Liagora hawaiiiana*); *c*, stalked monosporangia, stalked and sessile carpogonia (Marshall Islands, Taylor 46-608 in *Liagora hawaiiiana*); *d*, spermatangia and monosporangia (Marshall Islands, Taylor 46-608 in *Liagora hawaiiiana*).

2. *Acrochaetium rongelapense* Abbott IN Taylor, Plants of Bikini..., 117, 1950 (fig. 2, *b-d*).

Plants in small, stiff tufts to 1 mm. (usually less) in height, epiphytic to partly endophytic, with a persistent basal spore. Erect filaments unbranched or sparingly branched, dichotomous where present; erect branches occasionally from endophytic filaments below spore (fig. 2, *b*), but these short lower filaments usually unbranched. Monosporangia usually stalked, 12 to 15  $\mu$  in diameter in a

second series, or not stalked when opposite or alternate (fig. 2, *b*). Cells of erect filaments 8  $\mu$  in diameter, 23 to 30  $\mu$  in length, gradually becoming shorter near tips of plant, to 15  $\mu$  in length. Colorless hairs may occur on tips of filaments.

Persistent basal spore 15 to 17  $\mu$  by 22  $\mu$ . Spermatangia (fig. 2, *d*) about 4  $\mu$ , stalked, in small clusters; carpogonium sessile or on a one-celled stalk (fig. 2, *c*), cystocarps to 46  $\mu$  in diameter. Male and female elements on different plants, but occurring with monosporangia. Chromatophore parietal with a single pyrenoid.

Marshall Islands: type in *Liagora hawaiiiana*, Rongelap Atoll, Mellu Island, July 27, 1946, *Taylor 46-609* (MICH); isotype (IA); other specimens, same place and date, *Taylor 46-608* (MICH, IA).

*Acrochaetium rongelapense* is no doubt closely related to *A. barbadense*, especially to the entity which has been known as *A. angustum*, with which *A. rongelapense* shares two characteristics: (1) it is a smaller and broader plant than *A. barbadense* and (2) it has both pedicellate and sessile sporangia. From *A. angustum* it differs in having a simple invading endophytic filament; and its erect filaments, even in the mature plants, are unbranched or little-branched. The female reproductive organs in *A. rongelapense* are similar to those of *A. corymbiferum*; according to Hamel (1927) those of *A. corymbiferum* are similar to those of *A. barbadense*.

The differences shown by *A. rongelapense* as compared to *A. barbadense* are those of degree: the plants are smaller and stouter, the branching sparse, the filaments below the spore simple as compared to *A. barbadense* as understood in this study. Also, whereas the entities which compose *A. barbadense* have been shown to intergrade to a high degree, the same characters in *A. rongelapense* seem very stable by comparison.

*A. vanbosseae* Papenfuss (*Chantransia liagorae* Weber-van Bosse) grows upon *Liagora hawaiiiana* from Coetivy Island in the Seychelles (Indian Ocean). In its height (to 1 mm.), in its sparse branching, and in the fact that the internal (lower) filaments do not form a creeping base it compares well with *A. rongelapense*. However, Weber-van Bosse (1914) mentions nothing of its chromatophore, the persistence of the basal spore, nor whether the monosporangia are stalked. The plant described by her was female. When more facts are known about *A. vanbosseae*, *A. rongelapense* may be found to be conspecific with it.

As *Liagora hawaiiiana* is a particularly well-marked species of *Liagora*, the Coetivy specimen is probably properly identified. In the Hawaiian specimens of this species (Abbott, 1945), I saw no *Acrochaetium* species.

### 3. *Acrochaetium dotyi*, new species (figs. 3, 4).

Plantae erectae, ad 2 mm. vel supra alt., partim in textubus *Liagorae* sp. endophyticae, ex spora basili unica indivisa persistente tunica incrassata laud praeditis orta. Ramificatio erecta, furca basali prope sporam, remotior regulariter secunda, vel, bifurcationis ramis impariter evolutis, irregulariter secunda. Filamentorum erectorum cellula et longae et breves, brevibus in partibus fertilibus. Monosporangia pauca in partibus filamentorum erectorum inferioribus, e paene omnibus superioribus cellulis orta, atque frequenter in latere superiore cellularum ramorum secundorum duarum infimarum. Filamenta endophytica 1-2, e superficie inferiore sporae persistentis orta, plerumque linearia, ramificatione rara e spora remota.

