

The Liagoraceae (Nemaliales, Rhodophyta) of the Hawaiian Islands IV: the species of *Liagora* described by Butters (1911)

John M. HUISMAN* & Isabella A. ABBOTT

Department of Botany, University of Hawaii at Manoa,
3190 Maile Way, Honolulu, HI 96822, USA

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Abstract — The eleven species and one variety of *Liagora* attributed to the Hawaiian Islands by Butters (1911) are revisited. Most have been or are herein reduced to synonymy, and of the five species that were described as new by Butters, the only species still recognized is *Liagora hawaiiiana*. Published accounts of this species are lacking in some details of structure and reproduction. The present paper includes a detailed description of *L. hawaiiiana*, highlighting several of its distinctive features including a slightly diffuse gonimoblast, presence of a fusion cell, and prominent involucre. In addition, *L. hawaiiiana* is newly reported for Lord Howe Island, Australia. The current taxonomic placements of the remaining species are detailed and *Liagora hawaiiiana* Butters, *Liagora intricata* Butters [= *Yamadaella caenomyce*], and *Liagora maxima* Butters [= *L. albicans*] are lectotyped.

Hawaii / *Liagora* / Liagoraceae / Nemaliales / Red Algae / Rhodophyta

Résumé — Les Liagoraceae (Nemaliales, Rhodophyta) des îles Hawaii IV : les espèces du genre *Liagora* décrites par Butters (1911). Les onze espèces et une variété de *Liagora* attribuées aux îles Hawaii par Butters (1911) sont revisitées. La plupart ont été ou sont maintenant réduites en synonymie, et des cinq espèces décrites comme nouvelles par Butters, seule *Liagora hawaiiiana* est encore reconnue. Le présent article propose une description détaillée de *L. hawaiiiana*, mettant en lumière plusieurs de ses caractères distinctifs dont un gonimoblaste discrètement diffus, la présence d'une fusion cellulaire, et d'un involucre proéminent. En outre, *L. hawaiiiana* est nouvelle pour Lord Howe Island, Australie. La place taxonomique courante des autres espèces est détaillée; *Liagora hawaiiiana* Butters, *Liagora intricata* Butters [= *Yamadaella caenomyce*], et *Liagora maxima* Butters [= *L. albicans*] sont lectotypifiés.

Algues rouges / Hawaii / *Liagora* / Liagoraceae / Nemaliales / Rhodophyta

* Biological Sciences and Biotechnology, Murdoch University, Murdoch, WA 6150, Australia. Correspondence and reprints: J.Huisman@murdoch.edu.au

INTRODUCTION

In 1911, Frederic Butters published a paper entitled "Notes on the species of *Liagora* and *Galaxaura* of the central Pacific" (Butters, 1911) in which he described eleven species and one variety of *Liagora* Lamouroux from the Hawaiian Islands, plus an additional species from Tahiti. His work was based primarily on specimens in the herbarium of the University of Minnesota collected by Josephine E. Tilden in the Hawaiian Islands during the summer of 1900, some of which were distributed by Tilden as part of her "Centuries of American Algae" (Tilden, 1901). Other collections were made by the United States Fish Commission and by A.A. Heller.

Butters described five species and one variety as new to science. Of these, *L. maxima* Butters has been reduced to the synonymy of *L. albicans* Lamouroux and *L. intricata* Butters is a synonym of *Yamadaella caenomyce* (Decaisne) Abbott (Abbott, 1970). *Liagora subpaniculata* Butters, *L. tildeniae* Butters and *L. tildeniae* var. *lubrica* Butters are regarded as synonymous with *L. ceranoides* Lamouroux (Abbott, 1990a), although unfortunately there appear to be no useful extant collections to confirm those synonymies. However, the illustration of the cystocarp of *L. tildeniae*, at least, conforms exactly to current concepts of *L. ceranoides*.

The only remaining species is *Liagora hawaiiiana* Butters. Of the species he described, *Liagora hawaiiiana* is the best represented in terms of herbarium specimens from the original collection. We are aware of specimens housed in MIN, BISH, MICH, and UC, but others were no doubt distributed by Tilden. The species has been subsequently treated (see Abbott, 1945 and 1999), but some details of its morphology and reproduction (considered important in species delineation) are lacking. It can generally be recognized by gross morphology alone, but this can be a dangerous practice with most species of *Liagora* and even workers experienced with the genus will routinely undertake a microscopical examination before venturing to name a specimen. We therefore provide a characterization of *L. hawaiiiana*, based on an examination of type and recently collected material.

