OCCASIONAL PAPERS
OF
BERNICE P. BISHOP MUSEUM
HONOLULU, HAWAII

Volume XVIII | December 28, 1945 | Number 10

The Genus Liagora (Rhodophyceae) in Hawaii[1]

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INTRODUCTION

The genus *Liagora* (Rhodophyceae, Helminthocladiaceae) was first recorded for the Hawaiian Islands with the report by Schauinsland (19)[2] of three species from Laysan. Since there was no description accompanying the listing, for all practical purposes the record may be omitted.

Frederic K. Butters (6), in 1911, made the first study of Hawaiian members of the genus on material collected by Josephine Tilden in 1900. Butters described 12 species and one form. Of this number, five species and the one form were new to science. Of the new species described, one has since been reduced to synonymy. Of the remaining four, *Liagora maxima, L. hawaiiana, L. Tildenii,* and *L. subpaniculata,* I have found only the first two named.

It should be noted here that *Tildenii* has a masculine ending, whereas it should have a feminine ending. The name as amended is *Liagora Tildeniae.*

There are here listed for the first time six other *Liagora* from Hawaii: *L. Papenfussii, L. kahukuana, L. Setchellii, L. Boergesenii, L. pinnata,* and *L. divaricata.* The first two are proposed as new to science.

At the present time, and with present concepts, there are listed 18 species and forms of *Liagora* from Hawaii. There may be more or less than this number, especially when one must consider the section Validae. According to one's interpretation, this section may be split further, or grouped more in the larger sense of the species concept. There is evidence which is deemed pertinent by taxonomists of both

[1] University of Michigan Department of Botany, Paper 817.
[2] Numbers in parentheses refer to Bibliography, page 169.

points of view at this time, and further study seems necessary in order to clarify the Hawaiian members of this group.

After studying the early literature on *Liagora,* I selected *Fucus viscidus* Forskål as the technical type of the genus, founded by Lamouroux (15) in 1812. C. A. Agardh (1) seems to have overlooked Lamouroux's treatment when dealing with the species in 1822, and subsequent writers listed the species as *Liagora viscida* (Forskål) C. A. Agardh. This is now shown to be erroneous. The species is here amended to be listed as *Liagora viscida* (Forskål) Lamouroux.

Diverse ecological habitats were chosen for the collecting grounds where this genus was to be studied on the island of Oahu. It was found to be growing somewhat abundantly in all places selected. I made no collections of *Liagora* on other of the Hawaiian Islands, but several collections made by other persons have been available for study. The greatest number of specimens represented in my collections are from Makahoa Point, Laie Bay, in Kahuku, obtained from November through June; at Kawela Bay in April; Hanauma Bay, and Black Point in Kaalawai, in March; Nanakuli in June, and at Waikiki throughout the year. At Kahuku and Kawela Bay, coral reefs are occasionally interspersed with lava patches, and the waves are persistently backed by the trade winds. Hanauma Bay and Black Point, partly sandy beaches on black basalt, show a somewhat similar type of locality. Waikiki, a sandy beach with an eroded outer reef, is a good collecting place as far as currents and availability are concerned, but yields few species of this group.

Most of the species of *Liagora* here studied show a close relationship to the same flora in the western Pacific. Eight species may be so placed, although four of these seem to be cosmopolitan, and related as well to Caribbean and Mediterranean forms. Only three species may be considered endemic, but these are also closely related to Caribbean forms. Further collections of this genus throughout the Pacific and Indian Oceans will no doubt closely ally all species mentioned here. This is illustrated (23) by Weber-van Bosse's collection of *L. hawaiiana* in Coetivy Island in the Indian Ocean.

Calcification of specimens, especially those of the section Validae, varies much according to the habitat, and thus should not be considered a major character for classification. Much calcification is present in specimens growing in waveswept areas, whereas the converse is true of specimens growing in quiet tide pools.

ACKNOWLEDGMENTS

I wish to thank Dr. William Randolph Taylor of the University of Michigan under whose helpful guidance this study was made; Dr. George F. Papenfuss of the University of California, formerly of the University of Hawaii, who suggested the study and who cooperated in collecting and sending specimens; Dr. F. K. Butters and Dr. C. K. Tseng for the loan of specimens; and Dr. Harold St. John for generous aid in nomenclatural matters. Dr. H. L. Mason extended to me the facilities of the University of California herbarium.

SPECIES

The key to the Hawaiian species of *Liagora* which follows is based on Yamada's treatment of the genus (24). Two of his four sections of the genus are used here, the sections Validae and Farinosae. No members of the sections Mucosae and Orientales have been found in Hawaii.

Key to Species

1. Spermatangia borne in finger-like groups or in pairs at the tips of the assimilatory filaments ..... SECTION VALIDAE.
   2. Branching monopodial.
      A. Branching with an extended main axis, branches loosely paniculate ..... **1. L. maxima.**
      A. Branching without an extended main axis, branchlets densely paniculate ..... **2. L. kahukuana.**
   2. Branching dichotomous.
      B. Assimilatory filaments more than 10 μ in diameter in distal cells, frond geniculate at nodes with smooth incrustation in the internodes ..... **3. L. hawaiiana.**
      B. Assimilatory filaments less than 10 μ in diameter in distal cells.
         C. Assimilatory filaments irregularly corymbose at tips..... ..... **4. L. Setchellii.**
         C. Assimilatory filaments regularly corymbose.
            D. Plant 10 cm. or more high..... **5. L. Boergesenii.**
            D. Plant less than 10 cm. high.
               E. Plant canaliculate; mucoid when fresh, involucre poorly developed and little apparent.... **6. L. divaricata.**
               E. Plant not canaliculate, not mucoid, involucre well developed, often obscuring the cystocarp.
                  F. Plants with lateral proliferations prominent in the branches, farinose when dry, rhizoidal filaments much elaborated and conspicuous..... .... **7. L. ceranoides** form **pulverulenta**

F. Plants without lateral proliferations, chalk-like when dry, rhizoidal filaments simple and inconspicuous.
G. Branches slender, plant irregularly corymbose, cystocarps prominent as sunken red dots in the thallus.....**8. L. tenuis.**
G. Branches stout, plant regularly corymbose, cystocarps obscured by calcification macroscopically.
H. Cystocarps microscopically prominent with many repeatedly branched sporogenous filaments and large carpospores..**9. L. valida.**
H. Cystocarps microscopically little apparent with short simply developed sporogenous filaments and small carpospores.....**10. L. Cenomyce.**

1. Spermatangia in somewhat dense groups, capitate or nearly so.....SECTION FARINOSAE.
I. Assimilatory filaments moniliform.
J. Spermatangia terminal only, on ends of much elaborated branchlets, compactly globose.....**11. L. farinosa.**
J. Spermatangia terminal and lateral, simply stalked, not globose.....**12. L. Papenfussii.**
I. Assimilatory filaments not moniliform, spermatangia lateral, stalked, plant erect, caespitose, pinnate.....**13. L. pinnata.**

1. Liagora maxima Butters, Minn. Bot. Stud. **4**: 165, pl. 24, figs. 3-5, 1911 (fig. 1).

Plants up to 40 cm. in height, loosely paniculate, branching mostly at base. Calcification continuous, occasionally geniculate *in sicco*. Plant greenish when fresh, not flaccid, not gregarious.

