

***Ganonema farinosum* and *Ganonema dendroideum*
comb. nov. (Liagoraceae, Rhodophyta)
from Puerto Rico, Caribbean Sea¹**

David L. BALLANTINE* & Nilda E. APONTE

Department of Marine Sciences, P.O. Box 9013,
University of Puerto Rico. Mayagüez, Puerto Rico 00681

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Abstract — A detailed morphological account of *Ganonema farinosum* (J.V. Lamouroux) K.C. Fan et Yung C. Wang is presented. Calcification in this non-lubricous species consists of a cylinder surrounding the medulla and encompassing the inner cortical filaments. Carpogonial branches are unambiguously accessory being produced laterally from a median position on supporting cells. Specimens of *Liagora dendroidea* (P. et H. Crouan in Mazé et Schramm) I.A. Abbott were also examined and these conformed to *Ganonema*. Transfer to that genus is made.

Caribbean / *Ganonema* / *Liagora* / Liagoraceae / Nemaliales / Puerto Rico / Rhodophyta / western Atlantic

Résumé — *Ganonema farinosum* et *Ganonema dendroideum* comb. nov. (Liagoraceae, Rhodophyta) de Porto Rico, mer des Caraïbes. Un exposé détaillé de la morphologie de *Ganonema farinosum* (J.V. Lamouroux) K.C. Fan et Yung C. Wang est présenté. Chez cette espèce non-muqueuse, la calcification consiste en un cylindre entourant la moelle et renfermant les filaments corticaux internes. Les rameaux carpogoniaux sont, sans ambiguïté, accessoires, puisqu'ils sont produits latéralement et en position médiane à partir de cellules supports. Des spécimens de *Liagora dendroidea* (P. et H. Crouan in Mazé et Schramm) I.A. Abbott ont aussi été examinés et ils présentent les caractéristiques du genre *Ganonema*. Leur transfert dans ce genre a donc été effectué. (Traduit par la Rédaction)

Atlantique ouest / Caraïbes / *Ganonema* / *Liagora* / Liagoraceae / Nemaliales / Porto Rico / Rhodophyta

INTRODUCTION

In the tropical western Atlantic, the family Liagoraceae contains nine genera (Wynne, 1998; Wynne & Huisman, 1998): *Ganonema* K.C. Fan et Yung C. Wang, *Helminthocladia* J. Agardh, *Liagora* J.V. Lamouroux, *Liagoropsis* Yamada,

1. Dedicated to M.-T. L'Hardy-Halos, on the occasion of her retirement.

* Correspondence and reprints : d_ballantine@rumac.uprm.edu

Trichogloea Kützing, *Helminthora* J. Agardh, *Nemalion* Duby, *Trichogloeopsis* I.A. Abbott & Doty, and *Yamadaella* I.A. Abbott. *Ganonema*, *Helminthocladia*, *Liagora*, *Liagoropsis*, and *Trichogloea* are all known from the island of Puerto Rico (Ballantine & Aponte, 1997). These genera are segregated in part by the nature and position of the carpogonial branch, details of gonimoblast initiation, presence of sterile filaments from carpogonial branch cells or from adjacent cells, formation of a fusion cell, compactness of the gonimoblast, arrangement of spermatangia, and calcification pattern (Kraft, 1989). Of these genera, the highly speciose *Liagora*, has been recognized as being too broadly defined and this has led to the erection of the segregate genus *Ganonema* (Fan & Wang, 1974; Kraft, 1989; Huisman & Kraft, 1994). In light of Kraft's (1989) and Huisman & Kraft's (1994) suggestion that *Liagora* species of the section *Mucosae* may all belong to the genus *Ganonema*, we report herein a detailed examination of vegetative and reproductive morphology of Puerto Rican material of both *G. farinosum*, (J.V. Lamouroux) K.C. Fan et Yung C. Wang, the type species of *Ganonema*, and *Liagora dendroidea* (P. Crouan et H. Crouan in Mazé et Schramm) I.A. Abbott.