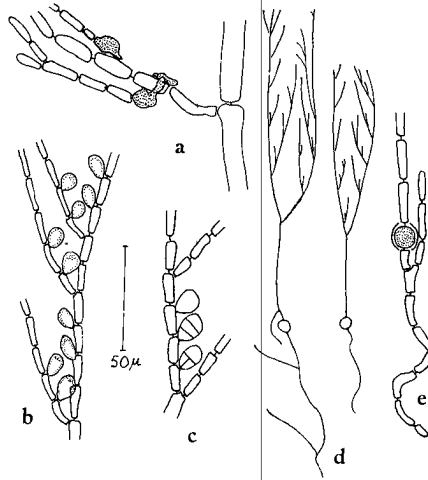


FIGURE 3.—*Acrochaetium dotyi* drawn from type, Doty 12466, Hawaiian Islands (*a, b, c, e* to scale): *a*, bases of two young plants, upper appearing to stick to *Liagora* filament, lower clasp a filament; *b*, habit of monosporangial plant; *c*, tetrasporangia on portion of plant, other parts showing monosporangia; *d*, two habit sketches, showing upper secund branching and relationship of lower branching to basal spore; *e*, branching below basal spore.

Ramus carpogonialis sessilis, 1-cellularis; fasciculi spermatangiorum in serie producti. Structurae masculae et femineae cum monosporangiis vel nullis in plantis diversis sejunctae. Tetrasporangia in plantis structuras sexules producentibus numquam orta, in tetraheda vel irregulariter in zonas divisa.

Chromatorphorum parietale, pyrenoideo unico.

Thallus 1.5 to 2 mm. high, rarely more, partly endophytic in tissues of *Liagora farinosa* and *Trichogloopsis hawaiiiana*, arising from single undivided persistent basal spore, 15  $\mu$  by 15 to 19  $\mu$  without a thickened wall (figs. 3, *e*; 4, *a*). Erect branching (fig. 3, *d*) with basal dichotomy shortly above spore (after plant clears *Liagora* tissues), then regularly secund toward inside surface, or branches unequally dichotomous, subsequent branching irregularly secund. Cells of erect filaments consisting of long cells 7 by 48  $\mu$ , and short cells 7  $\mu$  by 15 to

26  $\mu$ , the latter seemingly associated with fertile portions. Monosporangia few on main erect branches in lower portions, on nearly every cell in upper portions (fig. 3, *b*), obovate, 12 to 15  $\mu$  wide by 15 to 19  $\mu$  (mostly 17  $\mu$ ) long. Monosporangia commonly placed on upper side of two lowest cells of a secondary (second) branch.

Internal portions below basal spore consist of one to two long, colorless, penetrating filaments, which rarely divide to send up erect vegetative filaments close to (fig. 3, *e*) or remotely removed from basal spore and from each other. In some young plants, no "rhizoid" seems to form, the filament instead appearing to cement itself to the *Liagora* filaments, whereas in others spore may clasp *Liagora* filaments (fig. 3, *a*).

Sexual structures borne on inside surface of erect branches, carpogonium (fig. 4, *c*) sessile (one-celled), arising directly from vegetative filament, flask-shaped, 10  $\mu$  long, exclusive of trichogyne, by 5  $\mu$  wide. No cystocarps seen. Spermatangia (fig. 4, *a*) in stalked clusters, in a series, the clusters 12  $\mu$  in diameter, each spermatangium less than 2  $\mu$ . In development, spermatangial mother cells arranged linearly (fig. 4, *b, d*), spermatangia at first arranged to one side, cluster being circinnate in development. At maturity, cluster has a rounded top, but spermatangial mother cells remain to one side of cluster (fig. 4, *d*, lowest cluster). Youngest spermatangial branches strongly curved and at tops of plants (for developmental series, see fig. 4, *d*).

Monosporangia may or may not occur with male elements, do occur on female plants, which are separate. Tetrasporangia (fig. 3, *c*) on different plants from sexual structures, tetrahedrally to irregularly zonately divided, 17 to 19  $\mu$  by 24  $\mu$ , occurring in a short series on main axis or mixed with apparent monosporangia. Chromatophore parietal with a single pyrenoid (fig. 4, *c*).

Hawaiian Islands: type in *Trichogloeopsis hawaiiiana*, Oahu, Ha-nauma Bay, May 29, 1954, Doty 12466 (BISHOP, isotypes in PNH, UC, MICH, PAR, IA). Other specimens examined: in *Liagora fari-nosa*, same place and date, Doty 12465 (BISHOP, IA).