Over the course of many years working with the Hawaiian species of *Liagora* by the second author, some of the existing specimens have been examined and the identity of Butters' species clarified. Many have been reduced to synonymy. Our aim in the present study was to characterize, as far as possible, the Butters' species, lectotypify his names based on MIN specimens, and present a summary of their present taxonomic placement. Unfortunately, some of the specimens on which Butters based his Hawaiian records are lost, and not all of his identifications can be verified.

This paper is the fourth in a series describing the Liagoraceae of the Hawaiian Islands, the previous contributions dealing with *Gloiotrichus* Huisman *et* Kraft (Huisman & Abbott, 2003), the species of *Liagora* with quadripartite carposporangia (Abbott & Huisman, 2003), and *Ganonema* Fan *et* Wang (Huisman, Abbott & Sherwood, in press). Prior to the present series, the genus *Izziella* Doty (originally based on Hawaiian specimens) was re-examined by Huisman & Schils (2002).

MATERIALS AND METHODS

Dried specimens were rehydrated in water overnight. Portions of plants for microscopical examination were decalcified in 1N HCl, stained in 1% aniline

blue, then mounted in a 50 % Karo (Best Foods, Englewood Cliffs, N.J. USA) corn syrup solution and lightly squashed to separate the filaments. Herbarium specimens and slide preparations are held at the Botany Department, University of Hawaii at Manoa, or BISH. Herbarium abbreviations follow Holmgren *et al.* (1990). Slide preparations were examined with an Olympus BX3 microscope and photographed using an Olympus DP11 digital camera. Photographic plates were prepared using Adobe Photoshop v. 6. Where no specimens of the collections used by Butters are available for examination, we have cited the details from the original paper, followed by “*n.v.*” (*non vide*).

Note on Butters' citation of specimens: With regard to the citation of specimens, Butters was inconsistent and did not clearly indicate any holotypes. Since (at the time, at least) all of his specimens were in the collection of the University of Minnesota (MIN), any cited, extant collections housed there can be regarded as type material. He mostly gave a Tilden (J.E.T.) number, but these often represented several specimens and can be regarded as syntypes. Unfortunately the same number was also occasionally cited under two species (e.g., J.E.T. 1005 is given by Butters under both *Liagora hawaiiiana* and *Liagora leprosa*, J.E.T. 1221 is given under *Liagora leprosa* as well as *Liagora subarticulata*). Where possible, we have lectotypified Butters' new species with a MIN specimen. Given that these names have mostly been reduced to synonymy, this is unlikely to have any serious nomenclatural repercussions, but doing so will avoid further rearrangements if subsequent investigations reveal different taxonomic entities among the cited collections (a common problem with *Liagora*).

OBSERVATIONS

Liagora hawaiiiana Butters, 1911: 169, pl. 24, figs 8–9.
Abbott, 1945: 151, fig. 3; 1999: 85, fig. 14C-E.

Type locality and lectotype — Lā'ie Point, Koolauloa, O'ahu, Hawaiian Islands, on reef at low tide, June 16, 1900, *J.E. Tilden* 1005; **lectotype**: MIN 369840, upper specimen; isoelectotypes: BISH (Fig. 1); MICH 20346. Butters gave only the Tilden number when describing this species, which was initially based on wet-preserved material, part of which was later pressed by Butters and distributed by him to various herbaria. The type sheet in MIN was labeled by Butters with “part of the type material removed from formalin and pressed 3/14/1942. F.K.B.” and includes two specimens, the upper female and the lower male. Herein we lectotypify the name with the upper specimen. The remaining wet-preserved material is also in MIN.

Specimens examined — In addition to the MIN holdings, we have examined several specimens from the type collection housed in BISH and MICH. Also: (1) Mahakoa Point, Lā'ie Bay, Kahuku, O'ahu, on wave-washed sandy bottom of rocky lava coast, 12 April 1941, *I. Aiona* [Abbott] 63; MICH 20417. Neds Beach, Lord Howe Island, from outer reef, 27 January 1982, *G. Kraft* MELU, LHI10, 500 g.

