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Some *Liagora*-inhabiting species of *Acrochaetium*¹

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INTRODUCTION

The genus *Acrochaetium* (Rhodophyceae, Nemalionales) is known chiefly from floristic accounts, the most notable of which are those of Rosenvinge (1909),² 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

¹ 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.

² 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 lato*) 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; Børjesen 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. trichoglocae*, *A. papenfussii*, *A. tuticorincense*.

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. trichoglocae 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 μ 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

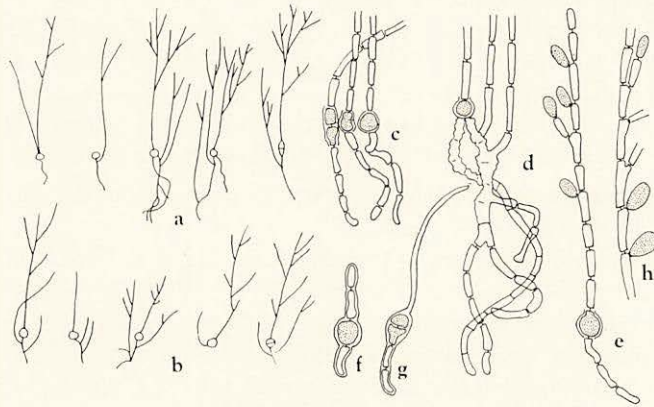


FIGURE 1.—*Acrochaetium barbadense*: a, habit diagrams, showing relationship of upper and decumbent branching to persistent basal spore (Bermuda, *Taylor 48-801* in *Liagora farinosa*); b, similar diagrams of specimens from Guadalupe Island (*Silva* in *Liagora californica*); c, basal spores, showing 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, *Achrochaetium 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 μ wide by 24 to 72 μ 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 μ wide by 17 to 21 μ 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.

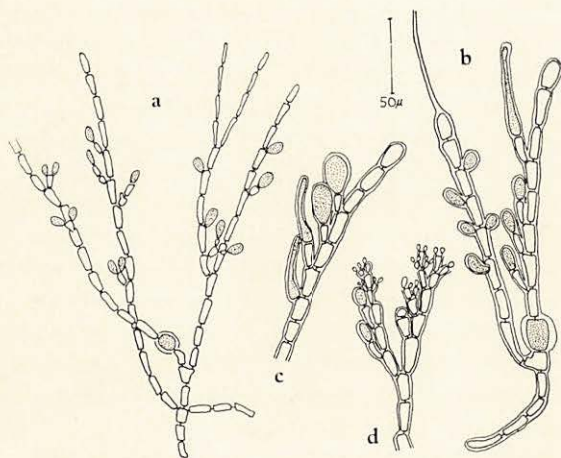


FIGURE 2.—*a*, habit of mature plant of type of *Rhodochorton angustum* (California, Gardner 4921 in *Liagora californica*). *b-d*, *Acrochaetium rongelapense*: *b*, habit, showing nature of monosporangia and carpogonium (stippled) of type specimen (Marshall Islands, Taylor 46-609 in *Liagora hawaiiiana*); *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 μ 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 ortae. Ramificatio erecta, furca basali prope sporam, remotior regulariter secunda, vel, bifurcationis ramis impariter evolutis, irregulariter secunda. Filamentorum erectorum cellulae 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.

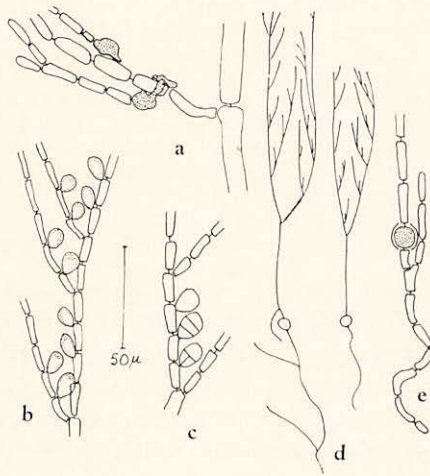


FIGURE 3.—*Acrochaetium dotyi* drawn from type, Doty 12466, Hawaiian Islands (a, b, c, e to scale): a, bases of two young plants, upper appearing to stick to *Liagora* filament, lower clasp a filament; b, habit of monosporangial plant; c, tetrasporangia on portion of plant, other parts showing monosporangia; d, two habit sketches, showing upper second 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 tetrahedra 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 μ by 15 to 19 μ 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 μ , and short cells 7 μ by 15 to

26 μ , 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 μ wide by 15 to 19 μ (mostly 17 μ) 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 μ long, exclusive of trichogyne, by 5 μ wide. No cystocarps seen. Spermatangia (fig. 4, *a*) in stalked clusters, in a series, the clusters 12 μ in diameter, each spermatangium less than 2 μ . 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 μ by 24 μ , 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, Hanauma 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 second 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. trichoglocae*, *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

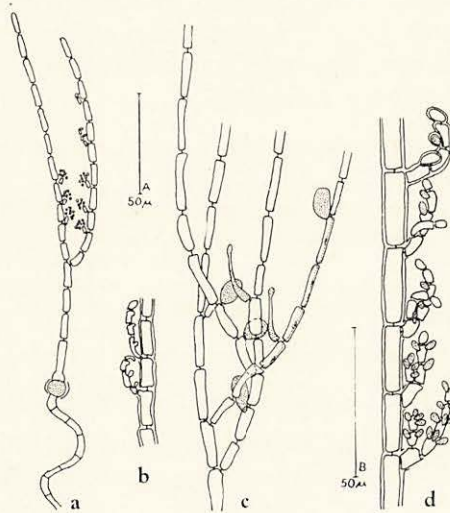


FIGURE 4.—*Acrochaetium dotyi* (*a*, *b*, *c*, to scale A; *d* to scale B): *a*, habit of male plant; *b*, linear spermatangial mother cells; *c*, sessile carpogonia, short cells of fertile areas, and monosporangia; *d*, detail of development of spermatangial clusters; most mature cluster not shown.

Acrochaetium 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 secund 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 μ 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 μ wide by 10 to 12 μ 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 μ in height, arising from a septate persistent spore (fig. 5, b), 7 to 12 μ by 24 to 33 μ 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

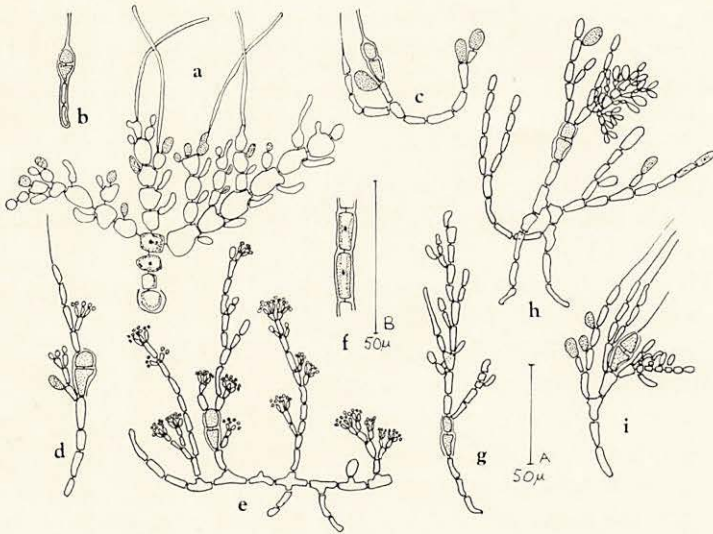


FIGURE 5.—*Acrochaetium catenatum*: a, habit of mature plant (Hawaiian Islands, Doty 12466), scale A. b-i, *Acrochaetium trichogloae* figures drawn from Abbott 1817 (Philippine Islands), scale A except f, which is scale B: b, germination of septate basal spore; c, young plant with stalked and sessile 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 μ beyond surface of *Liagora* filaments, irregularly and loosely branched. Hairs present (fig. 5, i) on young filaments. Monosporangia 7 to 10 μ wide by 12 to 19 μ long (average 16 μ), 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.³ 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.

Børgesen's material and his illustration of *Acrochaetium trichogloae* (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 Børgesen'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. trichogloae*, 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.