*Acrochaetium dotyi* is readily separated from other species of *Acrochaetium* growing on *Liagora*, in that its axes bear branches to the inside in a secund manner. From the species which have an aseptate basal persistent spore (*A. barbadense*, *A. rongelapense*) it may be further distinguished by the long and short cells of the erect filaments and by the large sessile monosporangia. The development of the spermatangia appears to be different from that in most other *Acrochaetium* species. In the species in which the spermatangia have been studied—*A. corymbiferum* [*A. bornetii* Papenfuss, 1945] and *A. rhipidandra* (Kylin, 1928), and in other spermatangial plants examined in this study (*A. trichogloaeae*, *A. papenfussii*, *A. rongelapense*, *A. tuticorinense*)—they appear as stalked or sessile structures at the tops of very small vegetative cells (some clearly spermatangial mother cells). Their formation appears to have no definite pattern; their final effect is that of being in corymbose clusters. In *A. dotyi*, on the other hand, the spermatangia are first produced in a linear, very incurved

lateral branchlet, the cells of which are clearly spermatangial mother cells. As growth proceeds, the branchlet (a circinnate lateral) opens out while each mother cell is producing spermatangia, first to the inside surface (fig. 4, *d*, top), then on all surfaces, the abaxial being the last. The final result is a clustered effect (fig. 4, *d*, for a developmental series), but these clusters in contrast to those of the other species mentioned are unequal laterally. Clusters of the others are unequal horizontally, as well as vertically. The only other species of

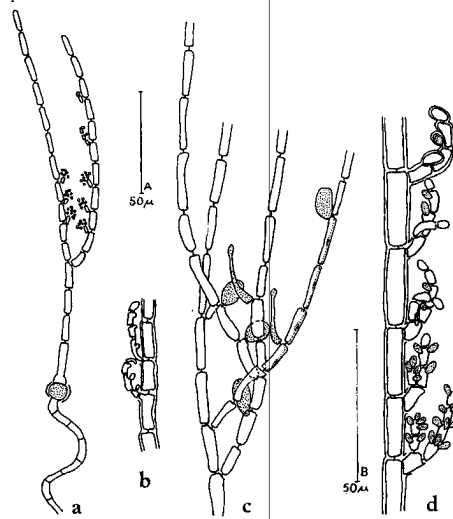


FIGURE 4.—*Achrochaetium dotyi* (*a, b, c*, to scale A; *d* to scale B): *a*, habit of male plant; *b*, linear spermatangial mother cells; *c*, sessile carpogonia, short cells of fertile areas, and monosporangia; *d*, detail of development of spermatangial clusters; most mature cluster not shown.

*Achrochaetium* known to approach this method of spermatangial formation are *A. botryocarpum* (Hamel, 1927; Levring, 1953) and *A. hyalosiphoniae* (Nakamura, 1941). In Levring's illustrations of *A. botryocarpum*, the spermatangial clusters do not show a unilateral development, although they may be borne in a second manner. In *A. hyalosiphoniae* the clusters are second and show an irregular unilateral development, branchlets of the third order being formed, whereas in *A. dotyi* the spermatangial branchlets develop to the second order only. Both *A. hyalosiphoniae* and *A. dotyi* show a single un-

divided persistent spore. The upper filaments of *A. hyalosiphoniae* frequently produce hyaline hairs which *A. dotyi* does not produce, and the endophytic system of branches is more developed than in *A. dotyi*. According to Nakamura (1941) the erect branches and branchlets are irregularly formed. They are more regularly formed in *A. dotyi*.

The material of *A. dotyi* is abundant, most of the plants being monosporangial only. Next in abundance are the male plants, then female, then tetrasporangial. They appear more commonly on the male plants of their "host" than on the female plants.

I take great pleasure in naming this species for my friend and colleague, Maxwell S. Doty of the University of Hawaii, who collected the material and who, in so many ways, has been most generous with algal materials for my examination.

**4. *Acrochaetium catenatum*** Howe, Marine algae of Peru, 84, 1914 (fig. 5, *a*).

Thallus microscopic, partly endophytic in superficial tissues of *Liagora*, up to 100  $\mu$  in height, arising from a persistent but little distinguished aseptate basal spore that bears no rhizoids or filaments from its lower surface. Erect portion linear for a short distance before branching once or twice dichotomously, each of the branches so formed bearing short few-celled laterals opposite, alternate or secund (fig. 5, *a*). Long colorless hairs are formed at the tips of these laterals, sometimes together with monosporangia. Cells nearly isodiametric, those of main axis 7 to 10  $\mu$  wide by 10 to 12  $\mu$  long; cells of laterals in same proportions but smaller. Chromatophore parietal with a single pyrenoid.