Assimilatory filaments long and slender, 500 μ in length, 5-dichotomous, the cells in the median section 6 μ in diameter, 36 μ in length. Terminal cells oval, 20 μ by 21 μ, not crowded. Lower cells 20-50 μ in length, 8-10 μ in width. Assimilatory cells of male plant more slender than those of female plants. Rhizoidal filaments conspicuous, slender, usually curved.

Species dioecious. Carpogenic branch greatly curved, 3-celled in the short-lived young stage, 4-celled when mature. Cystocarps 350 μ in diameter, attached laterally near second dichotomy of assimilatory filaments. Involucral filaments dense, forming early from supporting cells; curved, unbranched, slender at the base, the cells 3 μ in diameter and 7 μ in length. Gonimoblast filaments intermingle freely with the involucre. Carpospores are 8 μ in diameter. Spermatangia are 1.5 μ in diameter, stalked, occurring loosely, singly, or in pairs at different levels at the tips of the assimilatory filaments.

Because of the massive globular appearance of the cystocarp and the densely developed involucre, the cystocarp of *L. maxima* closely resembles the cystocarp of *L. decussata* Montagne. In the structure of the spermatangia and general habit, the species resembles *L. erecta* Zeh. I have seen a photograph of the type of *L. erecta* in the Univer-

sity of California herbarium, through the courtesy of the late W. A. Setchell; but, unfortunately, I have not examined any specimen. The present comparison rests chiefly with Børgesen's excellent description (5) of the Indian species, from which the Hawaiian species seems quite distinct.

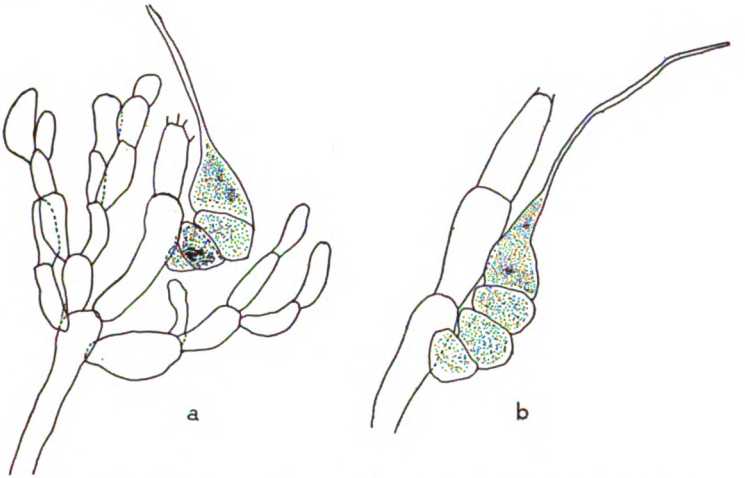


FIGURE 1.—*Liagora maxima:* **a, b,** carpogonial branches, × 513.

According to Minnie Reed (in notes to Setchell), the Hawaiians near Napoopoo, island of Hawaii, call this seaweed *limu alewalewa* and Hawaiians near Hana, Maui, call it *limu puaki.*

Type: Waianae, Oahu, *J. E. Tilden 418* in University of Minnesota Department of Botany; paratypes in American Algae Century V, as *Liagora decussata, Tilden 983, 1564.*

Range: restricted to the Hawaiian Islands.

Hawaiian Islands: Oahu: 1.8 miles west of Nanakuli at Maili, May, *Papenfuss 10450,* in herbarium of Papenfuss; Makua, *Reed 689.*[3] Molokai: Waialau [Waialua], *Reed 337* and *337a.* Maui: Hana, *Reed 527.* Hawaii: Napoopoo, *Reed 240.*

2. Liagora kahukuana, new species (fig. 2).

Frons valde calcareo-incrustata, usque ad 18 cm. alta, fragilis, teres, annulata rugosi-verucosa, paniculata dense ramosa, rosei-purpurea.

Axis centralis ex filamentis bulbosis constructus, filamenti circa 11-62 μ lati, ca. 210 μ longi. Cellulae filamentorum peripheralium cylindricae, breves, cellulae sursum distalae breviores crassioresque, doleiformes, 9 μ latae.

[3] All Reed specimens are in the herbarium of the University of California, Berkeley.

Species dioica. Rami carpogoniales 3-cellulosi subcurvati. Cystocarpia inconspicua, filamentis involucralibus circumdata. Spermatangia pedunculata circa 1 μ diametro.

Plant large, up to 18 cm. in height, heavily calcified, densely paniculate, clearly marked with annulations, rosy-purple when fresh.

Central axis composed of long, cylindrical cells, which are in the younger parts 11 μ in width to about 100 μ as long; in the older parts the filaments are 62 μ in diameter, and up to 210 μ in length, the cells very swollen through the middle, and tapering at one or both ends. The assimilatory filaments average 248 μ in length, usually 3-dichotomous with the branching chiefly at the distal ends. Cells somewhat cylindrical, short, 9-17 μ in the distal cells, larger below, the entire filament, however, retaining a rather uniform appearance.

Species dioecious. Carpogenic branches 3-celled, curved, situated above the second dichotomy away from the central axis. Cystocarps inconspicuous and in the early stages ill-defined, without the development of sterile filaments or other secondary cellular outgrowths of the carpogenic branch. Involucre surrounding a mature cystocarp slightly developed of very slender cells. Trichogyne not early deciduous, up to 112 μ in length. Spermatangia stalked loosely, singly or in pairs, at the tips of the assimilatory filaments. They are not crowded, and average 1 μ in diameter.

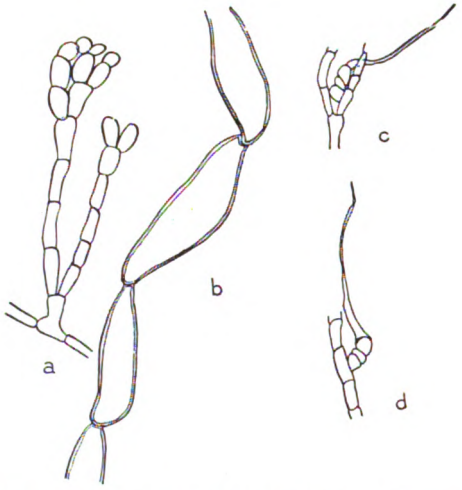


FIGURE 2.—*Liagora kahukuana:* **a,** assimilatory filaments, × 513; **b,** central filaments, × 513; **c, d,** carpogonial branches, × 258.

Type: Makahoa Point, Laie Bay, Kahuku, Oahu, Hawaiian Islands, June 22, 1941, *Abbott 125* in herbarium of Bishop Museum, isotype in herbarium of W. R. Taylor, Ann Arbor, Michigan.

Range: restricted to the Hawaiian Islands. Oahu: in addition to the type locality, at Waimanalo off rocky shore north of Makapuu Point in April, *Abbott 667,* 3 carpogonial, 2 spermatangial plants.

This colorful species is named for its type locality. In gross and internal anatomy, it is most nearly related to *L. decussata* Montagne. However, the latter shows the following characters which are not present in this new species: (1) a sharp, clear-cut cystocarp with an elaboration of cells at the base, (2) a corymbiform outline of assimilatory filaments at the tips, with smaller cells in these filaments, (3) a short trichogyne which is early deciduous, (4) only one size of cells in the central axis of fairly uniform shape. An additional character of *L. kahukuana* is the extremely dense paniculate branching.