³ I have seen no male plants bearing monosporangia, but Børgesen (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 μ 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 aspicias multum aggregata floccosaque. Cellulae terminales capilla longa incolore ornatae. Spora persistens ad septum 12-24 μ crass., longit. 20-24 μ . 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 μ in height, arising from a divided persistent spore near surface of *Liagora* or up to 75 μ 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 μ), 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 μ long, 12 to 14 μ 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.

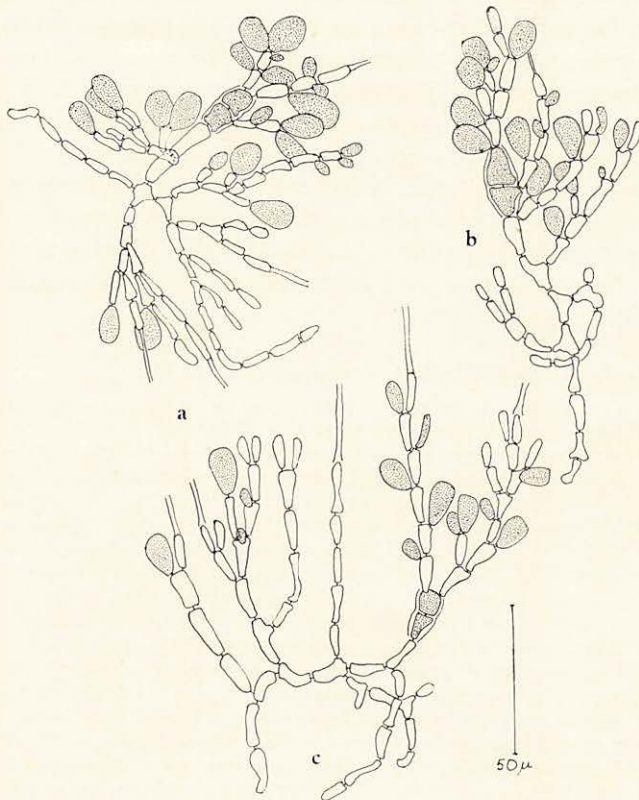


FIGURE 6.—*Acrochaetium nitidulum* drawn from *Abbott 1823*, Philippine Islands, type: *a-c*, habits of mature plants.

The divided persistent spore, bearing a compact system of erect branches on which large glistening monosporangia are borne, is characteristic of this species. It is smaller in stature than other species with septate persistent spores and may be further distinguished in that it lacks an extensive invasive branching system.

Three other species discussed in this paper have septate persistent spores: *Acrochaetium barbadense*, *A. trichoglocae*, and *A. papenfussii*. *A. barbadense* is a typically epiphytic species, with only its basal spore and subsequent decumbent filaments produced by it involved endophytically. *A. trichoglocae* is a slender species compared to *A. nitidulum*, with both epiphytic and endophytic branch systems, the epiphytic predominating. *A. papenfussii* is a primarily endophytic species in which the erect portions produced by the activity of the cells below the spore come to the surface of *Liagora* and there creep horizontally and produce spores. In cell measurements and size of plants, *A. nitidulum* is more like *A. papenfussii* than it is like other species, but the only other species which has the habit of vertical and horizontal growth so characteristic of *A. papenfussii* is *A. actinocladium*. Except for this feature, *A. actinocladium* is more like *A. liagorae*. Lacking the secondary horizontal growth of *A. papenfussii*, *A. nitidulum* also lacks the strongly developed decumbent system of branches shown by *A. papenfussii*. A comparison of figures 6, *b* and 7, *h* will show that the mature plants of the two species are very different.

Rosenvinge's figure of *Chantransia dumontiae* [*Acrochaetium dumontiae* (Rosenvinge) Hamel] shows his plant to have the crowded upper branching of *A. nitidulum* (1909, his fig. 52). Compare his figure with my figure 6, *b*. *A. dumontiae* has a creeping multicellular base and bears tetrasporangia, and it has an endophytic system of branches. It would be well to study these two species together.

3. *Acrochaetium papenfussii*, new species (fig. 7).

Planta in parte vel ex toto endophytica, e spora persistente, tunica paulo incrassata induta, 22-33 μ long., 14 μ lat., explicata. Ramuli breves, a cellulis paucis compositi, erecti, e spora cellula superiore orti, ex inferiore thallus ramificatus primum decumbens serius erectus, ramis ad *Liagorae* filamenta horizontaliter ramosis, ramos breves, erectos, ad 60 μ long., monosporangia gignente, producentibus. Monosporangia sessilia vel stipitata, ovata, 7-10 μ lat., 17-19 μ long. Cellulae terminales omnes atque bisporeae germinantes capillis incoloribus minoribus quam 2 μ crass. ornatae.

Membra mascula et feminea in planta eadem vel in diversis, monosporangia cum his vel in plantis aliis, producta. Spermantangia diam. minora quam 2 μ , in racemis pedicellatis, 1-2 in stipite incolori, suffulta. Carpoonium 1-cellulare, lagunculiforme, 5 μ diam. long., trichogyno excl., 12 μ . Cystocarpium 60 μ lat.,

cellulis terminalibus carposporis $7\ \mu$ lat. $12\ \mu$ long. Chromatophorum stellatum pyrenoïdem unam includens.

Plant partly to wholly endophytic, germinating from a septate persistent spore, 22 to $36\ \mu$ long by 12 to $14\ \mu$ wide, spore (fig. 7, a) with a slightly thickened wall that which, at maturity, may become obscure, the spore retaining its shape; upper cell somewhat bulbous, upper portion of lower divided spore cuneate, lower end possibly attenuate. Upper spore cell produces short erect branches (fig. 7, c, d) of only a few cells or, if more, most branches to only about $30\ \mu$ in height. Lower divisions produce a vigorous decumbent branch system (fig. 7, c, d), the cells $12\ \mu$ by 17 to $29\ \mu$, at first a linear filament (fig. 7, b) but soon branching to one or both sides and giving rise to strongly

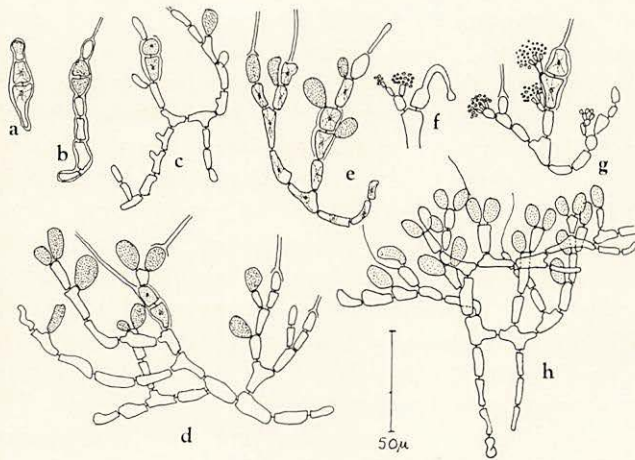


FIGURE 7.—*Acrochaetium papenfussii* drawn from *Abbott 1816*, Philippine Islands, type: a, germinating spore with immature upper cell; b, germinating spore with lower portion developing in advance of upper portion; c, germinating spore with well-developed decumbent system; d, young plant showing how erect branches are produced; e, monosporangium on original spore and elsewhere, chromatophores shown; f, portion of plant showing a carpogonium and spermatangial clusters; g, spermatangial clusters on original divided spore of young plant as well as elsewhere; h, habit of mature plant, showing vertical and horizontal branches.

developed erect branch systems up to $200\ \mu$ in height (fig. 7, c). At maturity, these branch at surface of *Liagora* filaments, rarely overtopping them, and growing horizontally among filaments, producing short (to $60\ \mu$, mostly less) erect branches bearing monosporangia (fig. 7, h). Monosporangia sessile or stalked, 7 to $10\ \mu$ wide by $19\ \mu$ long, on young plants irregularly and infrequently produced, on mature plants alternate or opposite and produced on nearly every erect cell, including the original bispore (fig. 7, d, g). Branching of horizontal portions of mature plant very crowded (fig. 7, h), plant assuming shape of a close tuft to $150\ \mu$ in diameter. Cells of horizontal filaments average

7 to 22 μ . Thin colorless hairs, usually less than 2 μ wide, common on all terminal cells and on germinating bispore. Chromatophore stellate with a single pyrenoid (fig. 7, e).