Geographical distribution: Peru (type locality), Tierra del Fuego (Kyllin), East Indies (Weber-van Bosse), and Ryukyus (Nakamura).

Hawaiian Islands, Oahu in *Liagora* spp.: Oahu, Hanauma Bay, May 29, 1954, Doty 12466 (BISHOP); Waianae, Kahanahaiki, May 30, 1959, Doty 19091, collected by Max and Meng Doty and Jan Newhouse (BISHOP, IA). All collections with other species of *Acrochaetium*.

The thalli of the Hawaiian specimens of *Acrochaetium catenatum* are very similar to those described by Nakamura (1941) from the Ryukyus except that hairs are much in evidence in the Hawaiian specimens. The scattered but very wide distribution of this species indicates that it is probably common. Its extreme smallness, even for species of *Acrochaetium*, would account for the fact that it is not more widely reported. *Acrochaetium unifilum* var. *mesogloiae* Jao and *A. compactum* Jao (Taylor, 1937, 1957) are similar species and may not, indeed, be distinct from *A. catenatum*. *A. catenatum*, however, does not resemble any other of the *Acrochaetium* species in this study.



## GROUP II

Growth from a persistent septate spore, plant partly to wholly endophytic.

1. *Acrochaetium trichogloae* Børgesen, Kgl. Danske Vidensk. Selskab., Biol. Meddel. 18 (19) : 13, 1952 (fig. 5, b-i).

Plant partly epiphytic, to 240  $\mu$  in height, arising from a septate persistent spore (fig. 5, b), 7 to 12  $\mu$  by 24 to 33  $\mu$  in length, which is at or near surface of *Liagora* filaments. Plant with well-developed decumbent system of branching, consisting of a short straight filament (fig. 5, d) or this filament soon giving

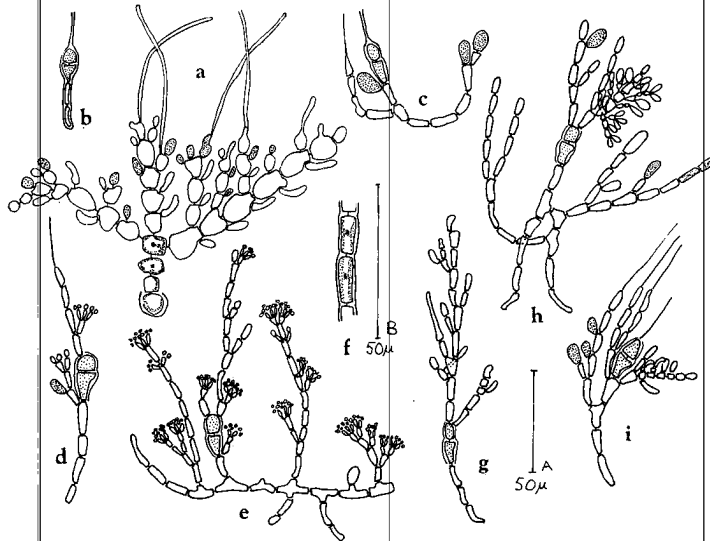


FIGURE 5.—*Acrochaetium catenatum*: a, habit of mature plant (Hawaiian Islands, Doty 12466), scale A. b-i, *Acrochaetium trichogloae* figures drawn from Abbott 1817 (Philippine Islands), scale A except f, which is scale B: b, germination of septate basal spore; c, young plant with stalked and sessile monosporangia; d, young plant with spermatangia; e, mature spermatangial thallus; f, detail of cells showing parietal chromatophore; g, young plant with young gonimoblast (upper, left and on spore at right) and a stalked carpogonium; h, mature cystocarp; i, young cystocarp from below a basal spore.