Ganonema farinosum is a broadly distributed species whose type locality is Suez, Egypt (Børgesen, 1942). It is also known from India (Desikachary *et al.*, 1990) and throughout the Caribbean as well as Brazil in the western Atlantic (Taylor, 1960, Joly, 1965; Norris & Bucher, 1982). In the eastern Atlantic it has been reported from the Canary Islands (Børgesen, 1927; Kvaternik *et al.*, 1996) and the west African coast (Lawson & John, 1982). In the Pacific Ocean *G. farinosum* has been reported from Hawaii (Abbott, 1945), Australia (Womersley, 1965; Cribb, 1983; Huisman, 2000), Japan (Fan & Wang, 1974; Yamada 1938) and China (Tseng, 1983). A number of *Liagora* species have been synonymized with *Ganonema farinosum* (Silva *et al.*, 1996). Huisman & Kraft (1994) and Afonso-Carrillo *et al.* (1998) have reviewed the taxonomic history of the genus *Ganonema*.

Liagora mucosa M. Howe was described based on material originally collected from the Bahamas (Howe, 1920). It is widely known from the Caribbean (Taylor, 1960) and has been reported from Puerto Rico (Almodóvar & Blomquist, 1961; Almodóvar, 1964a, 1964b), Santo Domingo (Almodóvar & Bonelly, 1977) and Belize (Littler & Littler, 1997). Abbott (1990) reported that *Liagora mucosa* was synonymous with an earlier-described species, *L. dendroidea*. That description was based on material from Guadeloupe in the eastern Caribbean (Mazé & Schramm, 1878).

Recent collections from a shallow back reef environment at La Parguera, Puerto Rico yielded a large number of specimens identified as *Ganonema farinosum*. Growing in the same habitat, specimens referable to *Liagora dendroidea* I.A. Abbott (= *L. mucosa*) were also collected.

MATERIALS AND METHODS

Ganonema farinosum and *Liagora dendroidea* were collected in the lee of Media Luna Reef (La Parguera, P.R.) at depths of 1.0 to 2.0 m. Specimens for morphological examination were preserved in 10% formalin/seawater. Microscope slides were prepared following decalcification in 10% HCl and staining with 1% aniline blue. Slides were then mounted in 60% Karo[®] syrup. Photomicrographs using Kodak Pan Technical black and white film were taken through an Olympus

BMAX light microscope. Herbarium abbreviations follow Holmgren *et al.* (1990) and authority designations are according to Brummitt & Powell (1992)². Voucher specimens are deposited in MSM.

Specimens examined

Ganonema farinosum: In MSM: *D.L. Ballantine 5304*, leeward Media Luna Reef, 1.0-1.5 m depth, La Parguera, Puerto Rico, 8 December 1998; *D.L.B. 5307, ibid.*, 15 December 1998; *D.L.B. 5326, ibid.*, 14 January 1999; *D.L.B. 5329, ibid.*, 5 February 1999; *D.L.B. 5330, ibid.*, 19 February 1999. In MICH: Anonymous, Red Sea (annotated by I.A. Abbott as *Liagora farinosa*, August 1980).