Male and female elements on same or on different plants (fig. 7, f, g); monosporangia borne on sexual individuals. Spermatangia less than 2 μ , borne in pedicellate clusters, 1 to 2 on a stalk. Carpogonial branches one-celled (carpogonium sessile), carpogonium flask-shaped, 5 μ wide at lowest and widest portion by 12 μ long exclusive of trichogyne. Cystocarp 60 μ wide, the terminal carpospores, 7 μ wide by 12 μ long.

Philippine Islands: type in *Liagora* sp., Cagayan Sulu Island, mouth of Jurata Bay, Sulu Sea, February 27, 1957, Abbott 1816 (BISHOP). Isotypes in PNM, MICH, UC, PAR, IA. (*Acrochaetium trichogloae* occurs with this species.)

The germinating stages of *A. papenfussii* are strikingly different from those of *A. trichogloae* and *A. nitidulum* though all of these species develop from a persistent septate spore. The germinating spore of *A. papenfussii* is at or near the surface of *Liagora* and early sends downward a strongly developed filament, which divides and immediately gives rise to one or two (on both sides) erect branches which seek the surface. These, in turn, expand horizontally and, from the upper surface, give rise to short entangled branches which bear monosporangia (fig. 7, h). In this horizontal growth, *A. papenfussii* is similar to *A. actinocladium* from the Hawaiian Islands. However, *A. actinocladium*, the germination of which has not been seen, is nearly twice as large as *A. papenfussii*. Both species have a stellate chromatophore.

Distinction should be made between *A. papenfussii* and *A. trichogloae*, since they occur together on the same species of *Liagora* in the Philippine material. Aside from the chromatophore difference—which, as in many *Acrochaetium* species, may be obscure unless a large number of specimens is studied—the main differences are in the germination of the spore and the aspect of the mature plants. In *A. trichogloae* the upper, or external and erect, portion of the plant is developed first. This portion, together with the secondarily produced branches, project beyond the surface of *Liagora*. The secondarily produced and erect branches are loosely and irregularly branched. The monosporangia are scarce, but the male and female elements are abundant in the material studied. In *A. papenfussii* the lower endophytic portion is developed first, and it appears that this portion may develop to the exclusion of the upper portions, which are usually only a few short filaments. The strongly developed secondarily produced branches

from the internal processes eventually creep horizontally near the surface of *Liagora*, there producing many sporangia. The male and female reproductive structures are produced there also, but I found few in my material.

I name this species for George F. Papenfuss, who has contributed to man's knowledge of this complex and who has been a stimulant to my work and to that of other students of algae. His unfailing help and interest have been constant sources of gratification to me.

GROUP III

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

1. **Acrochaetium liagorae** Børgesen, Dansk. Bot. Arkiv. 3 (1) : 58, 1915 (figs. 8, *a-j*; 9, *a-f*).

Chantransia liagorae Børgesen, op. cit., 57, 1915.

Acrochaetium collisianum Børgesen, op. cit., 454, 1920.

Acrochaetium liagoroides Børgesen, Indian Bot. Soc., Jour. 16 : 40, 1937.

[*non Acrochaetium liagorae* (Weber-van Bosse) Hamel, Recherches Acrochaetium, 92, 1927. See *Chomastrum liagorae* IN Papenfuss, Univ. Calif. Pub. Bot. 18 (14) : 324, 1945.]

Plants endophytic in upper portions of assimilatory filaments of *Liagora*, rarely projecting beyond filaments. Thalli creeping in various directions, only in isolated branches appearing linear. Basal filaments characteristically sausage-shaped (fig. 8, *d*), the cells broader through center than at either end, sometimes giving rise to upright branches on whose ultimate cells colorless hairs are often formed. Upright branches usually to 50 μ , sometimes to 250 μ . Monosporangia borne on erect branches, usually one (fig. 9, *a*) to each ultimate or penultimate cell, but occasionally opposite (fig. 8, *h*), or monosporangia borne directly (fig. 8, *e, i*) on basal cells (more commonly here than in upright branches). Monosporangia (fig. 8, *e, f*) usually sessile, or with short one- or two-celled pedicel (figs. 8, *i*; 9, *c*). Branching and monosporangia are to surface side of thallus, usually on that one side only.

Germination from an aseptate thin-walled spore, 12 to 19 μ by 12 μ , spore bearing one or more colorless hairs and basal portion usually developing first. (See figure 8, *b, c, e*.) Spore soon pulled out of shape and not recognizable from other sporangia, especially empty ones. By its inward growth among *Liagora* filaments (fig. 8, *g*) original spore is left at surface or sends up short filaments to surface.

Basal cells 7 to 14 μ (average 12 μ) at widest portions to 24 μ in length, erect cells 12 μ by 17 to 22 μ . Monosporangia 10 to 14 μ by 12 to 22 μ in length. Chromatophore stellate with a single large pyrenoid (fig. 8, *a*) in portions embedded 50 μ or more from surface of assimilatory filaments, or parietal if near or at surface of *Liagora* filaments (fig. 8, *h, j*). Each cell, regardless of shape of chromatophore, with a single pyrenoid.

Carpogonia borne on same filaments as monosporangia and sometimes also with spermatangia (figs. 8, *a*; 9, *b*, *f*); borne directly on basal filaments or laterally or terminally on short erect branches (fig. 9, *f*); sessile (one-celled, fig. 9, *b*, *f*) or, more rarely, two-celled (fig. 8, *d*). If sessile, up to $10\ \mu$ exclusive of trichogyne by $5\ \mu$ wide; if two-celled to $17\ \mu$ long by $7\ \mu$ wide; sessile type more common. Cystocarps not seen. Spermatangia borne in short panicle; developing spermatangial mother cells uniseriate on short terminal filament, spermatangia first developing to one side (fig. 9, *e*), then on all surfaces, the final cluster longer than broad (fig. 9, *b*). Spermatangia 2 to $4\ \mu$ wide.

Only one irregularly divided tetrasporangium seen in Philippine material (fig. 9, *d*), the source of sexual material.

Geographical distribution: Virgin Islands, the Dry Tortugas, Florida (Taylor, 1928), Juan Fernandez (Levring, 1941), and Kan-

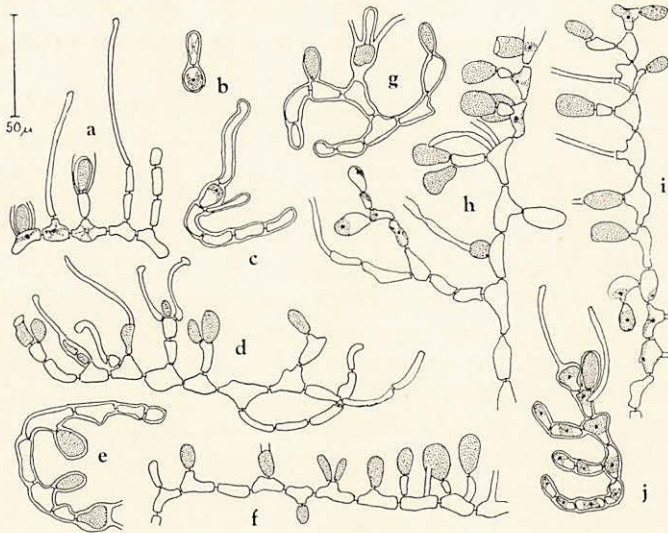


FIGURE 8.—*Achrochaetium liagorae*: *a*, portion of mature plant showing stalked and sessile monosporangia, hairs, and nature of chromatophore (Philippine Islands, Abbott 1825); *b*, germinating spore (Bermuda, Taylor 56-708); *c*, germinating spore with terminal hair and developing decumbent filament (Bermuda, Taylor 56-708); *d*, stalked and sessile carpogonia on a monosporangial thallus (Philippine Islands, Abbott 1824); *e*, original spore, bearing two hairs (Bermuda, Taylor 49-1614); *f*, mature plant bearing stalked and sessile monosporangia (Bermuda, Taylor 56-708, in *Liagora ceronoides*); *g*, young plant, showing early branching (Bermuda, Taylor 49-1614); *h*, monosporangial plant with parietal chromatophores (Bermuda, Taylor 49-1614); *i*, sessile and stalked monosporangia (Hawaiian Islands, Doty 10603); *j*, early branching of young plant (Philippine Islands, Abbott 1825).

garoo Island, Australia (Levring, 1953), all as *Acrochaetium collinsianum* Børgesen. The type locality (and only collection) of *A. liagoroides* is Mahabalipuram, India (in *L. erecta* Zeh).