rise to few to many upright branches (fig. 5, c, e, h), which themselves are little-branched, but in their erect growth growing with vigor equal to that of original erect branches. Erect portions developed from upper surface of spore project 150 to 200  $\mu$  beyond surface of *Liagora* filaments, irregularly and loosely branched. Hairs present (fig. 5, i) on young filaments. Monosporangia 7 to 10  $\mu$  wide by 12 to 19  $\mu$  long (average 16  $\mu$ ), sparsely produced, sometimes in a short series, or to either side alternately on a filament (fig. 5, c, h). Cystocarps

longer than wide when young ( $34\ \mu$  by  $24\ \mu$ ) and when mature  $48\ \mu$  by  $48\ \mu$ , up to  $60\ \mu$  wide. Cystocarps produced directly on a filament in place of a branch or a monosporangium or on short stalks which are 1- to 2-celled vegetative filaments. They may thus be axillary, lateral or terminal, and may be produced below and above persistent spore (fig. 5, *g-i*). Carpospores  $5$  to  $7\ \mu$  wide by  $12$  to  $14\ \mu$  long. Carpogonial branch consisting of carpogonium alone, or carpogonium on a 1- to 2-celled stalk, only carpogonium taking part in formation of carpospores. In mature cystocarp, daughter cells of fertilized carpogonium give rise directly to carpospores or produce short cell rows laterally, each of which in turn produces a carpospore. Carpospores may be produced successively in same carposporangium.

Cystocarps and spermatangia are produced on different plants. Monosporangia may be formed on same plant as cystocarps.<sup>3</sup> Spermatangia produced in clusters on short stalks, 1 to 3 on each stalk, and about  $2\ \mu$  in diameter; clusters appear both below and in erect portions above persistent spore (fig. 5, *d, e*).

Cells in erect portions above persistent spore wider ( $7$  to  $9\ \mu$ ) than those below ( $5$  to  $7\ \mu$ ) spore, but their length in either place ranging from shortest at tips of plants of  $10$  to  $22\ \mu$  (average  $17\ \mu$ ). All cells have one pyrenoid and a parietal chromatophore (fig. 5, *f*).

Philippine Islands: in *Liagora* sp., Cagayan Sulu Island, Jurata Bay, Sulu Sea, February 27, 1957, *Abbott 1817* (PNM, BISHOP, UC, PAR, IA).

Hawaiian Islands: in *Liagora* sp. "C", Oahu, Kawela Bay, April 13, 1941, *Papenfuss* (BISHOP, UC, IA).

Bermuda: in *Liagora* sp., south side of Paget Island, May 7, 1949, *Taylor 49-1614*, collected by Bernatowicz (MICH, IA).

Australia: Marino, near Adelaide, May 21, 1953, *H.B.S. Wormersley A 18634*, in *Liagora farinosa*, new record.

All specimens examined are new records.

Børgeesen's material and his illustration of *Acrochaetium trichogloee* (1952, pp. 13-15, figs. 6, 7) shows that he had young plants to which my figure 5, *c, f* are comparable. The more mature plants (fig. 5, *e, h*) illustrate a different habit than that of the young plants. They are more strongly branched from the lower internal portions than Børgeesen's drawings indicate. The measurements of the cells and monosporangia of the Mauritian and Philippine plants are similar. The female plants offer little information as the development is similar to that of most other cystocarpic plants of *Acrochaetium*. *A. trichogloee*, unlike most other species of *Acrochaetium*, produces spermatangia and cystocarps both below and above the germinating spore, a diagnostic feature. In other species, these organs are produced only above such a spore.

<sup>3</sup> I have seen no male plants bearing monosporangia, but Børgeesen (1952) has seen them.

*A. trichogloae* can be distinguished from others in this series having a septate germinating spore in that its filaments are more slender than those of *A. papenfussii* and *A. nitidulum* and in that its primary growth is external to *Liagora*, even the secondarily produced branches (fig. 5, *e*). *A. papenfussii* is, by contrast, primarily endophytic. It can be distinguished from the partly endophytic *A. nitidulum* by its loose branching and by the fact that whereas monosporangia are sparsely produced in *A. trichogloae*, they are richly produced in *A. nitidulum*. Their size in *A. nitidulum* is nearly twice that of *A. trichogloae*.

The Hawaiian and Bermudan specimens cited above are young plants, the Hawaiian ones more sparsely branched and the Bermuda ones more irregularly branched than the Philippine specimens. The measurements of their vegetative cells and of monosporangia, however, compare well with the Philippine and Mauritius specimens. They should be placed here until more mature specimens show their position more accurately.

As Børgesen (1952) says that the chromatophore of *A. trichogloae* is axial, it is not clear whether he means stellate or peripheral. In all the plants cited above the chromatophore is parietal, in the young portions covering most of the cell but without prolongations and in older cells restricted to the edges. Each cell contains one pyrenoid.