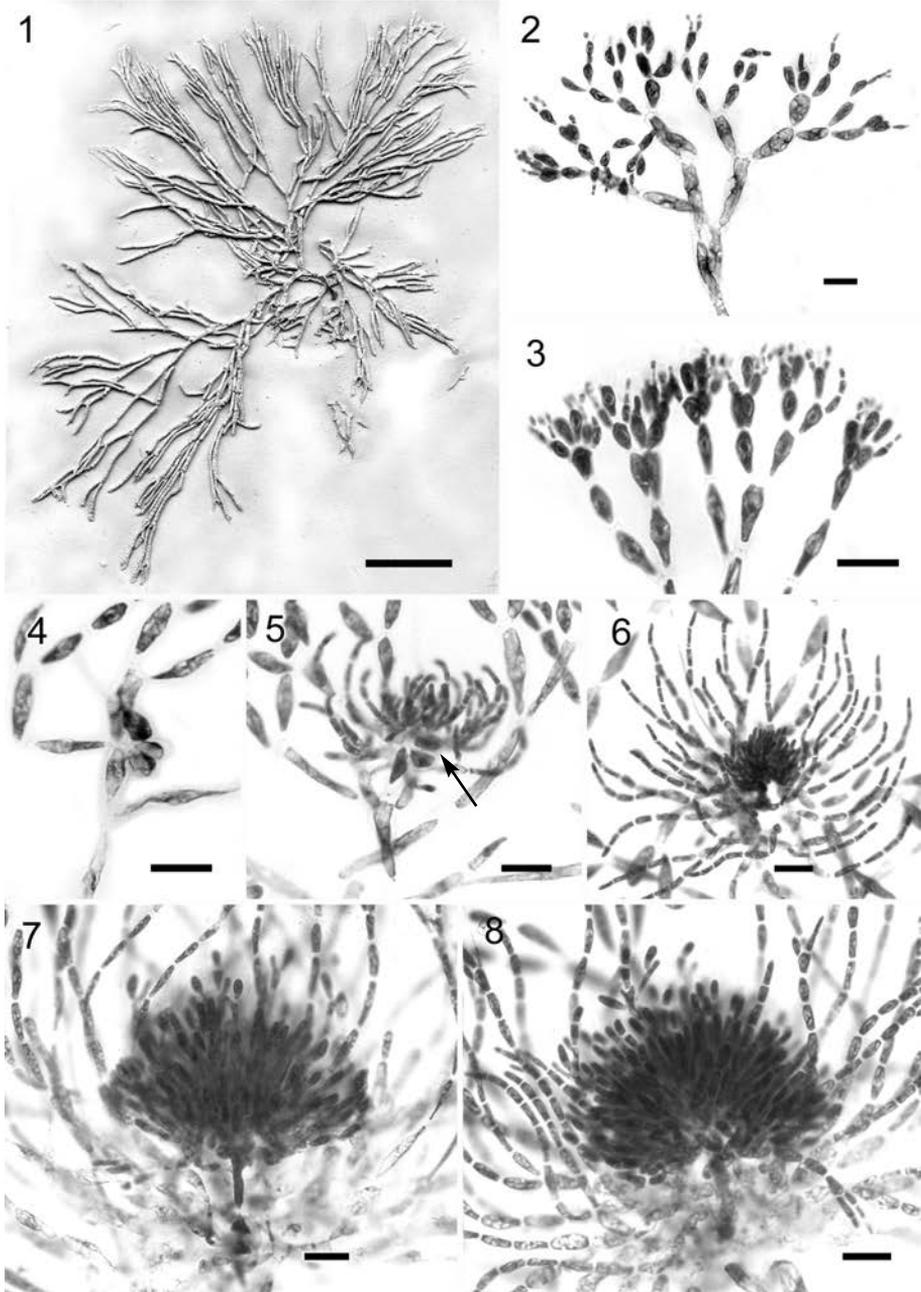
Habitat — Intertidal, favoring exposed eroded coral reefs and edges of platforms. The type locality was visited during June, 2003, but no specimens were encountered.