Type locality: south coast of St. Croix, Virgin Islands.

Philippine Islands: Balabac Island, south end of Gnat Reef, Sulu Sea, March 4, 1957, *Abbott 1823, 1824, 1829, 1830* (BISHOP, PNM, UC, PAR, IA); in two separate collections of *Liagora* spp., reef west of Cagayan Sulu Island and south of Bulissuan Island, Sulu Sea, February 28, 1947, *Abbott 1825, 1826* (BISHOP, PNM, IA, MICH, UC).

Hawaiian Islands, Oahu: Kawela Bay, March 29, 1953, *Doty 10603*, collected by Doty and Newhouse (BISHOP, IA); in *Liagora tetrasporifera* Børgesen, Kawela Bay, April 13, 1942, *Papenfuss* (UC, BISHOP, IA); Waianae, Kahanahaiki, May 30, 1959, *Doty 17261*, collected by Max and Meng Doty and Newhouse (BISHOP, IA).

Bermuda: in *Liagora valida* Harvey, south side of Paget Island, May 7, 1949, *W. R. Taylor 40-1614*, collected by A. J. Bernatowicz (MICH, IA); in *Liagora ceranoides* Lamx., Whalebone Bay, St. George's Island, April 19, 1956, *Taylor 49-698 (56-708)* (MICH, IA). All records are new.

Australia: Kangaroo I., Pennington Bay, Jan. 22, 1947, *H.B.S. Wormersley A 4443*, in *Liagora harveyana*, specimens examined.

I have been fortunate in receiving from W. R. Taylor properly preserved material of *Liagora* from Bermuda in which I have been able to see the development of the endophyte; the variation, and size, and shape of cells, and the disposition of the branches and spores. Since Bermuda is not too far from the type locality of this species, and since the marine algal flora of both places is largely similar, I gave special attention to this material for a basic understanding of the limits of the species.

The Bermuda plants, as exemplified by figure 8, *e, f, h*, represent the "typical" aspect of this species and by far the most commonly observed condition. The creeping portions are relatively short, bearing no (or only short) erect branches to one side and bearing monosporangia directly on the basal cells or on short pedicels. This form is the most commonly encountered in the study of *Liagora* species. Figure 8, *b, c* shows germinating stages, probably exemplifying the youngest stage in the essentially creeping thallus. Figure 8, *h* shows such a thallus with an erect branch bearing monosporangia.

A mature thallus from Hawaii is shown in figure 8, *i*. The basal cells in this material showed evidence of being compressed by *Liagora* tissues in their knobby and irregularly shaped outlines.

Though the Philippine material (figs. 8, *a-d*, 9, *a-c*) shows a creeping habit, it also shows a more robust development of erect filaments (those to about 80 μ , common; those to 240 μ , rare). Variations in the branching, in the size of the cells, in the shape and disposition of the spores, and in the germination (figs. 8, *g, j*; 9, *a, b, f*) should be compared with those of plants from Bermuda (fig. 8, *e, f, h*). It is especially important to compare my figure 9, *a* with Børgesen's figures

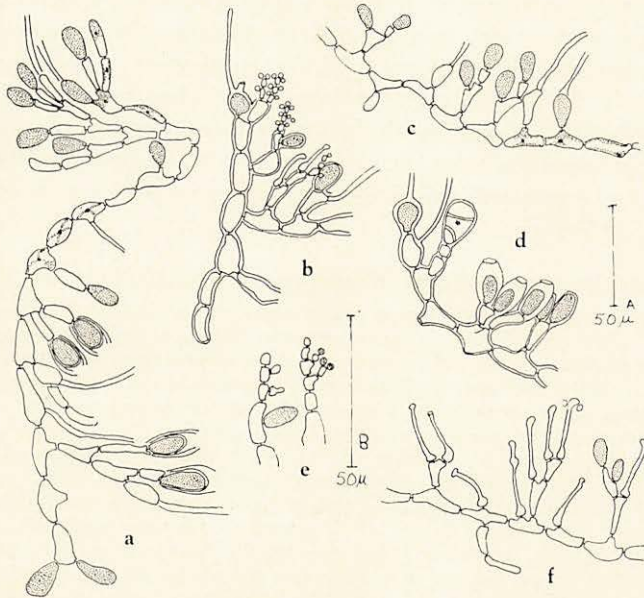


FIGURE 9.—*Acrochaetium liagorae* (*a-d, f*, scale A; *e*, scale B): *a*, mature thallus, showing manner of branching to be similar to that of *A. liagoroides*, and both stellate and parietal chromatophores (Philippine Islands, *Abbott 1829*); *b*, plant with original spore (stippled and with hairs) still intact, showing spermatangia, carpogonia, and monosporangia (Philippine Islands, *Abbott 1829*); *c*, parietal chromatophores on a monosporangial plant (Philippine Islands, *Abbott 1829*); *d*, irregularly divided tetrasporangium, intact original spore, and stalked monosporangia (Philippine Islands, *Abbott 1825*); *e*, formation of spermatangia from linear spermatangial mother cells (Philippine Islands, *Abbott 1825*); *f*, carpogonia and monosporangia (Philippine Islands, *Abbott 1825*).

24 and 25 (1937). It is partly on the basis of such comparison that I am placing *A. liagoroides* in synonymy with *A. liagorae*.

The differences between the chromatophore of the immersed thalli and those of the superficial areas are most striking in the Philippine plants. This was first observed by Børgesen (1937) in *A. liagoroides*. In examining the Bermuda material (of thalli that were creeping only, as well as thalli with erect branches), I note the same situation: the chromatophore is parietal in the superficial thalli and stellate in the immersed thalli. In general, however, the stellate chromatophore is more commonly encountered.

The spermatangial clusters of *A. liagorae* are, to my knowledge, the only ones showing a paniculate nature. Most species of *Acrochaetium* show corymbose to irregularly shaped terminal clusters of spermatangia such as may be seen in *A. rongelapense*, *A. papenfussii*, and *A. trichoglocae*. Some species (*A. hyalosiphoniae*, *A. botryocarpum*, *A. dotyi*) show unilateral development of clusters and still others (*A. imitator*, *A. gynandrum*) show a few large, terminal spermatangia.

Tetrasporangia have been reported for *A. liagoroides* (Børgesen, 1937) and occur terminally in position where monosporangia are borne in upright branches.

2. *Acrochaetium imitator*, new species (figs. 10, 11).

Thallus endophyticus repens uniseriatus, ramos laterales erectos breves habens. Germinatio linearis e spora aseptata. Monosporangia plerumque terminalia pedicellata singulatim producta. Rami carpogoniales unicellulares, e carpogonio constantes, post fertilizationem transverse divisi, carposporas directe efficientes. Spermatangia non stipitata terminaliter aggregata bina vel terna. Chromatophorus parietalis pyrenoideo singulo praeditus.

Thallus endophytic, creeping, up to 500 μ , uniseriate with short, simple laterals and with or without short, erect, clustered branches which reach surface of *Liagora*; erect branches straight or curved, irregularly dichotomous when near the surface (fig. 10, *a*). Vegetative cells sausage-shaped, especially in basal portions, becoming doleiform-elongate in upper portions of thallus. Germination linear, from a simple aseptate spore (fig. 10, *b*), occasionally retaining its original shape (12 μ by 12 μ) but more frequently pulled out of shape. Unicellular colorless hairs 2 to 5 μ wide at base, frequent on terminal cells. Monosporangia average 12 by 17 μ , borne singly (fig. 10, *c*) usually on a one-celled stalk. Carpogonial branches one-celled, produced on basal filaments or laterally on erect filaments (fig. 10, *d, e*). After fertilization, carpogonium divides only once transversely (fig. 11, *a*); each daughter cell, in turn, cuts off cells which surround original carpogonium like segments of an orange (fig. 11, *b*). Spermatangia formed in small terminal groups, 2 to 3 to each mother cell; each spermatangium 5 μ wide by 6 to 8 μ long (fig. 11, *c*).

Chromatophore parietal (fig. 10, *b*) with a single pyrenoid.