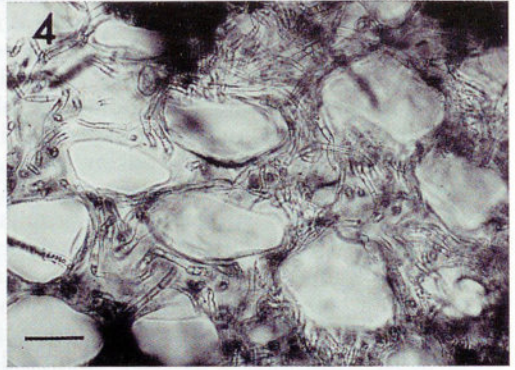
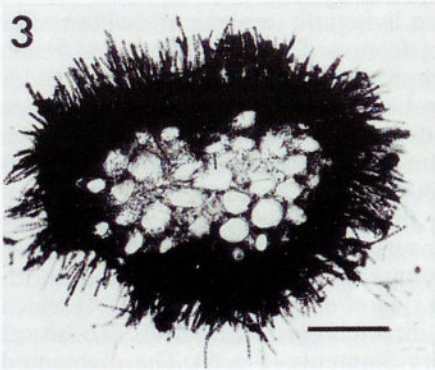
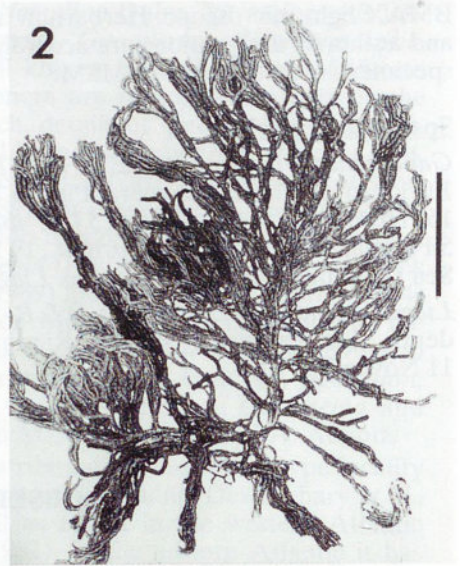
Liagora dendroidea: In MSM: *D.L.B. 5246*, leeward Media Luna Reef, 1.0-1.5 m depth, La Parguera, Puerto Rico, 5 November 1996; *D.L.B. 5294, ibid.*, 11 November 1998.

OBSERVATIONS

Ganonema farinosa occurred either solitarily (Fig. 1) or in dense stands, attached to coral rubble and limestone. When living, these algae are wine-red in color and are non-lubricous. Thalli are erect from a discoid holdfast and reach 30 cm in height. Branching is unevenly dichotomous (Fig. 2) with many older plants developing numerous short twig-like branch proliferations on the axes which obscure the dichotomous aspect. Axis diameters measure to 2.0 (- 2.8) mm in mature plant portions, decreasing to 1.0 mm near the apices. Axes are multiaxial with a compact medulla composed of 20-30 filaments. In section of older plant axes, rhizoids closely surround the medullary filaments (Figs 3, 4). Longitudinally oriented colorless medullary cells mostly measure to 200 μm but reach 300 μm in diameter and are to 1500 μm in length. Surrounding the medulla and incorporating the inner cells of the cortical fascicles is a ring of calcification (Figs 3, 4) which measures to 385 μm in thickness. Outwardly directed cortical fascicles are cut off unilaterally from the distal ends of medullary filaments (Fig. 5). The pigmented assimilatory filaments project beyond the calcification layer. Initially the basal cell of the cortical fascicles are little differentiated (Fig. 5); however, with distance from the apex, the basal cells become enlarged (Fig. 6). As they continue to mature, additional proximal cells of the cortical fascicles may enlarge as well (Fig. 7). The enlarged basal cells measure 35-45 \times 75-90 μm in diameter. Lower cells of the cortical fascicles cut off rhizoids, 3-7 μm in diameter, which are directed inwardly towards the medulla. The rhizoids only very rarely produce adventitious cortical initials and these never support carpogonial branches. Cells of the assimilatory filaments are cylindrical, measuring an average of 14 μm in diameter, and are irregularly alternately branched.