Morphology — Plants to 11 cm tall, white to pale pink, dichotomously branched with long segments (Fig. 1), 5-13 mm between dichotomies, axils somewhat divaricate but becoming acute when the calcification cracks; axes terete, 0.8-1 mm in diameter, heavily calcified, smooth, brittle with age, sometimes with striations (the cystocarpic lectotype is smooth, but the male isolectotype is noticeably striated). Structure multiaxial, with a central medulla of longitudinally aligned filaments bearing anticlinal assimilatory fascicles. Medullary filaments slender, 10-30 μm in diameter, mixed with intertwining rhizoidal filaments, mostly hyaline but some cells staining with aniline blue; assimilatory filaments (Fig. 2) 200-300 μm long, regularly dichotomously divided except near the outer cortex, where trichotomous divisions often occur. In younger parts of the plant, lower cells cylindrical, 10-12 μm in diameter, upper cells ellipsoidal, obovoid or pyriform, 6-7.5 μm in diameter. In older portions of the plants, the lower cells are 12-15 μm and the upper cells are 7-10 μm in diameter, the outermost cells often clavate and cutting off a terminal “glandular” cell. Most cells with a conspicuous central pyrenoid. Plants dioecious or monoecious. Spermatangia spherical, 2-3 μm in diameter, borne singly or in pairs on elongate mother cells arising 1-3 from outer cortical cells (Fig. 3). Carpogonial branches 3(rarely 4)-celled, curved, with an elongate carpogonium (Fig. 4). Following presumed fertilization the zygote (= post-fertilization carpogonium) divides transversely and the gonimoblast initials arise from the distal cell. At the same time involucreal filaments arise from the cells adjacent to the supporting cell and are sparsely branched with cylindrical cells, slightly more slender than the cortical filaments (Figs 5, 6). The gonimoblast is initially dense (Fig. 6) but becomes slightly diffuse, although not intermingling with the involucreal filaments or the cortical filaments, with terminal, ellipsoidal to clavate, carposporangia, 12-17 \times 5-7 μm . An extensive fusion cell is formed from the cells of the carpogonial branch, the supporting cell, and sometimes cortical filament cells below the supporting cell. Mature cystocarps (Figs 7, 8) with a gonimoblast 125-175 μm in diameter, the involucreal filaments spreading to about twice the size.

Remarks — Butters’ description of the cystocarp of *Liagora hawaiiiana* gave very few details other than it being involucreate. Subsequent treatments of this species (Abbott, 1945: 151; Abbott, 1999: 85) have provided additional details, but have not included some features considered important in current taxonomic schemes, including the presence of a fusion cell and a slightly diffuse mature gonimoblast.

Liagora hawaiiiana has been attributed to several locations other than the type, including Japan (Yoshida, 1998: 517), the Philippines (Meñez, 1961: 69, pl. 7: figs 81, 82), the Marshall Islands (Taylor, 1950), and Coetivy Island in the Indian Ocean (Weber-van Bosse, 1913: 111-112; Weber-van Bosse, 1914: 275-276). The species was also recorded for the Great Barrier Reef, Australia, by Cribb (1983: 20), but that record was referred to *L. boergesenii* Yamada by Huisman (2002). In

Figs 1-8. *Liagora hawaiiiana* Butters. Fig. 1. Isotype specimen (BISH). Fig. 2. Detail of assimilatory filaments showing lower cells slightly broader than upper cells (BISH). Fig. 3. Spermatangia borne in terminal spermatangial mother cells (MELU, LHI10, 500g). Fig. 4. Three-celled carpogonial branch (MELU, LHI10, 500 g). Fig. 5. Post-fertilization showing transversely dividing carpogonium (arrow) and initiation of involucreal filaments (MELU, LHI10, 500 g). Fig. 6. Later stage of carposporophyte development, with compact gonimoblast and narrow, unbranched, involucreal filaments (MELU, LHI10, 500 g). Figs 7 & 8. Mature cystocarps showing the development of a fusion cell formed from cells of the carpogonial branch (MELU, LHI10, 500 g). Scales: Fig. 1 = 2 cm; Figs. 2-8 = 20 μm .



the collection of the second author (which will eventually be housed at BISH), are several specimens labeled *L. hawaiiiana* from Japan, the Philippines, and the Marshall Islands, some of which formed the basis for the above records. An examination of these has shown that none agree with the species as characterized above. The specimen from the Philippines is *Liagora valida* Harvey, those from the Marshall Islands do not have a distinct involucre and possibly represent *Liagora divaricata* Tseng. These observations cast doubt on most non-Hawaiian records, but we have not examined all specimens on which these records are based. We anticipate that our characterization of the species will allow others to confirm or refute them. We have, however, examined material of this species from Lord Howe Island, Australia, that is entirely compatible with the type material, and represents an authentic new record of the species for Australia.