Hawaiian Islands: type in *Liagora* sp., Oahu, Waianae, Kahana-

haiki (BISHOP), *Doty 19091*, collected by Max and Meng Doty and Newhouse. Isotypes in BISHOP, UC, PAR, IA. All with *Acrochaetium nemalionis*.

In isolated segments, the thallus and habit of *A. imitator* are so much like those of *A. liagorae* that, were it not for the differing sexual structures, this species might be identified with *A. liagorae*. This fea-

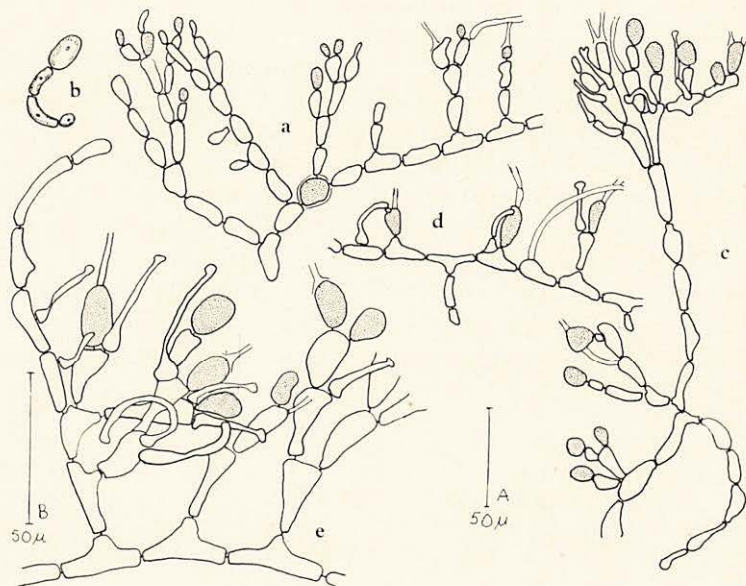


FIGURE 10.—*Acrochaetium imitator* drawn from *Doty 19091*, Hawaiian Islands, type (*a-d*, scale A; *e*, scale B): *a*, unusually persistent spore on mature plant with branch at right typical of species; *b*, germination from aseptate spore, showing parietal chromatophores; *c*, portion of thallus, showing stalked monosporangia and carpogonia; *d*, portion of thallus, showing sessile carpogonia on cells of basal filaments, lateral when on erect filaments; *e*, numerous carpogonia on erect filaments with strong unilateral development of branches.

ture of *A. imitator* gives it the specific name. In other respects it appears to resemble *A. gynandrum*.

The carpogonial branches, or carpogonium, of *A. liagorae* are one-celled and are borne on basal cells as well as on erect portions of the thallus. Cystocarps of *A. liagorae* have not been seen, but those of *A. imitator* are remarkable in their great simplicity. In the other species

discussed in this paper that exhibit cystocarps, the carpospores are produced terminally (and sometimes laterally) on short filaments, but they are never produced directly from the carpogonium (fig. 11, *a*), as is the case in *A. imitator*. One of the simplest cystocarps in the genus is that produced by *A. gynandrum* (Rosenvinge) Hamel (Rosenvinge, 1909; Kylin, 1944), but it is a few-celled filamentous structure which forms carpospores terminally.

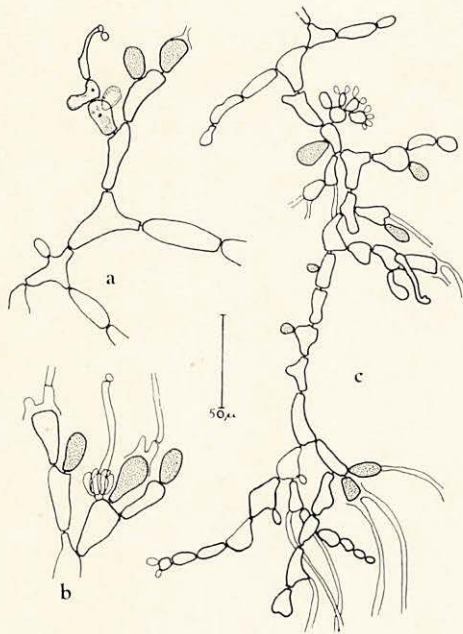


FIGURE 11.—*Acrochaetium imitator*: *a*, transverse division in fertilized carpogonium, spermatium at tip of trichogyne, lower cell of divided carpogonium producing carpospore directly; *b*, carpospores being produced around fertilized carpogonium; *c*, single, paired, and clustered spermatangia, one carpogonium, monosporangia, and hairs on mature thallus. (Doty 19091, Hawaiian Islands, type.)

The spermatangia of *A. imitator* resemble those of *A. gynandrum* more than do those of *A. liagorae*, the spermatangia of which are produced on all surfaces of short uniseriate branches of spermatangial mother cells. This is in contrast to the spermatangia which terminate

ultimate cells singly or in groups of two to three in *A. imitator* (fig. 11, *c*).

In *A. liagorae* the chromatophore is of two kinds: in cells near the surface of *Liagora* they are parietal; in cells more remote from the surface they are stellate. In *A. imitator* all chromatophores seen, whether of superficial cells or of deep internal ones, were parietal.

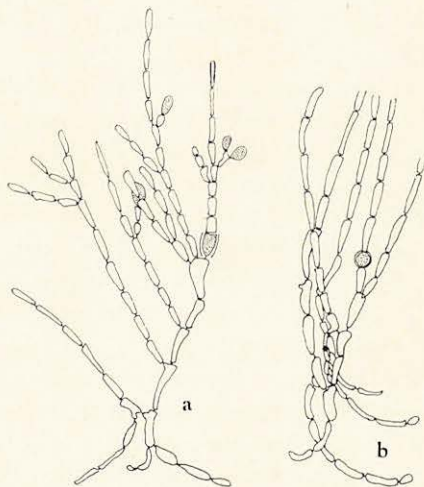


FIGURE 12.—*Acrochaetium nemalionis* (Doty 19091, Hawaiian Islands; the type and isotypes of *A. imitator*): *a*, habit of thallus with simple base, original spore identified by position; *b*, basal portion of a thallus showing entangled basal "rhizoidal filaments," and intact germinating spore in filament at right.

3. *Acrochaetium nemalionis* (De Notaris) Bornet, Soc. Bot. France, Bull. (Suppl) 51 : xx, 1904.—Rosenvinge, 126, 1909.—Hamel, 30, 1927 (fig. 12, *a*, *b*).

Thallus up to 2 mm. in height, generally less, chiefly epiphytic, only basal portions within tissues of *Liagora*. Erect filaments formed as soon as they clear "host" tissues, and are branched irregularly at this juncture (fig. 12, *a*). Upper portions branch dichotomously or are little-branched. Cells of erect branches cylindrical, in basal portions 7 to 12 μ wide by 12 μ long, upper cells 7 μ wide by 19 μ long, tapering to less than 2 μ wide by as much as 36 μ long. Basal portions much entangled, producing secondary branches, some of which may become erect; others of rhizoidal nature (fig. 12, *a*), these from lower lateral portions of cells. Rhizoids may penetrate beyond central axis of "host," to more than 250 μ . Basal portions rarely showing original basal germinating spore, 12 μ by 12 μ (fig. 12, *b*); usually without such a well-marked spore (fig. 12, *a*). All cells of basal (rhizoidal) portion of thallus pigmented.

Monosporangia borne on one-celled stalks, usually bifurcate and bearing two or more spores, 10 by 17 μ , one of which is generally wider (by about 4 μ) than its sister spore.

Chromatophore parietal with a single pyrenoid.

Hawaiian Islands: in *Liagora* spp., Oahu, Waianae, Kahanahaiki, May 30, 1959, *Doty 19091*, collected by Max and Meng Doty and Newhouse (BISHOP, UC, IA); same place and date, *Doty 19096* (BISHOP, IA). Both collections with *Acrochaetium imitator*.

This is a new record for *A. nemalionis* in the Pacific. It has been previously reported in *Liagora* from the Canary Islands by Bornet (1904). In the past there has been a question as to the nature of the germinating spore of this species, and no such spore can be found in most thalli. However, it is not surprising to find that the plants germinate from a simple aseptate spore (fig. 12, *b*) which usually becomes obscure subsequently, owing to elongation or the production of rhizoids. Except for being shorter than the Danish specimens, the Hawaiian specimens agree so well with Rosenvinge's description and illustrations (1909) that nothing more can be added.