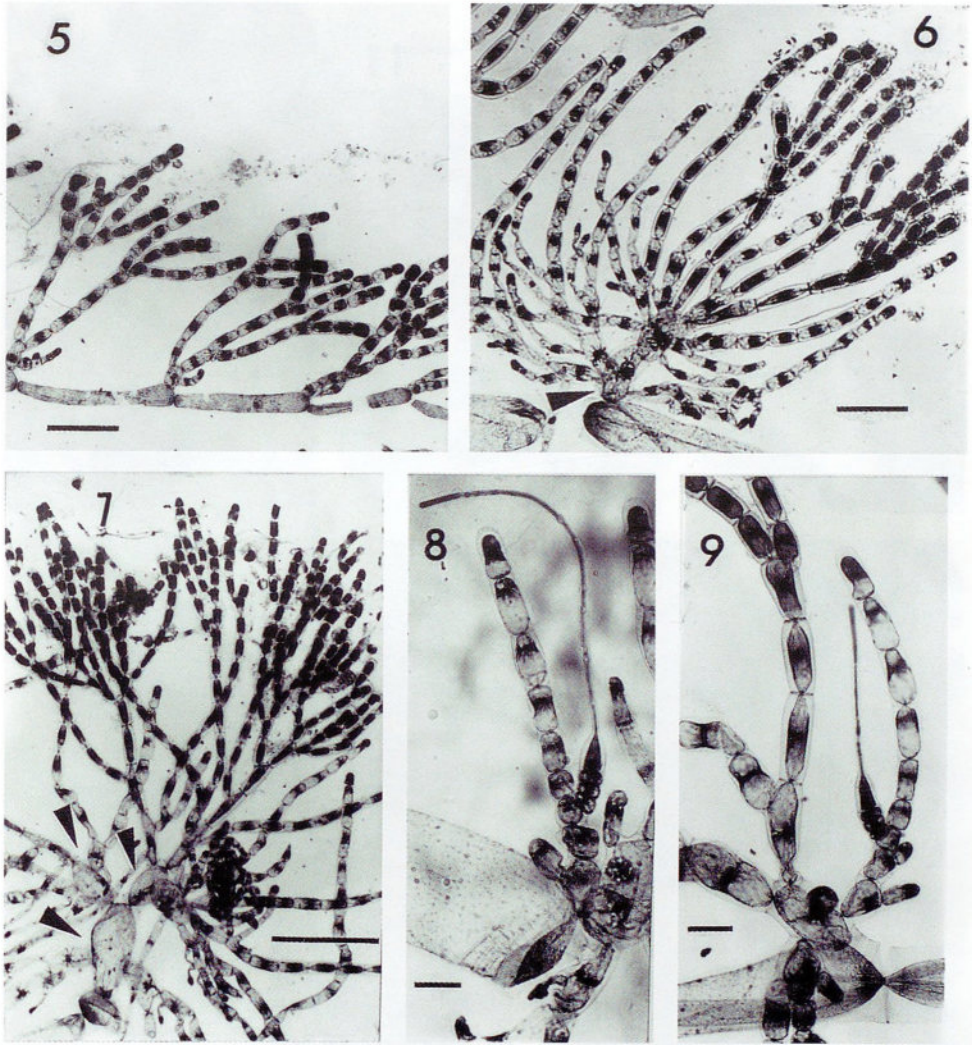
Plants are dioecious. Carpogonial branches are almost always four cells in length (Figs 8-10) although three- and five-celled carpogonial branches were rarely observed. They are borne laterally from a median position on one of the proximal cells of the assimilatory filaments. The carpogonial branch cells are gen-