Liagora hawaiiiana can be distinguished by its dichotomously divided thallus with smooth to faintly striated, slender axes and long internodes, di-trichotomously branched assimilatory filaments, 3(-4) celled carpogonial branch, initially compact gonimoblast becoming slightly diffuse, formation of a fusion cell, and distinct involucre of slender, mostly unbranched filaments. The most closely related species appears to be *Liagora robusta* Yamada, but that species is coarser and has regular transverse striations (Yamada, 1938; Huisman, 2002).

Liagora cheyneana Harvey. Butters, 1911: 173.

= *Ganonema farinosum* (Lamouroux) Fan et Wang.

Cited specimen — Kaua'i. June 23, 1902, 18-41 fathoms. S. For. Co. R. (U.S. Fish Com. 4023C), *n.v.*

Remarks — *Liagora cheyneana* is generally regarded as a synonym of *G. farinosum*, and the description given by Butters agrees with that species, particularly the “cortical ... filaments of almost cylindrical cells” and that the “distal cells of the filament often bear globose antheridia consisting of short branched filaments with cells about 1.5 mic in diameter”. These two features are characteristic of *Ganonema farinosum* (Huisman, 2002). No specimens are available to confirm this placement, but the species is common in the Hawaiian Islands.

Liagora corymbosa J. Ag. (?) Butters, 1911: 171.

= *L. ceranoides* Lamouroux?

Cited specimen — Wai'anae, O'ahu, June 12, 1900, *J.E. Tilden* 1564C, *n.v.*

Remarks — This record was attributed to *L. valida* Harvey (as *L. fragilis*) by (Abbott, 1990b: 312), but Butters' description is not compatible with that species as currently understood (Abbott & Yoshizaki, 1982; Huisman, 2002). His illustration shows corymbose assimilatory fascicles with di-trichotomous branching, whereas fascicles in *L. valida* are not corymbose and only rarely trichotomously divided. Unfortunately no specimens are available, and it is impossible to tell with any certainty what this record represents. The cortical structure is similar to that of *Liagora divaricata* Tseng (see Abbott & Huisman, 2003), but in that species cystocarps do not have the prominent involucre described by Butters. The habit as described by Butters suggests *L. ceranoides* Lamouroux.

Liagora intricata Butters, 1911: 167, pl. XXIV, fig. 6.

= *Yamadaella caenomyce* (Decaisne) Abbott, *vide* Yamada, 1938: 6; Abbott, 1945: 162 (as *Liagora caenomyce*); 1970: 117; 1999: 62; and herein.

Type locality and lectotype — Diamond Head, Oahu, *A.A. Heller* no. 2285a; also Tahiti, Society Islands, September 1910, *J.E. Tilden*. These two speci-

mens were cited by Butters and a type was not indicated. Herein we **lectotypify** the name with the specimen from Diamond Head, Oahu (*A.A. Heller* 2285a); MIN 4064, a fragment of which is in the collection of the second author. This specimen is labeled as the type of “*Galaxaura rugosa* var. *attenuata*”, a name that was apparently never published.

Remarks — Examination of the type confirms this placement. The specimen is female with the distinctive carpogonial branch and diffuse gonimoblast of *Yamadaella caenomyce* (Abbott, 1970; Wynne & Huisman, 1998). Despite Butters’ claim to the contrary, the Hawaiian specimen has mature cystocarps.

Liagora leprosa J. Agardh. Butters, 1911: 163.

= *L. ceranoides* Lamouroux.

Specimen examined — Lā’ie Point, Koolauloa, O’ahu, on rocks at low tide, 18 June 1900, *J.E. Tilden*, Tilden American Algae Cent. V. no. 417, MIN 4044 (Fig. 9).

Remarks — This specimen agrees with *Liagora ceranoides* as currently understood (Abbott, 1999; Huisman, 2002), the species with which *Liagora leprosa* is generally synonymized. *Liagora ceranoides* is common at Mālaekahana¹, O’ahu, which is just north of Lā’ie Point, one of the collection localities cited for this species by Butters (1911: 163).