In comparison with other species growing on *Liagora*, *A. nemalionis* shows some similarity to *A. barbadense*. Both species germinate from an aseptate spore and both bear many erect branches terminating in hairlike filaments. Their basal portions differ in that *A. barbadense* does not show the massive, basally much-entangled filaments characteristic of *A. nemalionis*. In all *A. barbadense* studied the persistent germinating spore was present, whereas the germinating spore of *A. nemalionis* had usually disappeared. The monosporangia in the two species differ also, most of those of *A. barbadense* being borne singly whether pedicellate or not, most of those of *A. nemalionis* being pedicellate with two or more sporangia. The distinguishing characteristic of *A. nemalionis* is the secondary production of rhizoidal decumbent filaments produced from the lower lateral portions of the cells in the region of the basal germinating spore (fig. 12, *b*). Though other species may have invading decumbent filaments, none of them form these filaments in the same way as *A. nemalionis*.

4. *Acrochaetium laxum*, new species (fig. 13, *a-f*).

Thallus ad 5 mm. alt., 1.5 mm. lat., in *Liagora* app ex toto vel in parte endophyticus. Explicatio e spora singulari breviter persistente tenuitunicata 12-14 μ crass., 17 μ long. in superficie superiore capillam incolorem unam vel plures gerente. Plantae ramos multos rectos irregulariter ramosos complanatos infra supraque sporam ortos totos *Liagorae* textuum superficiem versus promittentes, proferentes. Monosporangia ovata vel late ovata, pro modo 12 μ crass., 12-17 μ

long., sessilia vel pedicellata, e filamentis irregulariter orta. Cellulae pyrenoidem unam chromatophorumque parietale exhibentes.

Plants to 5 mm. high (2 mm. average) and to 1.5 mm. broad, partly to wholly embedded in tissues of *Liagora mucosa* and *L. ceranoides*. Growth from a single shortly persistent spore, 12 to 17 μ in length, 12 to 14 μ in width, spore not surrounded by a thick wall and always bearing one or more colorless hairs on its upper surface (fig. 13, b, c). Spore remains near surface of *Liagora*. In mature plants its shape is sometimes retained although cell may be empty, but more often it is pulled out of shape and not possible to mark with certainty in mature plants. Elongation from lower surface of spore favored first, spore appearing to be in lateral isolation (fig. 13, c, d), but repeated lower divisions

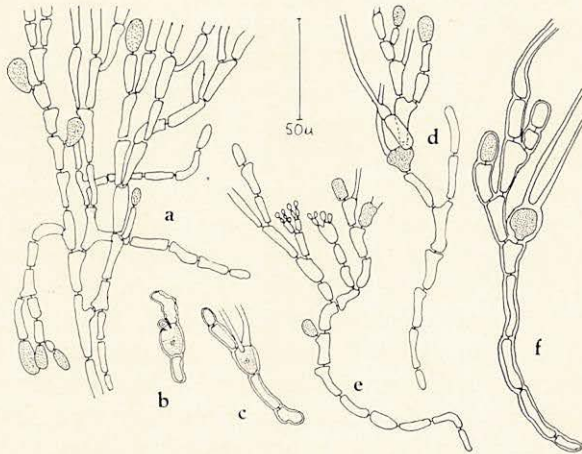


FIGURE 13.—*Acrochaetium laxum*: a, habit of internal portions of mature plant in *Liagora mucosa* (Bermuda, Taylor 49-801, type); b, germination of spore in *Liagora mucosa* (Taylor 49-801, type); c, germination of spore, showing hairs on upper surface, a young erect filament, and growth of decumbent filament in *Liagora mucosa* (Bermuda, Taylor 49-801, type); d, young plant, showing how filaments grow to one side of original spore in *Liagora mucosa* (Bermuda, Taylor 49-575); e, spermatangial plant (original spore is stippled cell to upper right of branch on right; Bermuda, in *Liagora ceranoides*, Taylor 56-708); f, young plant showing isolation of original spore from which has developed a decumbent system and an erect system of branches to left (Bermuda, in *Liagora ceranoides*, Taylor 56-708).

produce a loose, looping effect near lower portions of assimilatory filaments of *Liagora* and give rise to numerous upright, flattened branches (fig. 13, a) bearing monosporangia. Branches come to level of tips of assimilatory filaments, rarely overtopping them. Internal portions unequally branched, colorless, or only weakly staining. Monosporangia and upper cells deeply staining, monosporangia (fig. 13, a, d) ovate to broad-ovate, averaging 12 μ in width, 17 μ in length;

sessile or stalked, opposite or alternate, and irregularly disposed. Hairs (fig. 13, *d, f*) commonly produced by ultimate cells and 7 to 10 μ wide at base, are feature of both young and old thalli.

Spermatangia (fig. 13, *e*) were seen only once. They appear on broad stalks or directly on small ultimate vegetative cells and are 3 to 4 μ , which is large for spermatangia in *Acrochaetium*. Monosporangia were seen on this plant. No female plant was seen.

Cells of decumbent filaments 7 to 9 μ wide by 24 to 48 μ long (mostly nearer 24 μ); of erect filaments 7 to 12 μ wide by 14 to 24 μ long (mostly 14 μ), filaments bearing monosporangia usually stouter than other filaments. Cells with one pyrenoid and a parietal chromatophore.

Bermuda: in *Liagora mucosa*, west side of causeway between Hamilton Island and St. George's Island, April 16, 1949, *Taylor 49-801*, collected by Bernatowicz (MICH); isotypes in UC, PAR, IA. Along Hamilton to St. George's Causeway, west side of Castle Harbor, March 31, 1949, *Taylor 49-575*, collected by Bernatowicz (MICH, UC, PNM, IA); (in *L. ceranoides*) St. George's Island, Whalebone Bay, April 19, 1956, *Taylor 56-708* (MICH, BISHOP, IA).

Many species of *Acrochaetium* can, and do, grow on a wide variety of "hosts," partly because the structure of the plant permits this. This new species of *Acrochaetium* appears to be restricted to only a small number of "hosts" because of its lax intertwining endophytic habit, which gives the specific epithet. In this respect, it may best be compared with *A. liagorae* Børgesen (1937) from India. However, in the latter species the germinating spore is basal to the plant and persistent, whereas in *A. laxum* the germinating spore is lateral to the main plant and in the upper portions of the plant. It is usually pulled out of shape.

The erect portions of *A. laxum* bearing spores do not resemble those of *A. liagorae* in which the spores are pedicellate and borne in a series. The spores in *A. laxum* are sometimes pedicellate, but their disposition is irregular: sometimes opposite and sometimes alternate, as well as scattered.

The aseptate germinating spore of this species is similar to that of *A. liagorae* and *A. imitator*, but the very large size and erect filamentous habit of *A. laxum* distinguish it from both of these species. The two species are of essentially creeping habit, whereas *A. laxum* is clearly an erect plant.

A. laxum is a nearly wholly endophytic plant, but it has the erect filamentous habit of purely epiphytic species. This is in contradistinction to other endophytic species of *Acrochaetium* which creep either partly or wholly within the tissues of the "host."

These large plants have cells as large or larger than the *Liagora* filaments, and their extensive complanate branching appears to push aside the filaments of *Liagora*. In lateral growth, they may extend over several fascicles of assimilatory filaments.

5. *Acrochaetium actinocladium*, new species (fig. 14).

Planta ex toto endophytica, ramis et recte et horizontaliter dispositis inter *Liagorae* textus sitis. Partes verticales ad $240\ \mu$ vel longiores, usque ad $50\text{--}75\ \mu$ sub *Liagorae* superficie haud ramosae, superius per vias horizontales varias ramos emittentes, ramis ramulos breves monosporangiiferos rectos gigantibus. Ramorum horizontalium atque ramulorum rectorum cellulae rotundae vel allantoideae, inter se irregulariter junctae et specie facile separatae. Monosporangia nonnulla e ramis horizontalibus orta, 1-4 (vulgo 2) a cellula quaque producta, plerumque sessilia, rarius stipitata, $7\text{--}12\ \mu$ lat., $17\ \mu$ long., medius crassiora. Cellulae monosporangiferae et monosporangia haud superficiem excedentia. Cellulae ultimae capillis incoloribus ornatae. Chromatophorum stellatum pyrenoide una indutum.