2. Authors were spelled in full by the Editor.



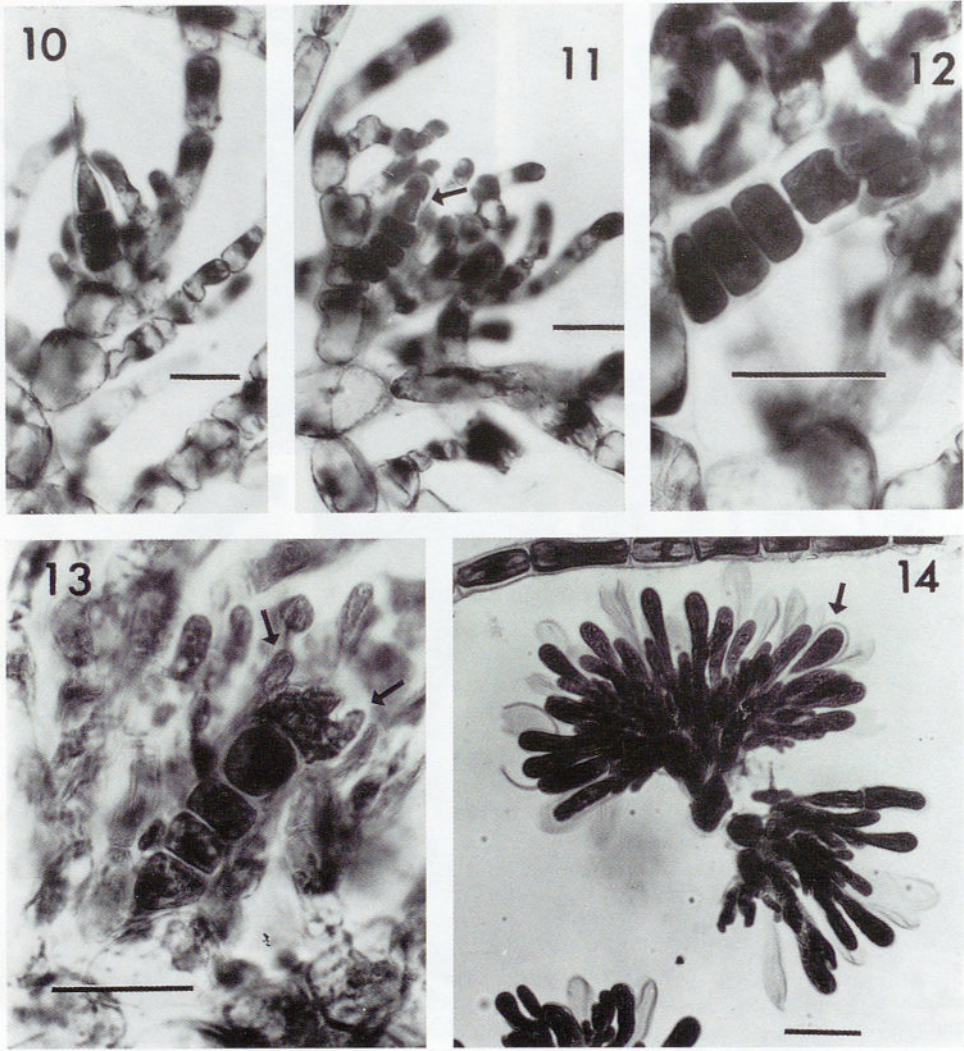
Figs 1-4. *Ganonema farinosum*. Fig. 1. Underwater photograph of living *Ganonema farinosum* growing at Media Luna Reef, La Parguera, Puerto Rico; depth = 1.0 m. Fig. 2. Dried herbarium specimen of Puerto Rican *Ganonema farinosum*. Scale bar = 5 cm. Figs 3,4. Transverse section of non-decalcified axis. The photographically opaque region is the calcification layer. Fig. 3. Section showing compact medulla and calcified cylinder surrounding medulla with assimilatory filaments projecting beyond the calcification. Scale bar = 500 μm . Fig. 4. Section showing dense rhizoids between medullary filaments. Scale bar = 100 μm .

erally rectangular in shape and are clearly differentiated from normal vegetative cells. Commonly, consecutive cortical cells bear carpogonial branches; more rarely, up to two carpogonial branches may be formed from the same supporting cell. All of the carpogonial branch cells are modified, i.e. they differ from vegetative cells of the cortical filaments, and prior to fertilization, none of the carpogonial branch cells take up the aniline blue stain. The carpogonial branches are normally slightly curved with trichogynes of the carpogonia extending up to 450 μm in length. Following presumed fertilization, the supporting cell may cut off one or more