3. **Liagora hawaiiana** Butters, Minn. Bot. Stud. **4**: 164, pl. 24, figs. 8, 9, 1911 (fig. 3).

Plants 4-9 cm. in height, regularly dichotomous with long uninterrupted internodes, with smooth incrustation, often canaliculate when dried. Frond terete, articulate at base of each dichotomy. Cells of central axis about 14 μ in diameter, 3-4 times as long. Cells of assimilatory filaments cylindrical, obovate at tips, 10-17 μ in distal cells, corymbose. Rhizoidal filaments grouped at bases of assimilatory filaments, thin, usually unbranched. Assimilatory filaments slender and graceful in aspect.

Species commonly dioecious, occasionally monoecious. Spermatangia attached singly on short stalks at tips of distal cells, crowded. Spermatangia 1.1-1.7 μ in diameter. Carpogenic branches 3-4-celled, lateral, slightly curved. Mature cystocarp with slender, abundant involucre.

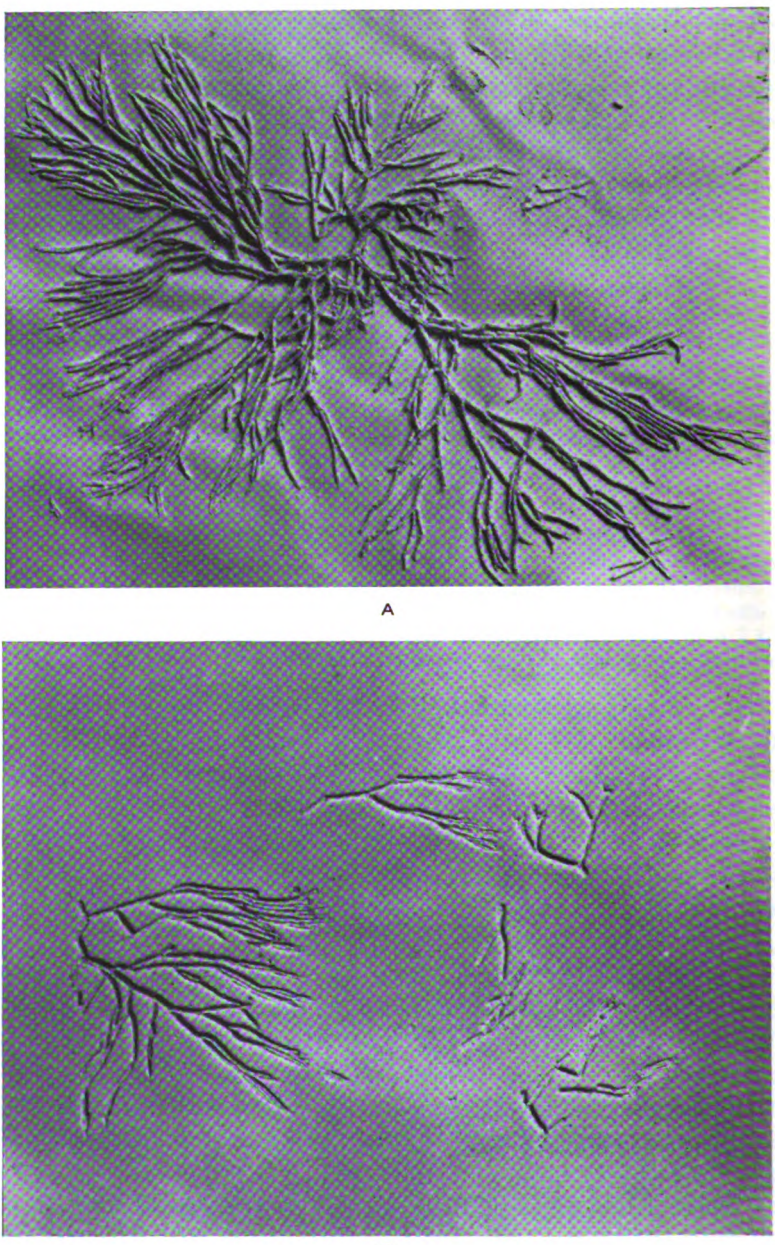
Type: Laie Bay, Koolauloa, *Tilden 1005,* in University of Minnesota Herbarium.

Range: Hawaiian Islands at the type locality, and Coetivy Island, near Seychelles, Indian Ocean.

Hawaiian Islands: Oahu: on wave-washed coral reef off rocky lava coast at Makahoa Point, Laie Bay, Kahuku, in March (*Abbott 17,* spermatangial), and in April (*Abbott 67, 71,* monoecious; *63, 66, 73, 77,* carpogonial).

These specimens are in substantial agreement with the type specimens, parts of which Dr. Butters kindly sent to the University of Michigan. Butter's specimens are entirely dioecious, but, since this character is variable in other members of this genus, it is deemed of little significance here. Butters observes that the male plants are more slender in gross appearance than the female plants of the type specimens.

The slender aspect of the assimilatory filaments, and the characteristic acute-angled, crowded spermatangia will separate *L. hawaiiana* easily from all other Hawaiian specimens studied. Externally, the



A

B

FIGURE 3.—*Liagora hawaiiana*, type specimens: **a**, cystocarpic; **b**, spermatangial.

geniculate character of the branches and the very smooth incrustation of calcium carbonate will set this species apart from other *Liagora*. No Hawaiian members of the genus seem closely related to *L. hawaiiana*.

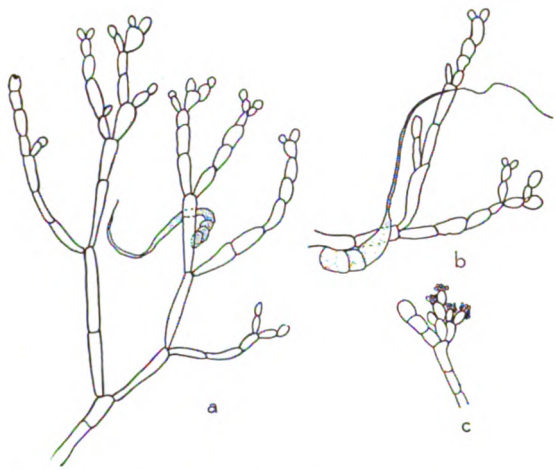


FIGURE 4.—*Liagora Setchellii:* **a, b,** assimilatory filaments with carpogonial branches, × 258; **c,** spermatangial clusters, × 258.

4. Liagora Setchellii Yamada, Inst. Alg. Res., Fac. Sci., Hokkaido Imp. Univ., Sci. Pap. 2(1): 13, pl. 3, fig. 2, text figs. 7-8, 1938 (figs. 4, 5).

Frond flaccid, 7 cm. in height, corymbose, densely branched. Calcification heavy, occasionally geniculate at the nodes. Branching regularly dichotomous.

Cells of the central axis 22 μ in diameter, 280 μ in length, cylindrical. Assimilatory filaments 376-450 μ long, generally 4-dichotomous. Cells cylindrical, 11 μ in diameter at tips, more narrow below, 7 μ in width and 34 μ in length.

Species monoecious or dioecious; the Hawaiian specimens show the two conditions. Carpogenic branches 4-celled, slightly curved, the involucral cells resemble those of the assimilatory filaments. Spermatangia on short stalks, 3 μ in diameter, the spermatangia crowded at the tips of the penultimate and ultimate cells.