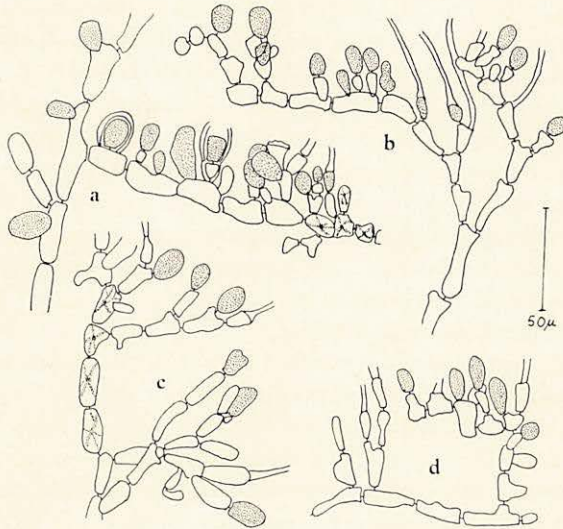


FIGURE 14.—*Acrochaetium actinocladium* from Hawaiian Islands, Waimanalo, Abbott 1832, type: a, portion of mature plant, showing inner horizontal and vertical nature of branching, sessile, and stalked monosporangia; cells at right show stellate nature of chromatophore; b, portion of mature plant, showing upper horizontal and vertical nature of plant bearing monosporangia; c, portion of mature plant showing inner repeated horizontal and erect branches borne on vertical branch system; d, portion of plant, showing secondary horizontal nature of branching on erect system.

Plants wholly endophytic, with both vertical and horizontally disposed portions embedded among *Liagora* tissues. Germination not seen. Vertical portions as long as assimilatory filaments of *Liagora*, about $240\ \mu$ and longer, unbranched to $50\ \mu$ to $75\ \mu$ of surface of *Liagora*, then branching in various horizontal directions, the horizontal branches creeping among ultimate branches of *Liagora*, to $360\ \mu$ in length, usually less. Cells of vertical branches $36\ \mu$ to $48\ \mu$ long by $12\ \mu$ or more wide. Horizontal portions bear short (to $75\ \mu$), erect, dichotomously disposed branches (fig. 14, *d*), the tips of which bear monosporangia, or spores borne directly on horizontal branches. Monosporangia usually $12\ \mu$ in length and width ($7\ \mu$ to $12\ \mu$ by $12\ \mu$ to $17\ \mu$), one to four to a cell, either sessile or stalked. Monosporangia rarely divided into a bispore. Lower cells (fig. 14, *a*) of horizontal branches irregularly sausage-shaped, $24\ \mu$ to $36\ \mu$ long, $10\ \mu$ to $14\ \mu$ wide at widest portions ($7\ \mu$ at narrowest); erect cells (fig. 14, *b*) $24\ \mu$ to $48\ \mu$ long by about $10\ \mu$ wide, topped by rounded cells $12\ \mu$ by $16\ \mu$, these cells commonly irregularly attached to each other and appearing to be easily disconnected (fig. 14, *d*). On these rounded cells may be borne monosporangia.

Monosporangia, borne on a level with tips of assimilatory filaments, do not project beyond. Colorless hairs (fig. 14, *b, d*) sometimes borne at tips of ultimate cells. Chromatophore stellate (fig. 14, *c*) with a single pyrenoid.

Hawaiian Islands: in *Liagora* sp., Oahu, Waimanalo, July 25, 1945, *Abbott 1832*, collected by D. P. Abbott, A. H. Banner, and I. Abbott (BISHOP); isotypes (PNM, UC, MICH, IA).

This new species of *Acrochaetium* most nearly resembles *A. liagorae* Børgesen in the habit of the ultimate cells and the position of the monosporangia. It differs markedly in that it has erect, long internal branches. The cells in this species are up to twice as large as those of *A. liagorae*, and the monosporangia are more equal in length and width, whereas those in *A. liagorae* are usually longer than broad. Indeed, the size of the filaments in *A. actinocladium* nearly dwarfs the filaments of the *Liagora* it inhabits.

Only *A. papenfussii* approaches the habit of this species. Both have horizontal branches from which shorter upright branches are given off; but in *A. actinocladium* the branching of these horizontal elements, as well as their number, is much more extensive than in *A. papenfussii*. The horizontal branches in *A. actinocladium* are given off at successive levels (fig. 14, *c*; compare with fig. 7, *h*).

From the top view, *A. actinocladium* has a raylike appearance, which accounts for its specific name. This particular characteristic seems unique to this species.

A. liagorae is a widely distributed species and, from my studies of it, shows wide variation. When more is known of its habits and structure, *A. actinocladium* may well be included within the limits of *A. liagorae*.

GROUP IV.

Germination of other kinds than those above; only bases embedded in *Liagora*, bases multicellular.

1. ***Acrochaetium seriatum*** Børgesen, Dansk. Bot. Arkiv. 3 (1) : 32, 1915 (fig. 15, a-c).

Plants with bases endophytic, base multicellular, disklike, giving rise to several erect branches 0.75 to 1 mm. in height (fig. 15, a). Main axis branched to both sides, sometimes pectinate but more usually irregularly branched. Cells of middle portion of filaments $12\ \mu$ to $14\ \mu$ long by $7\ \mu$ wide, tapering to $7\ \mu$ by $5\ \mu$ at tip. Monosporangia borne in a series, sessile or pedicellate or two on a pedicel, one of which is stalked, the other not (fig. 15, b). Chromatophore parietal (fig. 15, c) with a single pyrenoid.

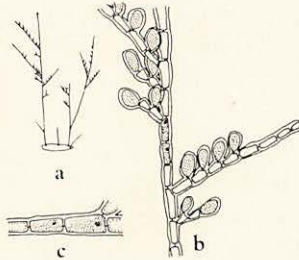


FIGURE 15.—*Acrochaetium seriatum* from Abbott 1824, Philippine Islands, Balabac Island: a, diagram, showing habit of branching and disposition of spores in relation to disk-shaped base; b, portion of monosporangial plant, showing both sessile and stalked sporangia; c, detail to show parietal chromatophore.

Philippine Islands (in *Liagora* sp.): Balabac Island, south end of Gnat Reef, Sulu Sea, March 4, 1957, Abbott 1824 (PNM, BISHOP, IA). A new record.

These specimens compare well with descriptions of the West Indian material, differing only in the fact that monosporangia may be borne on short bifurcated pedicels in addition to being borne in a series or one on a pedicel. Børgesen (1915, p. 34, figs. 29, 30) points to the seriate condition as differentiating this species from *A. flexuosum* Vickers, and his illustrations emphasize this point. Hamel's figure of *A. flexuosum* (1927, p. 78, fig. 47, a) shows the habit differs from that of *A. seriatum* as shown by Børgesen and the plants at hand; but it also shows the monosporangia on short pedicels or branched on a pedicel. Further study of these species is needed to determine whether they should be separated or combined.

A. seriatum was originally reported to be epiphytic upon *Centroceras* and a variety of other algae. When growing on *Liagora*, only the base is embedded in the *Liagora* tissues.

2. *Acrochaetium tuticorinense* Børgesen, Indian Bot. Soc., Jour. 16: 30, 1937 (fig. 16).

Plants to 240 μ in height, arising from a creeping base one-cell wide (fig. 16, a), originating from a single spore about 8 μ in diameter but soon pulled out of shape by development of a linear row of cells at both ends. Erect branches few, not from original spore, with sparse upper branching, each erect branch tipped by a hyaline hair (fig. 16, a, b).

Monosporangia few, sessile, irregularly placed, 10 μ by 12 μ in young plants, to 14 μ by 24 μ (10 μ by 19 μ) in mature plants. Reproduction also sexual, sessile carpogonium laterally placed directly on a filament, or stalked, cystocarps 17 μ by 29 μ , only end cells functioning as carpospores (fig. 16, b, d). Spermatangia clustered on terminal cells, each with a short stalk, spermatangia less than 2 μ in diameter (fig. 16, b). Chromatophore parietal with a single pyrenoid (fig. 16, c).