Liagora maxima Butters, 1911: 165-167, pl. XXIV, fig. 3-5.

= *L. albicans* Lamouroux, *vide* Abbott 1990a; 1999: 81; and herein.

Type locality and lectotype — Two miles north of Wai’anae, O’ahu, on rocky peninsula attached to rocks on sandy beach at low tide, 12 June 1900, *J.E. Tilden*; **lectotype**: Tilden American Algae Cent. V. no. 418, MIN 4039 (Fig. 10). Butters cited several specimens and did not indicate a holotype. Four specimens of Tilden no. 418 are housed in MIN and we herein lectotypify the name with MIN 4039. The remaining specimens are mounted on a single sheet (MIN 48608) and are isolectotypes. Several wet preserved paratype specimens are also in MIN (Tilden no. 1564); these also conform to *L. albicans*, as was noted by Abbott (1990a).

Liagora paniculata sensu Butters, 1911: 174 (non J. Agardh).

= *Ganonema papenfussii* (Abbott) Huisman, Abbott *et* Sherwood, *vide* Abbott, 1990a: 125 (as *Liagora papenfussii* Abbott); and herein.

Specimen examined — Diamond Head, O’ahu, 12 Apr. 1895, *A.A. Heller* 2132, MIN 4045, 4046 (Fig. 11).

Remarks — This specimen has medullary filaments over 50 µm in diameter and assimilatory filaments that are sparsely branched and composed of barrel-shaped cells, features indicative of *Ganonema* (Huisman & Kraft, 1994; Huisman, 2002; Huisman *et al.*, in press). Butters’ description and the microscopical features observed in the present study indicate that this specimen is *Ganonema papenfussii* as currently understood (Huisman, 2002; Huisman *et al.*, in press).

Liagora subarticulata sensu Butters, 1911: 174, pl. XXIV, figs 14, 15 (non Grunow).

= *L. valida* Harvey, *vide* Abbott, 1990b: 312; 1999: 93; and herein.

Specimens examined — Hanalei, Kaua’i, 26 July 1900, *J.E. Tilden* 1221.

1. e.g. Mālaekahana, on shallow reef flat, 16 June 2003, *J. Huisman* & *D. Spafford*, IA 30641.

Remarks — Butters listed J.E. Tilden 1221 under *Liagora leprosa* as well as *L. subarticulata*. This specimen conforms to *L. valida* as currently understood (Abbott & Yoshizaki, 1982; Huisman, 2002).

Liagora subpaniculata Butters, 1911: 168, pl. XXIV, fig. 7.
= *L. ceranoides* Lamouroux, *vide* Abbott, 1990a: 117.

Syntype localities and cited specimens — North of Hotel, Wai'anae, Oahu, May 26, 1900, *J.E. Tilden* 863, 864; Wai'anae, Oahu, June 12, 1900, *J.E. Tilden* 1564b; Kaua'i, June 23, 1902, 18-41 fathoms, S. For. Co. R. (U.S. Fish. Com. 4023A), *n.v.*

Remarks — No specimens were available to confirm this placement, but the description and figure given by Butters are compatible with *L. ceranoides* as presently understood (Abbott 1990a; Huisman 2002).

Liagora tenuis J. Agardh. Butters, 1911: p. 164, pl. XXIV, fig. 2. = *Liagora valida* Harvey.

Cited specimen — Wai'anae, O'ahu. May 26, 1900, *J.E. Tilden* 861, *n.v.*

Remarks — No specimens were available but this species is generally regarded as synonymous with *L. valida*, which is a fairly common species on the Wai'anae coast of O'ahu. The description and figure given by Butters are compatible with that placement.

Liagora tildeniae Butters, 1911: 171, pl. XXIV, figs 11, 12.
= *L. ceranoides* Lamouroux, *vide* Abbott, 1990a: 119.