Type: not designated by Yamada.

Range: western Pacific at Ryukyu, Formosa, Ogasawara Islands; **central Pacific in Hawaiian Islands at Kawela Bay, Oahu, *Papenfuss 10205*.**

The specimens representing this species in my collection differ from Yamada's description in the size and shape of the spermatangia. These are spherical in shape and smaller than those of the Japanese specimens. Yamada's specimens have long ovoid spermatangia which are somewhat larger than the Hawaiian specimens. These differences, however, may be justified when considering the wide distribution.

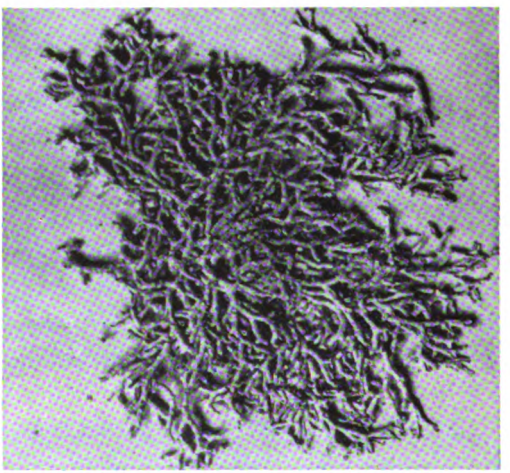


FIGURE 5.—*Liagora Setchellii*, spermatangial.

5. Liagora Boergesenii Yamada, Inst. Alg. Res., Fac. Sci., Hokkaido Imp. Univ., Sci. Pap. 2(1) : 11, pl. 2, figs. 5-6, text fig. 9, 1938 (fig. 6).

Plant large, corymbose, about 12 cm. in height, heavily calcified throughout. Calcification rugose at tips, smooth below. Frond flaccid.

Filaments of the central axis about 20 μ in diameter, 4-5 times longer. Assimilatory filaments more than 300 μ long, 5-dichotomous, branching mostly at the distal ends. Rhizoidal filaments 8 μ in diameter at the base of the assimilatory filaments. Cells of assimilatory filaments cylindrical, clavate at distal ends where cells are 5 μ by 13 μ, branching corymbose.

Hawaiian species dioecious. Carpogenic branch median in assimilatory filaments, 3-celled, slightly curved, laterally attached. Carpospores large, 5-5.6 μ in diameter. Involucre slightly developed of long, slender cells.

Type: not designated by Yamada.

Range: western Pacific, at Ryukyu and Formosa; central Pacific, in Hawaiian Islands: Oahu: Makahoa Point, Laie Bay, Kahuku, *Abbott 123*, carpogonial.

In its general outward appearance, this member of the Valida group resembles, to a large degree, other members of the group, especially some forms of *L. valida* and *L. Setchellii*. It seems to be larger than most *L. valida* specimens, and is more ramified and rougher in appearance than *L. Setchellii*. In size and form of the cystocarp, this species is distinctly different. Macroscopically the cystocarps may be seen as red dots in the surface of the frond, crowded near the apices. Yamada does not clearly indicate whether the species is dioecious or monoecious. It is recorded here as dioecious, with no male specimens seen.

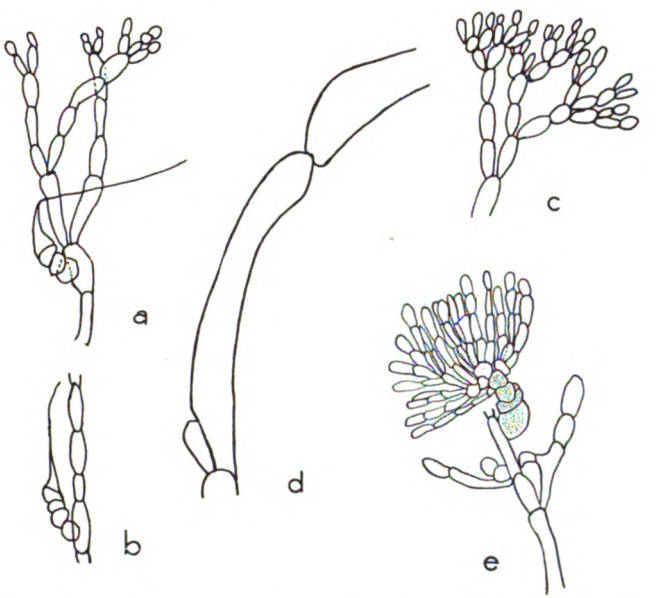


FIGURE 6.—*Liagora Boergesenii:* **a, b,** carpogonial branches, showing 4- and 5-celled stages, × 387; **c,** tip of assimilatory filaments, × 387; **d,** central cells; **e,** young cystocarp, × 387.

6. Liagora divaricata Tseng, Fan Mem. Inst. Biol., Bot. Ser., Bull. **10**: 268, figs. 2-4, 1941 (fig. 7).

Plant 5-8 cm. in height, moderately calcified, compressed below, regularly dichotomous, the tips strikingly divaricate. Base much entangled with lateral proliferations appearing as far up as the axils of the lower branches.

Cells of the central axis broadly cylindrical, averaging about 24 μ in diameter, 10 or more times as long. Rhizoidal filaments conspicuously clustered at the base of the assimilatory filaments, slender and long, 4 μ in diameter. Assimilatory filaments about 250 μ long, branching four or five

times toward the tips, corymbiform. Distal cells ovate, occasionally somewhat clavate, 4-11 μ wide, 7-18 μ long. Cells below rarely more than 3 μ wider, 3-4 times as long as distal cells.

Species dioecious. Carpogenic branch variable in length, 4-6 cells placed above the second dichotomy away from the base, slightly curved. Involucre slight. Spermatangia in loose clusters at tips of distal cells, 2 μ in diameter. Spermatangial stalks inconspicuous.

Type: Hainan Island, *Tseng 777,* in herbarium Tseng.

Range: known only from Hainan, and Makahoa Point, Laie Bay, Kahuku, Oahu, *Abbott 64,* spermatangial, *65, 70, 75,* carpogonial.

Specimens of this group resemble in habit *L. ceranoides* form *pulverulenta,* but are strikingly different anatomically. Except for the lateral proliferations in the axils of the branches, the Hawaiian specimens compare favorably with the Chinese specimens. The many monosporangial discs found among the filaments may account in part for the irregular outward appearance of the frond.

7. **Liagora ceranoides** Lamouroux form **pulverulenta** (C. A. Agardh) Yamada, Inst. Alg. Res., Fac. Sci., Hokkaido Imp. Univ., Sci. Pap. 2(1): 20, 1938. Lamouroux, J. V. F., Hist. nat. Polyp. corall. flex., 239, 1816. Agardh, C. A., Species Algarum I, 1(2): 396, 1822. (See figures 8, 9.)

Liagora pulverulenta C. A. Agardh, Species Algarum I, 1(2): 396, 1822.