## 2. *Acrochaetium nitidulum*, new species (fig. 6).

Plantae ex toto vel in parte endophyticae, ad 180  $\mu$  alt., e spora divisa (bispora) persistente Liagorae textuum superficiem versus posita ortae. Rami partim erecti partim decumbentes, superiores qual inferiores magis explicati. Ramulus ortus vel monosporangium e latere uno vel ambobus cellularum paene omnium in ramis superioribus sitorum, unde thalli aspiciunt multum aggregata floccosaque. Cellulae terminales capilla longa in colore ornatae. Spora persistens ad septum 12-24  $\mu$  crass., longit. 20-24  $\mu$ . Partes plantarum superiores nitidae. Monosporangia late ovate, plerumque sessilia, raro breviter stipitata, quaque cellula 1-4 gesta. Chromatophorum parietale, pyrenoide una indutum.

Plants partly to wholly endophytic to 180  $\mu$  in height, arising from a divided persistent spore near surface of *Liagora* or up to 75  $\mu$  within tissues. Mature plant sending from lower surface of spore a decumbent system of branches to lowest branches of assimilatory filaments of *Liagora* (to 240  $\mu$ ), decumbent branches sending up erect branch systems (fig. 6, *c*) or little-branched. Decumbent filaments as long as those above spore, usually consisting of irregularly shaped cells. Persistent spore 20 to 24  $\mu$  long, 12 to 14  $\mu$  at broadest (septate) portion. Upper portions of plant from upper surface of basal spore dichotomizing or with monosporangia at nearly every cell, crowded, distal cells frequently hair-tipped (fig. 6, *b*). Branching fuller when overtopping *Liagora*, sparse when within tissues. Mature plants, because of secondarily produced erect branches

(from decumbent system), describing loops at lower ends (fig. 6, c), but these secondary branches weakly developed (fig. 6, a), not as fully branched nor bearing as many spores as main erect system which arises from persistent spore. Monosporangia borne to one or both sides of erect filaments, large, frequently broad and flat at distal end (fig. 6, b, c), otherwise obovate, averaging  $12\ \mu$  broad and  $17$  to  $24\ \mu$  long. Monosporangia deeply staining, glistening, 1 to 4 to each cell on which they occur.

Cells of filaments  $7$  to  $10\ \mu$  wide, cells of upper (free) portions  $10$  to  $15\ \mu$  long, lower decumbent cells up to  $36\ \mu$  long. Cells with one prominent pyrenoid, and a parietal, chromatophore.

Philippine Islands: type in *Liagora* sp., south end of Balabac Island, Gnat Reef, Sulu Sea, March 4, 1957, *Abbott 1823* (BISHOP). Isotypes in BISHOP, PNM, MICH, UC, IA.

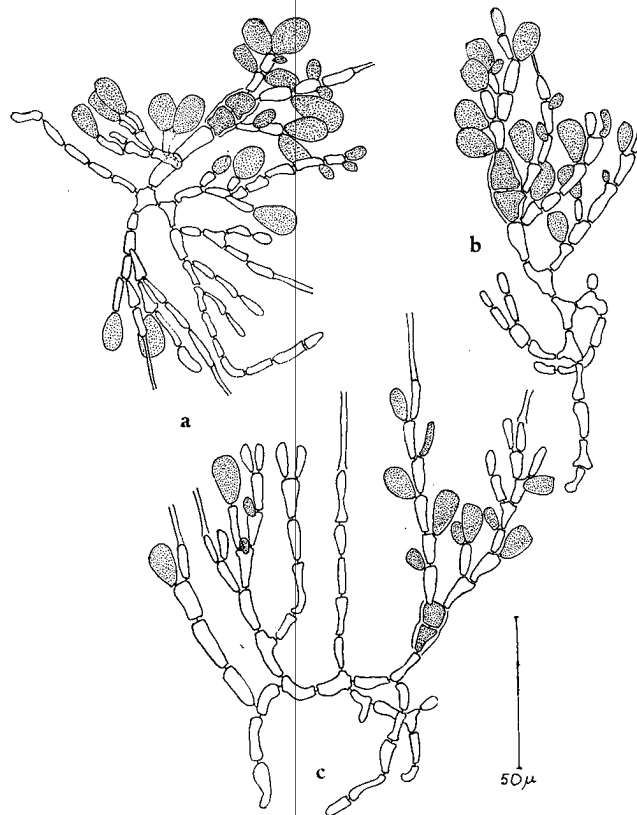


FIGURE 6.—*Acrochaetium nitidulum* drawn from *Abbott 1823*, Philippine Islands, type: a-c, habits of mature plants.