Figs 5-9. *Ganonema farinosum*. Figs 5-7. Cortical fascicles. Scale bars = 100 μ m. Fig. 5. Apex of medullary filament with three cortical fascicles. Note that the basal cell of the fascicles are little-differentiated (arrow heads). Fig. 6. Mature cortical fascicle with single enlarged basal cell (arrow head). Fig. 7. Mature cortical fascicle with three enlarged basal cells (arrow heads). Figs 8-9. Carpoogonial branches. Scale bars = 25 μ m. Fig. 8. Four-celled carpoogonial branch showing lateral insertion from median position on the supporting cell. Fig. 9. Four-celled carpoogonial branch with involucrel filament initials being cut off from cells proximal to the supporting cell.

involucrel filaments. These filaments may be cut off from the hypogenous cell, the suprahypogenous cell and the cell proximal to the supporting cell as well (Figs 9, 10). Cells of the involucrel filaments also give rise to short laterals which may surround the carpoogonial branch. The degree of involucrel development is variable. The first division of the fertilized carpoogonium is transverse (Fig. 11) after which



Figs 10-14. *Ganonema farinosum*. Fig. 10. Four-celled carpogonial branch with involucral filaments produced both from cells proximal to the supporting cell and from the supra hypogenous cell. Figs 11-12. Early post fertilization divisions. Scale bars = 25 μ m. Fig. 11. First transverse division of the fertilized carpogonium (arrow). Involucral filaments are out of focus. Fig. 12. Second post fertilization division. The distal division product of the first division here divides longitudinally. Fig. 13. Early post fertilization, gonimoblast initials (arrows). Scale bar = 25 μ m. Fig. 14. Cystocarp extruded by cover slip pressure. Note development of a new carpospore within the old sporangial wall (arrow). Scale bar = 25 μ m.

the distal cell divides at an oblique angle perpendicular to the plane of the previous division (Fig. 12). There is no fusion of the carpogonial branch cells following fertilization. Subsequent divisions of the distal cell and its daughter cell give rise to several gonimoblast initials (Fig. 13) which develop outwardly. Lower assimila-



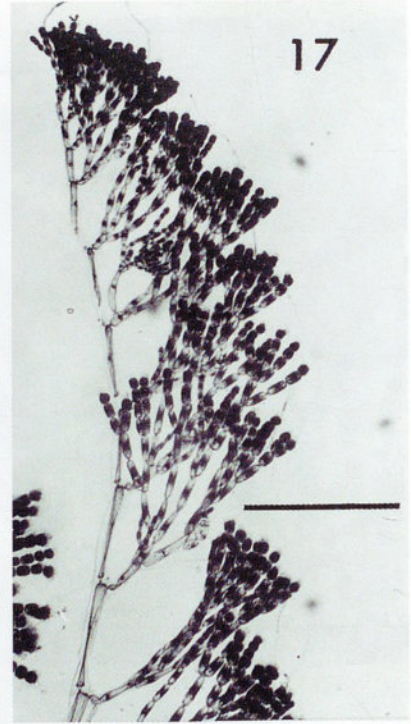
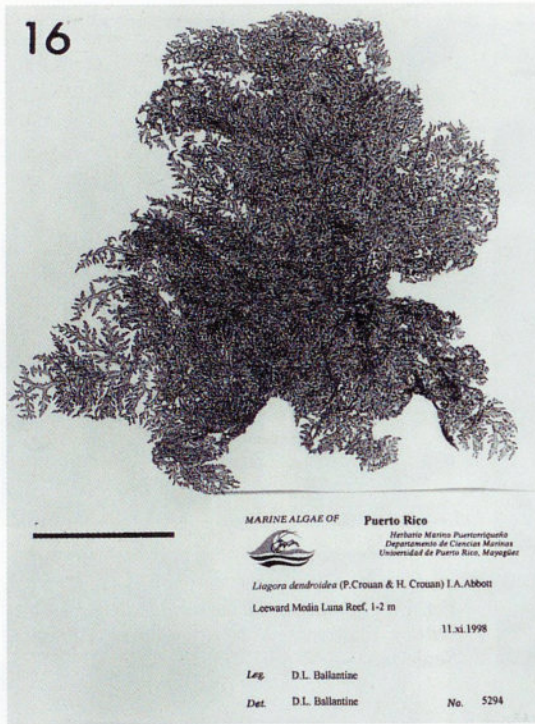
Fig. 15. *Ganonema farinosum*. Cortical assimilatory filaments with apical spermatangia. Scale bar = 100 μm .