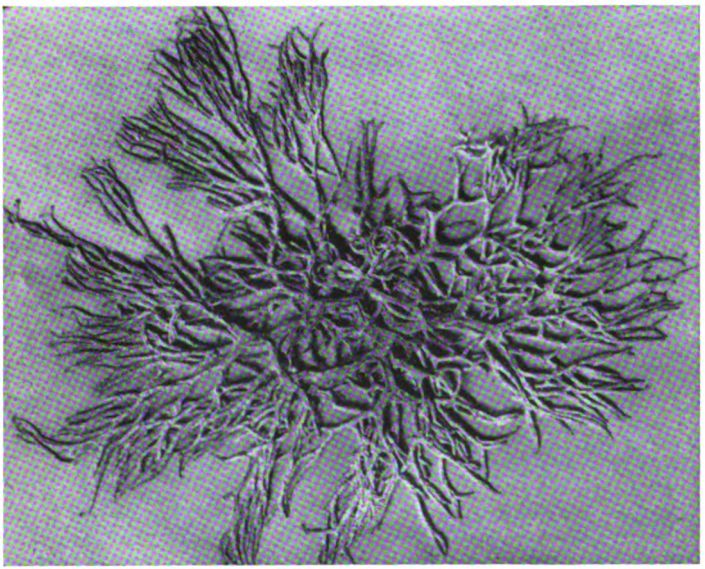
Plant 4-7 cm. in height, regularly dichotomous except for deciduous lateral proliferations near the base of the dichotomies and occasionally in the axils of younger branches. Frond corymbose with moderate incrustation, farinaceous when dried. Cells of assimilatory filaments cylindrical ovoid, smaller in male plants than in female plants, in the latter 3-6 μ in diameter, 4-10 μ in length in the distal cells, lower cells as broad, but often 6 times longer. Rhizoidal filaments frequent, branched or unbranched, prominent, slender.

Species dioecious. Carpogenic branch above second dichotomy of assimilatory filaments, lateral, slightly curved, 4-5-celled. Mature cystocarps moderately involucrate with thin, usually unbranched filaments. Spermatangia ovoid, 0.8-2.5 μ long, placed singly or in pairs, occasionally more than two, on long stalks, crowded at tips of assimilatory filaments.

Type locality: St. Thomas, Virgin Islands.

Range: cosmopolitan in distribution in subtropical and tropical seas: Malay Archipelago, China, Japan, Brazil, Mexico, through the islands of the West Indies north to Bermuda.

Hawaiian Islands: Oahu: on coral reef, Makahoa Point, Laie Bay, *Abbott 13,* carpogonial, *12,* spermatangial, Laie Bay, *J. E. Tilden 417;*



A

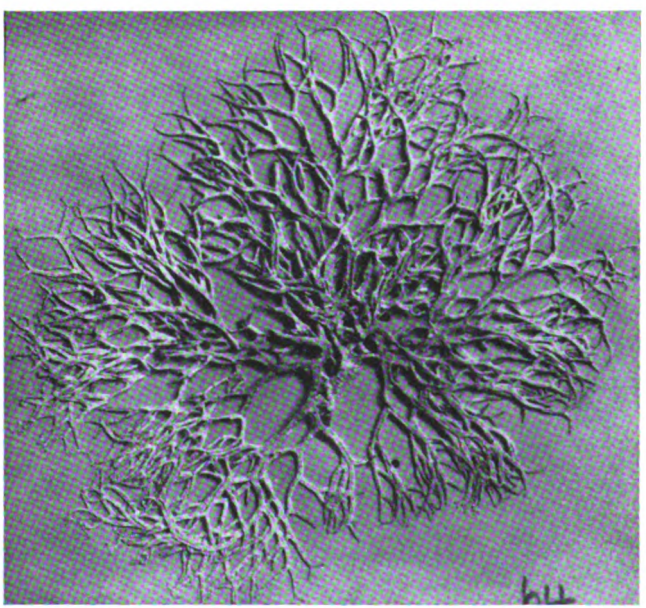


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FIGURE 7.—*Liagora divaricata:* **a,** cystocarpic; **b,** spermatangial.

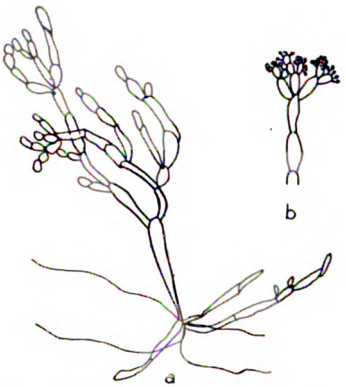


FIGURE 8.—*Liagora ceranoides* form *pulverulenta:* **a,** assimilatory and central filaments, × 258; **b,** spermatangial cluster, × 258.

Waikiki, in front of marine laboratory, *Abbott 372,* carpogonial and spermatangial; between Halona and Kaloko, *Abbott 427,* carpogonial and spermatangial. A specimen collected by G. P. Andrews with no data but presumably from Waikiki was also examined and found to be carpogonial.

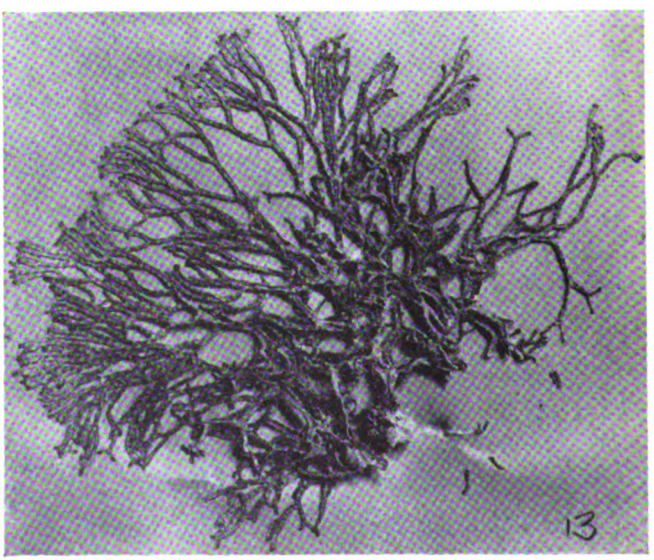


FIGURE 9.—*Liagora ceranoides* form *pulverulenta,* cystocarpic.

The Hawaiian specimens are notably lacking in lateral proliferations, except at the bases of the first dichotomies and, occasionally, in the axils of branches farther upward in the plant. These proliferations are rugose and crowded and appear unlike the normal proliferations for this species in specimens examined at Michigan and California. In habit, these specimens greatly resemble *L. divaricata*. The latter, however, is strikingly divaricate at the tips, with false lateral proliferations in the Hawaiian specimens, and is more compressed throughout.

8. Liagora tenuis J. G. Agardh, Analecta algologica, Soc. Physiogr. Lund, Acta, new ser. 2: 101, 1896 (figs. 10, 11).

Frond 1.5-4 cm. in height, dichotomously branched, attenuate, loose, irregularly corymbose, caespitose. Distal cells of assimilatory filaments 2.24-4.4 μ in width, 4.4-6.7 μ in length, corymbose at tips.

The specimens here are dioecious or monoecious. Cystocarps appear macroscopically as sunken red dots in the thallus. Carpogenic branch 4-celled, lateral, curved, the cystocarp covered with a dense involucre. Spermatangia stalked at tips of distal cells, in pairs, less than 1 μ in diameter.

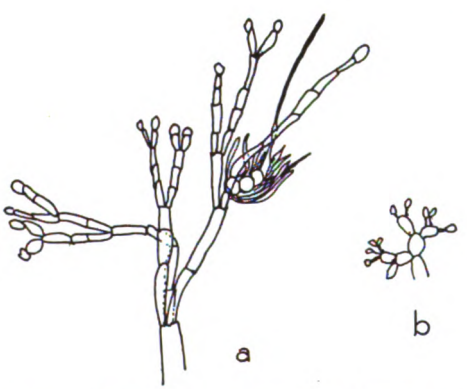


FIGURE 10.—*Liagora tenuis:* **a**, assimilatory filaments with carpogonial branch and developing involucre, × 387; **b**, spermatangial branch, × 775.