Type localities and cited specimens — North of Hotel, Wai'anae, O'ahu, May 26, 1900, *J.E. Tilden* 861A; Lā'ie Point, Koolauloa, O'ahu, June 18, 1900, *J.E. Tilden* 1007; Kealia Beach, Kaua'i, July 25 1900, *J.E. Tilden* 1202, *n.v.*

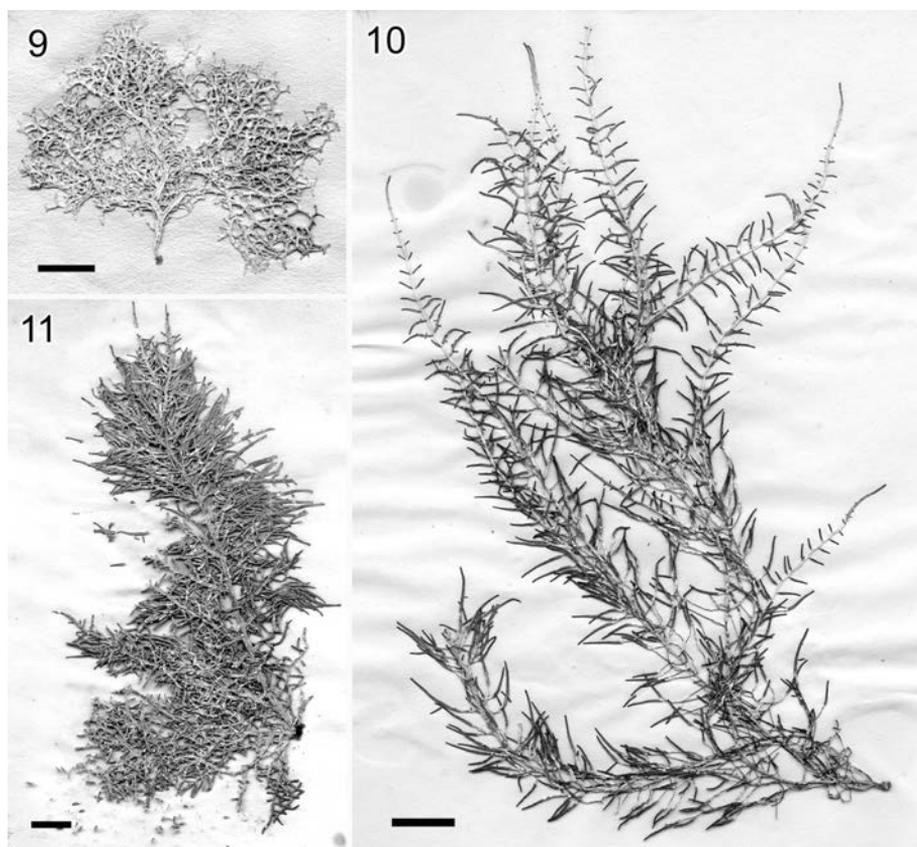
Remarks — From the description and illustrations this species is almost certainly synonymous with *L. ceranoides* Lamouroux, but unfortunately no material is available in MIN to confirm that placement. As mentioned above under *L. leprosa*, *L. ceranoides* is common at MÇlaekahana, just north of LÇ'ie Point, one of the collection localities cited by Butters.

Liagora tildeniae var. *lubrica* Butters, 1911: 172, pl. XXIV, fig. 13.
= *L. ceranoides* Lamouroux, *vide* Abbott, 1990a: 119.

Type locality and specimen — Kaua'i, 23 June 1902, 18-41 fathoms. S. For. Co. R. (U.S. Fish Com. 4023B).

Remarks — Butters' illustration (1911, pl. 24: fig. 13) shows a very broad medullary filament, suggestive of *Ganonema* (see Huisman & Kraft, 1994; Huisman, 2002; Huisman *et al.*, in press), but in that genus cortical filaments are generally distally unbranched, unlike the dichotomously divided filaments shown by Butters (1911, pl. XXIV, fig. 13). A liquid preserved specimen with this number (but labeled "*Liagora pseudo-paniculata*") is in the MIN collection, but it is in a very poor state and not at all informative. The specimen was apparently sterile, and its identity cannot be ascertained.

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Figs 9-11. *Liagora ceranoides* Lamouroux, *L. albicans* Lamouroux, and *Ganonema papenfussii* (Abbott) Huisman, Abbott et Sherwood. Fig. 9. Specimen of *Liagora ceranoides*, recorded by Butters as *L. leprosa* (MIN 4044). Fig. 10. Lectotype specimen of *Liagora maxima* Butters [= *L. albicans*] (MIN 4039). Fig. 11. Specimen of *Ganonema papenfussii*, recorded by Butters as *Liagora paniculata* (MIN 4036). Scales: Figs 9, 11 = 1 cm; Fig. 10 = 2 cm.

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