tory filaments of a cortical fascicle, which support developing carposporophytes, cut off numerous inwardly directed rhizoids. The mature carposporophyte is compact, hemispherical in shape and measures to 220 μm . The carposporangia are sausage-shaped (botuliform) and measure to 40 μm in length. Carpospores may regenerate within the sporangial wall of released carpospores (Fig. 14). Gonimorhizoids were never observed.

Spermatangia branch initials are cut off from the ultimate three or four distal cells of the cortical filaments. Initials are two (-three) cells in length and may have single-celled branches. The branch cells cut off spermatangial mother cells which cut off three to four oval-shaped spermatangia, which measure 2 (- 2.5) μm \times 3.5 (- 4) μm . The entire spermatangial masses appear as dense heads (Fig. 15) reaching 70 μm in diameter.

The genus *Ganonema* displays the following features: medullary filaments that are greater than 40 μm in diameter; subsodiametric differentiated basal cells of cortical fascicles; spermatangia arranged in dense heads at ends of cortical filaments; straight to slightly curved carpogonial branches borne on inner cortical supporting cells; occasional polycarpogonial condition; four-celled carpogonial branches; presence of sterile filaments produced by cells adjacent to the carpogonial branch; lack of a fusion cell; initial transverse division of the fertilized carpogonium; compact gonimoblast, and regeneration of carposporangia within old carposporangial cells walls (Kraft, 1989; Huisman & Kraft, 1994). Puerto Rican specimens of *Ganonema farinosum* conform in all respects to previous published accounts.

Ganonema farinosum, however, is unique from other members of the genus in several respects. Principal among these is the nature of its calcification. Kraft (1989) regarded the feature of possession of a calcified cylinder to be one of the most distinctive features of *Cylindraxxis*. This feature is otherwise shared only by the genera *Dotyphycus* and *Trichogloea* (Kraft, 1989). Calcification in all



Figs 16-19. *Ganonema dendroideum*. Fig. 16. Dried herbarium specimen of Puerto Rican *Ganonema dendroideum*. Scale bar = 5 cm. Fig. 17. Apex of medullary filament with unilaterally produced cortical fascicles. Scale bar = 250 μm . Fig. 18. Four-celled carpogonial branch. Scale bar = 25 μm . Fig. 19. Rhizoids wrapped around carpogonial branch. Scale bar = 25 μm .

other *Ganonema* species is absent or light. In the two Australian species, *Ganonema helminthaxis* Huisman et Kraft lacks calcification altogether (Huisman & Kraft, 1994) while *G. codii* (Womersley) Huisman et Kraft possesses light calcification (Huisman, personal communication). The degree of calcification is also reported as being light in *G. lubrica* Afonso-Carr., M. Sansón et J. Reyes (1998). *Ganonema farinosum* also differs from other members of the genus in lacking regular development of adventitious cortical filaments from rhizoids, although these do occur. *Ganonema farinosum* is also non-lubricous, while all other species are. Species of the Mucosae group of *Liagora* (Yamada, 1938), which Kraft (1989) and Huisman & Kraft (1994) have suggested belong in *Ganonema*, are lubricous as well. Finally Huisman & Kraft (1994, p. 83) indicated that the placement of the carpogonial branch in *Ganonema* occupies "positions of primary or subsidiary vegetative cortical laterals ...". Norris & Bucher (1982) depicted a carpogonial branch in *Liagora farinosa* (= *Ganonema farinosum*) that is laterally inserted in a median position similar to that reported herein for Puerto Rican *G. farinosum*. Kvaternik *et al.* (1996) however, in addition to laterally inserted carpogonial branches, illustrated one for *G. farinosum* in a terminal position. Kraft (1989) and Huisman & Kraft (1994) discussed the ambiguity concerning the term accessory vs non-accessory with respect to placement of carpogonial branch cells in Liagoraceae as it relates to homology of the structures. We would argue that the lateral median position of carpogonial origin in *Ganonema farinosum* differs from the position of vegetative laterals and is unambiguously accessory.