Type locality: West Indies.

Range: West Indies.

Hawaiian Islands: Oahu: Hanauma Bay in March, *Abbott 43, 44, 45, 47, 48,* carpogonial, *49,* monoecious; Black Point in April, *Abbott 98,* carpogonial; Waikiki at Elk's Club in April, *Abbott 94,* monoecious; Waikiki at marine laboratory in December, January, *Abbott 215, 336,* carpogonial, *340* monoecious; Kawela Bay in April, *Papen-*

fuss 10111, 12 specimens, some carpogonial, spermatangial, and monoecious.

It is with some uncertainty and dissatisfaction that this species is placed here, as I have seen no type specimen, and only such authentic specimens as are no better than those in my collection, from the point of view of morphology. Howe (13) and Børgesen (3) who have

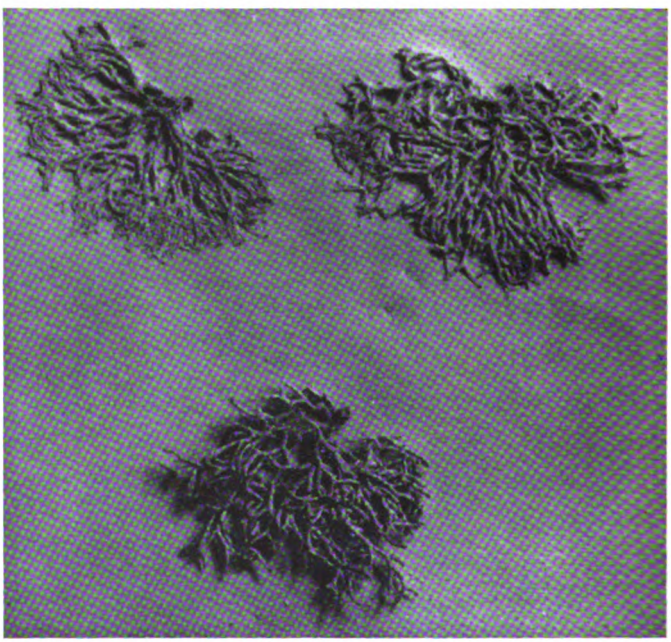


FIGURE 11.—*Liagora tenuis:* cystocarpic and spermatangial plants.

studied the species from the type area seem to agree that this species is synonymous with, or a form of, *L. valida.* Specimens which I ascribe to this species seem to be constantly different enough in habit and in morphology of the cystocarp and spermatangia to place them here, until further detailed studies may be made.

9. **Liagora valida** Harvey, Smithsonian Contr. Knowledge **5** (art. 5) : 138, pl. 31 A, figs. 1-5, 1852 (figs. 12, 13).

The habit of the frond of the specimens which I refer to this species is extremely variable. A few specimens placed here are widely branching, sprawling in a dichotomous manner, loosely corymbose, others are

definitely crowded in corymbose form, very densely branched, others are small, the dichotomies appearing regularly at short intervals, giving a crowded effect, with the true dichotomies only apparent at the tips.

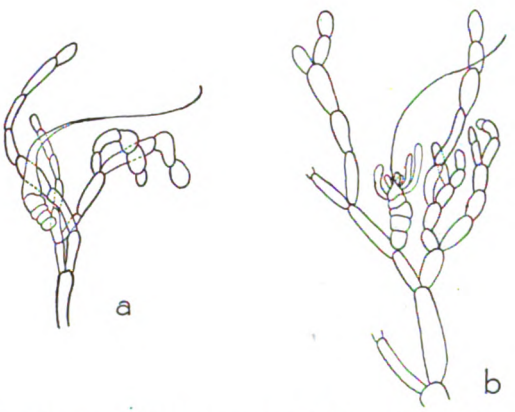


FIGURE 12.—*Liagora valida:* **a,** carpogonial branch, × 387; **b,** gonimoblast, × 387.

The size, shape, and general distribution of the assimilatory filaments are most variable, some possessing the typical corymbiform outline referred to by Børgesen, others having tips of the filaments mostly free. In cell sizes, there is a variance of 2.4 to 12 μ in diameter for the distal cells; in shape they are moniliform, or nearly so, to broadly oval or cylindrical.

In the carpogenic branches, there is much variety in the size, shape, and disposition of involucral filaments. It therefore seems necessary to make a further study of this group and, for the present time, to indicate only that this species is present in abundance over a wide collecting range in the islands.

Type: from Sand Key, Florida, in herbarium Dublin University.

Range: widely distributed in warmer waters of the Atlantic, very common in the Caribbean area.

Hawaiian Islands: Kauai: Lawai Beach in December, *John Harris* and *Yoshio Kubo,* carpogonial. Oahu: Makahoa Point, Laie Bay in March and April, *Abbott 16, 76,* spermatangial; in June, *Abbott 121, 122, 126, 127,* carpogonial. Black Point, Kaalawai, *Abbott 97, 99, 100,* carpogonial. Nanakuli, east of Kalanianaole Park, *Abbott 107, 108,*

carpogonial. Kawela Bay, *Papenfuss 10209,* 6 specimens carpogonial, 1 spermatangial.

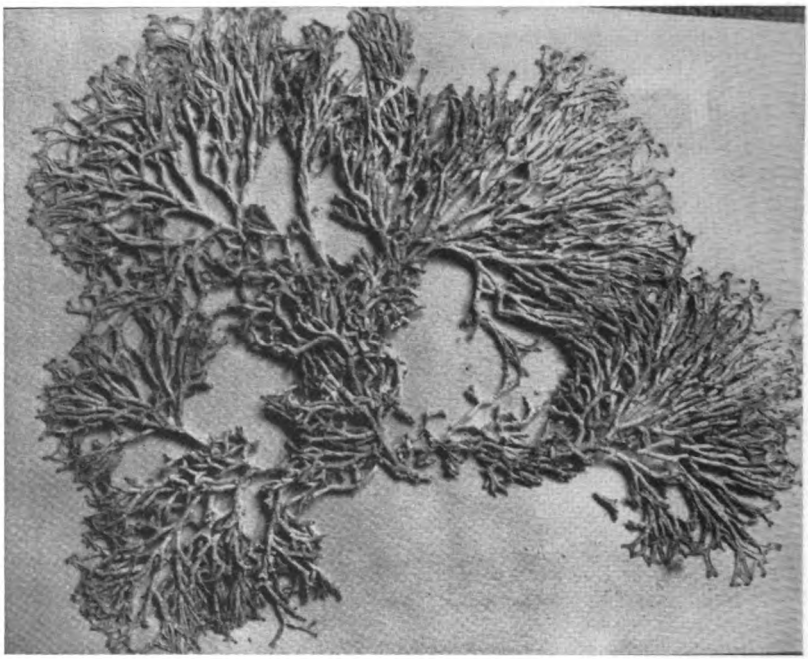


FIGURE 13.—*Liagora valida,* cystocarpic.

10. Liagora Cenomyce Decaisne, Sci. Nat., Ann., Botanique II, **18**: 107, 1842.

Liagora intricata Butters, Minn. Bot. Stud. **4**: 167, 1911.