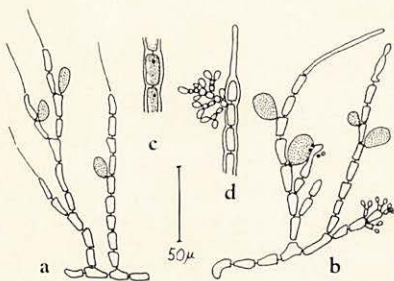


FIGURE 16.—*Acrochaetium tuticorinense* from *Abbott 1824*, Philippine Islands, Balabac Island: a, diagram of habit, showing creeping base, disposition of branches, hairs, and monosporangia; b, habit showing stalked carpogonium with spermatia about trichogyne, and spermatangia and monosporangia on same plant; c, detail to show parietal chromatophore; d, mature cystocarp appearing subterminally.

Philippine Islands: in *Liagora* sp., Balabac Island, south end of Gnat Reef, Sulu Sea, March 4, 1957, *Abbott 1824* (BISHOP, UC, PAR, IA). Newly reported from the Philippines.

Most of the plants examined were young, short in stature, and bearing only a few monosporangia. These young stages are, however, abundantly found on this *Liagora*.

The plants which Børgesen described from India as growing upon a piece of sea grass are larger than the plants discussed here. They

have a disklike base, which I could not find in my material, nor did I find plants with the long erect upper filaments of Børgesen's material. However, the general nature of the two plants (see Børgesen's figure 16, *b*) is strikingly similar and leaves no doubt in my mind that the Philippine plants are identical with those of India. The Philippine plants are sexual, a condition not reported for the Indian plants; but the morphology of the sexual organs does not mark them as much different from other species of *Achrochaetium* showing this condition.

In Papenfuss' Group II (1945, p. 311) of species with a multicellular basal layer, only *A. thuretii* was reported to show sexual reproduction. *A. tuticorinense* belongs to this group and adds a second species which may be sexual. *A. canariense* Børgesen (1927), somewhat similar in habit, originates in a divided spore which is persistent and which produces a discoid base. Its erect system of branches is both more prolific and more robust than that of *A. tuticorinense*. It reproduces by monospores, bispores, and tetrasporangia, and was found growing upon *Gelidium pusillum*. Because of these differences, it is probably not identical with *A. tuticorinense*.

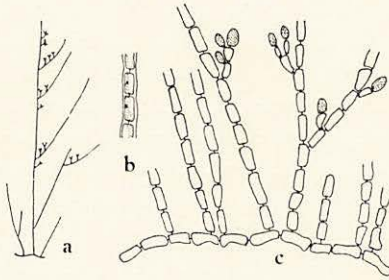


FIGURE 17.—*Acrochaetium gracile* from Abbott 1824, Philippine Islands, Balabac Island: *a*, diagram of habit, showing branching and disposition of monosporangia, plant with multicellular base; *b*, detail to show parietal chromatophore; *c*, habit of plant, showing stalked nature of monosporangia and nature of basal filaments.

3. *Acrochaetium gracile* Børgesen, Dansk. Bot. Arkiv. 3 (1) : 26, 1915 (fig. 17).

Plants slightly over 1 mm. in height, one to many erect branches rising from a creeping, multicellular base describing a loose disk (fig. 17, *a*), the base wholly embedded (to 30-50 μ) in the assimilatory filaments of *Liagora*. Basal (horizontal) cells of filaments 5 by 12-14 μ ; of the erect portions 7 μ by 22 μ ,

tapering at the tips to 5 μ by 17 μ . Upper branching sparse, bearing monosporangia on both main axis and laterals, spores pedicellate, two or more on each pedicel (fig. 17, c). Chromatophore parietal, with single pyrenoid (fig. 17, b).

Philippine Islands, in *Liagora* sp.: Balabac Island, south end of Gnat Reef, Sulu Sea, March 4, 1957, *Abbott 1824* (with *A. seriatum* and *A. liagorae*) (PNM, BISHOP, IA). A new record for the Philippines.

These plants compare favorably with Børghesen's description. My observations add only the fact that the basal portion is wholly embedded in the tissues of *Liagora*. The measurements (30 μ to 50 μ) within the assimilatory filaments do not take into account the chalky incrustation (to 1 mm.) which was removed before examination.

The plants from the West Indies were found growing epiphytically upon *Sargassum vulgare*; those from the Canary Islands, on *Gelidium pusillum* (Børghesen, 1927).

GENERAL DISCUSSION AND CONCLUSIONS

All of the known species of *Acrochaetium* which inhabit *Liagora* are classifiable into four main groups, if the main emphasis is placed on the nature of the germinating spore and the relationship of the developing plant to this spore. The shape of the chromatophore has been utilized secondarily. This system is a modification of those used by Rosenvinge, Hamel, Kylin, and Papenfuss, which apply to the genus as a whole, whereas in this study they are applied to a relatively small group of species. It would be extremely difficult to find other characters as useful.

The species studied in this report show two methods of germination: (1) from a persistent spore usually with a thickened wall which endures through the life of the plant and is clearly demonstrable at any stage of growth or (2) from a spore which soon loses its identity and, neither by position nor wall thickening, can be recognized at any but the young stages. In method 2 are included incidental species, chiefly epiphytic, in which the basal portions are modified into multicellular, disk-shaped, circular or creeping structures. This condition is more common in species of this complex which inhabit genera other than *Liagora* or *Liagora*-like plants.

Also of great value is the relationship in endophytic species of the decumbent and erect filaments to the germinating spore. This rela-

tionship shows whether a plant is primarily endophytic or primarily epiphytic. Whereas on other species of algae, depauperate growth may be attributable to the external environment, primarily endophytic species in *Liagora* seem to have adjusted themselves superbly to their particular environment. The protection afforded by their "host" is manifested in the rather stable characters of growth for the species, yet is diversified among the species. The one big morphological and physiological obstacle that these species must overcome to grow on *Liagora* is the calcium-carbonate layer produced by filaments of *Liagora*. The bases of the epiphytes and most of the thalli of the endophytes lie embedded in this layer, but this does not seem to have discouraged their development.

The shape of the chromatophore, which seems to be a useful character, has been used at the species level in this paper. If it can be demonstrated to be a stable character, which Feldmann doubts, it will have great value in the study of *Acrochaetium* species. The difficulty with both germination and chromatophore characters is that they require properly preserved material in order to be fully utilized. Thus, in *Acrochaetium vanbosseae*, the shape of the chromatophore may never be known, since Weber-van Bosse (1913), in her original descriptions, states that she could not determine the nature of the chromatophore because the specimens were preserved first in formalin, then in alcohol. Herbarium specimens are sometimes equally difficult because the dried plants do not respond well to soaking. The alternative is full descriptions from properly preserved material so that poorly prepared or fragmentary specimens can be compared with the descriptions.

At the species level, the systematists have mostly been concerned with the method of branching, the disposition and character of the spores, and the nature of the sexual plants. In the species of *Acrochaetium* on *Liagora*, the branching is irregular and the disposition of spores highly irregular. I re-emphasize the view that a group of characters should be used wherever possible and the fact that no one of those already in use is highly reliable by itself.

It has been some time since all sexual plants in this complex have been placed in the genus *Chantransia* (Bornet and Thuret 1867, Bornet 1904). Even supposing that *Chantransia* were valid, which according to Papenfuss (1945) it would not be for the Rhodophyceae, my studies show that the female plants add little of systematic value at the species level, but that the spermatangial plants may. It should

be noted, however, that Feldmann (in press) places great emphasis on the nature of the cystocarp formation and on formation of spermatangia at the generic level.

The number of endophytic species of *Acrochaetium* which grow on *Liagora* indicates that the frequently loose and slimy vegetative construction of *Liagora* bears a relationship to the vegetative characteristics of these endophytes. It is possible that if some of the primarily epiphytic species (*A. barbadense*, *A. trichogloeeae*) were found on other species of algae with a different vegetative construction (for instance, *Gracilaria*) the endophytic portions might be entirely suppressed. On the other hand, species with a primary endophytic growth (*A. papenfussii*, *A. actinocladium*) might not be able to grow on any other type of alga than those with loose vegetative construction (other helminthocladiaaceous genera and *Dudresnaya*, *Crouania*, and so forth). However, incidental species such as *A. gracile* and *A. tuticorinense* are clearly recognizable as the same ones growing on genera of different vegetative structure than that of *Liagora*. Baardseth (1941) has already pointed out this problem and I agree with him that careful investigation of species on various "hosts" may contribute much to the reduction in number of species in this genus.

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