Liagora Holstii Zeh, Berlin Bot. Garten, Notizblatt **5**: 269, 1912.

Frond 3 cm. in height, terete, dichotomously branched and much intertwined, continuously calcified, annulate throughout. (I have only a small fragment in my collection.)

Assimilatory filaments nearly 200 μ in length, corymbose at tips, repeatedly dichotomous. Cells cylindrical-ovate, about 1 μ in diameter at distal cells, larger below. Central axis composed of uniformly large cylindrical cells, 14 μ in diameter. Rhizoidal filaments long, slender, curving around base of assimilatory filaments.

Species dioecious. Carpogenic branches 3-celled, curved, laterally situated. Cystocarps small in comparison to cystocarps in this group. Dense involucre surrounds cystocarp. (Male plants lacking in my collection.)

Type: Manila, Philippine Islands, *Cuming,* Exsicc. *2222* in herbarium of Paris Museum.

Range: Philippine Islands, Japan, China, Malaya, Tahiti, Tonga, East Africa.

Hawaiian Islands: Oahu: Makahoa Point, Laie Bay in April, *Abbott 74,* carpogonial; Waikiki, *Reed 893.* Molokai: Pukoo, *Reed 329a.* Hawaii: Puna, *Setchell 8,* Punahou [Punahoa], *Reed 1141.*

East Africa: *Holst 127B* (type of *L. Holstii* Zeh, part of type in herbarium of University of California).

Philippine Islands: Numerous specimens collected by H. H. Bartlett and others, in herbarium University of Michigan.

For many years, *L. Cenomyce* has been labeled *L. caenomyce.* This is found to be incorrect from the original description, especially in light of the fact that the specific name is taken from a genus of lichens, *Cenomyce.* In the field, this species resembles the small rugose forms of *L. valida,* but it is very different morphologically.

11. Liagora farinosa Lamouroux, Hist. nat. Polyp. corall. fléx., 240, 1816 (figs. 14, 15).

Liagora hirta Harvey et Bailey, Boston Soc. Nat. Hist., Proc. **3**: 373, 1851.

Liagora Preissii Sonder var. *pacifica* Grunow, Mus. Godeffroy, Jour. **3**(6): 36, 1874.

Liagora Cheyneana sensu Weber-van Bosse, an Harvey, Siboga Exped. Monogr. **59b**(2): 200-201, 1921.

Liagora elongata sensu Børgesen, an Zanardini, Dansk. Bot. Arkiv. **3**(1): 67-70, 1915.

Liagora Cayohuesonica sensu Howe, an Melvill, in Britton and Millspaugh, Bahama Flora, 554, 1920.

Liagora corymbosa sensu Howe, an J. G. Agardh, in Britton and Millspaugh, Bahama Flora, 554, 1920.

Liagora crassa sensu Howe, an Dickie, in Britton and Millspaugh, Bahama Flora, 554, 1920.

Liagora farionicolor sensu Howe, an Melvill, in Britton and Millspaugh, Bahama Flora, 554, 1920.

Liagora lurida sensu Howe, an Dickie, in Britton and Millspaugh, Bahama Flora, 554, 1920.

Plant 5-7 cm. in height, moderately calcified, farinose throughout, with many lateral proliferations. Size and appearance of frond variable.

Cells of central axis large, up to 200 μ in diameter and about 8 times as long. Assimilatory filaments are 300 μ long, laterally or dichotomously branched, cells nearly uniformly moniliform throughout, 15.5 μ wide by 21.8 μ in length in the distal cells on which spermatangia are attached.

Species monoecious and dioecious. Carpogenic branch 4-celled, lateral, sometimes almost straight but generally slightly curved. Involucre of stout filaments, slightly developed. Spermatangia compactly capitate, stalked, in more or less dense clusters. Reproduction also by monospores.

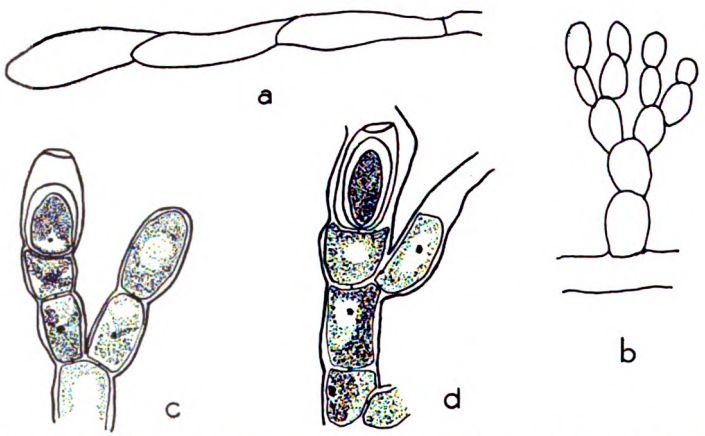


FIGURE 14.—*Liagora farinosa:* **a**, central filament, × 387; **b**, assimilatory filaments, × 387; **c**, monospore showing one old wall, × 775; **d**, monospore showing two old walls, × 775.

Type locality: Red Sea, near Suez.

Range: throughout warmer seas.

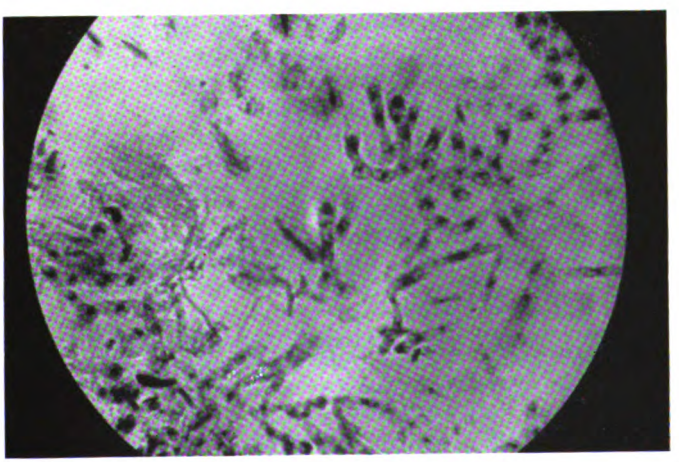
Hawaiian Islands: Oahu: Makahoa Point, Laie Bay, Kahuku, in April, *Abbott 69,* spermatangial, *72,* monoecious; in February, *Abbott 722,* carpogonial, with endophytic *Acrochaetium.*

Pacific Ocean: Japan, Ryukyu, Formosa, China, Samoa, New Guinea, Palau.

Atlantic and Caribbean at Florida, Dry Tortugas, various islands of West Indies, Canary Islands.

The addition of *L. Preissii* variety *pacifica* as a synonym to an already lengthy list is based on a study of an authentic specimen from the herbarium of Grunow. This specimen, procured by Setchell, is on sheet 370251 in the herbarium of the University of California. There are typical capitate spermatangia, typical moniliform cells. The plant is loosely pinnately branched. A second specimen, on sheet 94547 at

A



B

FIGURE 15.—*Liagora farinosa:* **a**, spermatangial-cystocarpic; **b**, photomicrograph, showing figure 14, *c*, *d*, at center and right respectively, × 47.

California is this species. A specimen of *L. hirta* from the Brown University herbarium of Bailey was also examined at California, and I agree with Yamada (24) that this species is synonymous with *L. farinosa.*

The species has been found to be dioecious by Howe, Weber-van Bosse, Yamada, and Tseng, and monoecious by Børgesen. It is reported in both conditions here.

Asexual reproduction is here indicated for the genus *Liagora* for the first time. Monospores were found in *Liagora farinosa* (*Abbott 72,* collected at Makahoa Point), of the type described by Svedelius for the genus *Scinaia.* These occur at the tips of the assimilatory filaments and appear as swollen cells. Many empty monosporangia are seen, and the naked protoplast escapes to leave the sporangial wall intact except at the apex. Thus, as in *Scinaia,* liberation of the monospore is followed by the production of a new monospore within the old monospore wall, and this has been seen to occur at least three times. There are, then, two methods by which this species of *Liagora* may at times produce new gametophytes: by the germination of the 1 N asexual monospore, and by the germination of the 1 N sexual carpospore.

Liagora pinnata is morphologically closely related to this species but it lacks the globose capitate spermatangia which are so very characteristic of *L. farinosa.*

12. Liagora Papenfussii, new species (fig. 16).

Frons 9 cm. alta, mollissima, lubrica, calce modice incrustata, in sicco farinacea, ramis dense pinnatis, ramellis alternis.

Axis centralis 33 μ ad 115 μ diametro, 250 μ vel 300 μ longis ex filamentis cylindricis compositus. Filamenta assimilatoria circa 230 μ longa, 4-dichotoma, cellulis cylindricis 12 μ crassis, 17 μ longis, eis dichotomiae primae circa 12 μ crassis, 28 μ longis, eis partium superiorum brevioribus.

Species monoica et tetrasporica. Rami carpogoniales 20 μ lati, 42 μ longi, 3-cellulosis media in filamentis assimilatoris instructis. Cystocarpia sublaxa. Involucra tenuia, filamentis eis assimilatoriis similibus. Tetrasporae circa 3.4 μ lata, 5.6 μ longa. Spermatangia diam. 2.8 μ, haud capitata, terminalia et lateralia in cellulis parvis ramorum fertilium 3.4 μ crassorum.

Plant small, up to 9 cm. in height, moderately calcified, pinnately branched, with branchlets alternate, appearing somewhat farinaceous when dried.

Central axis composed of long, cylindrical cells, 33.6-112 μ in width, 257-300 μ in length. Assimilatory filaments averaging 234.4 μ in length, usually 4-dichotomous, branching mostly at corymbose distal ends. Assimilatory filaments compact, little diverging, cells moniliform or nearly so, cylindrical, 12.3 μ by 16.8 μ at distal cells, retaining nearly the same width throughout;

cells at the base of the first dichotomy away from the central axis averaging 12.32 by 28 μ.

Species monoecious and tetrasporic. Carpogenic branches usually 3-celled, sometimes 4, curved. Carpogenic branch situated in the middle of the assimilatory filaments. Involucre slightly developed, in structure resembling the assimilatory filaments. Tetraspores 3.3 by 5.6 μ. Spermatangia occurring terminally and laterally on small cells at the tips of the fertile branches, 3.4 μ in diameter. Spermatangia stalked, not capitate, 2.8 μ in diameter.

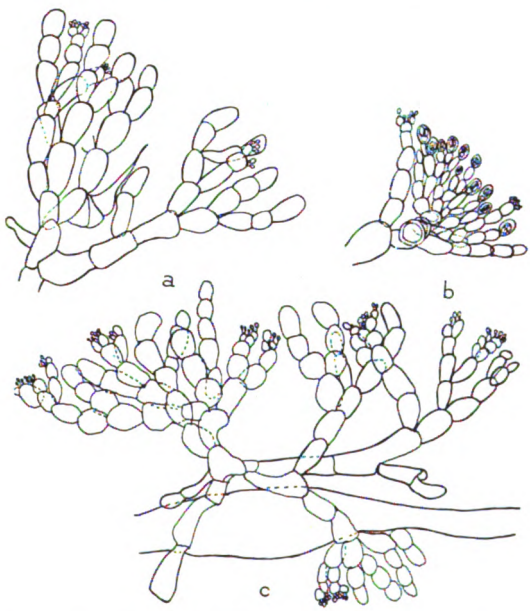


FIGURE 16.—*Liagora Papenfussii:* **a,** assimilatory filaments showing young carpogonial branch and spermatangia, × 513; **b,** mature cystocarp showing tetraspores, old carpogonial branch and spermatangia, × 513; **c,** assimilatory filaments on a central cell, with spermatangia, × 513.

Type: between Camp Erdman, Mokuleia and Kaena Point, Oahu in September, *Papenfuss 10016,* in herbarium Papenfuss, paratype in herbarium of Bishop Museum.

Range: known only from the Hawaiian Islands and collected only on Oahu: Makahoa Point, Laie Bay, *Abbott 15, 124;* Diamond Head, *Garber 438, Reed 76.* (All specimens tetrasporic, carpogonial and male. A sterile specimen without locality or collecting date, *Reed 600C,* belongs to this species). Specimens on sheets 508038 and 508039 at California are this species.

This interesting species is named for George F. Papenfuss, who brought it to my attention. Besides being tetrasporic, a condition reported for *Liagora* by Børgesen and later by Kylin and Yamada, the species differs from *L. pinnata,* which it closely resembles, in that it is smaller in habit and has large and only narrowly divergent assimilatory filaments. This gives the cortex a compact aspect not generally found in most species of this genus. In addition, the formation of spermatangia both laterally and terminally on the distal cells is markedly different from spermatangial formation in other species.

Tetrasporic specimens of *Liagora* are probably not to be regarded in the light of tetrasporic specimens of other red algae. In *Liagora,* tetraspores are rather the exception than the rule, and this condition has been found only in *L. tetrasporifera* Børgesen from the Canary Islands and the French coast and in specimens of *L. pinnata* Harvey from Japan. It is thought that the tetraspores are merely a quartet of carpospores. No definite proof has been presented to explain this phenomenon, and cytological studies are planned for this species in an effort to settle the anomaly.

13. Liagora pinnata Harvey, Smithsonian Contrib. Knowledge **5** (art. 5) : 138, pl. 31 B, figs. 1-5, 1852.

Liagora paniculata sensu Howe, an J. G. Agardh, in Britton and Millspaugh, Bahama Flora, 555, 1920.

Frond terete, paniculate, the branchlets alternate. Calcification moderate with cystocarps appearing as small red dots in the whitened tips of branches.

Central axis composed of large, cylindrical cells 40 μ in diameter, 320 μ in length. Rhizoidal filaments mixed with large filaments of central axis near divergence of assimilatory filaments. Cells of the assimilatory filaments cylindrical, large at the base, narrow at the center, and widening again at the tips. Distal cells occasionally clavate, about 18-20 μ in diameter.

Species monoecious. Carpogenic branch laterally situated, composed of 4 cells, slightly curved. Small involucre with cells the same size as those of assimilatory filaments. Spermatangia clustered below tips of the filaments on small cells. Spermatangia 2 μ in diameter.

Type: Sand Key, near Florida, in herbarium of Dublin University.

Range: West Indies, China, Japan.

Hawaiian Islands: Oahu: Makahoa Point, Laie Bay, Kahuku, *Abbott 146,* in formalin; *J. F. Rock 29,* exact locality unknown.

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