Without further discussion, Yamada (1938), erected the section Mucosae for *Liagora* with the following characters: terminal, subterminal or lateral carpogonial branches of three or more cells, comparatively large carpospores and cystocarps lacking involucre, antherida terminal on assimilatory filaments and being lubricous nature. At that time Yamada placed *L. mucosissima* Yamada and *L. formosana* Yamada into the section. Of the four sections of *Liagora* established by Yamada, the Caribbean species *Liagora dendroidea* fits into Section Mucosae. Puerto Rican *Liagora dendroidea* (Fig. 16) are up to 15 cm in height. Algae are lightly calcified throughout and highly lubricous. Cortical fascicles, cut off from the distal ends of axial cells, are issued unilaterally (Fig. 17). The cortical (assimilatory) filaments are moniliform and measure to 18 μm in diameter. Assimilatory cells are four to five times longer than broad proximally and become isodiametric distally. Basal cells of lateral fascicles are to 20 μm in diameter and are elongate, to five times longer than broad, in younger algal portions. In older plant portions they are swollen, to 50 μm in diameter, and are two to three times longer than broad. The basal cells of the cortical fascicles cut off three, rarely two, cortical branchlets which are directed outwards. They also give rise to downwardly coursing rhizoids which may cut off cortical laterals. Medullary cells are colorless and measure to 125 μm in diameter.

Carpogonial branches are normally cut off singularly, although, polycarpogonial branches are occasionally produced. In one instance a two-celled carpogonial branch was observed to be cut off from carpogonial branch cell two of another carpogonial branch. The carpogonial branches are most commonly laterally inserted towards the distal end of the supporting cell (Fig. 18) and are always located towards the base of the cortical fascicle. Following presumed fertilization, cortical branch cells immediately adjacent to the carpogonial branch cut off rhizoids which wrap around the carpogonial branch (Fig. 19). Carpogonial branch cells do not fuse and the first division of the fertilized carpogonium is transverse. The carposporophytes are compact, measuring to 200 μm in diameter, and carposporangia are ovate to pyriform in shape, measuring to 25 in width and to 37 μm in length.

In the field, *Liagora dendroidea* is virtually indistinguishable from *Trichogloeopsis pedicellata* (P. Crouan & H. Crouan in Mazé & Schramm) I.A. Abbott with which it grows sympatrically. Howe (1920) made a similar observation concerning the two species (as *Liagora pedicellata* and *L. mucosa*) in the Bahamas. Female specimens of the former species are readily differentiated on the basis of the elongate basal carpogonial branch cell and the possession of gonimorhizoids.

In transferring *Liagora mucosa* to *L. dendroidea*, Abbott (1990) indicated that she was unable to locate the type specimen; basing her conclusions on examination of material from the type locality as well as Howe's type of *L. mucosa*. Our specimens are in complete agreement with Howe's (1920) account with the exception that we have measured greater medullary cell diameters than did Howe. Examination of Puerto Rican material of *L. dendroidea* also indicates that most of Huisman & Kraft's (1994) criteria for their emendation of *Ganonema* are met. These include possession of cortical fascicles borne on differentiated basal cells (even though they are not isodiametric in *L. dendroidea*); medullary cells greater than 40 µm in diameter; straight or slightly curved carpogonial branches borne from the base of the cortical fascicles; occasional polycarpogonial condition; and lack of a fusion cell. Details of vegetative and reproductive morphology thus indicate that the alga should be referred to *Ganonema* and the combination is proposed here:

Ganonema dendroideum (P. Crouan et H. Crouan in Mazé et Schramm) comb. nov.

Basionym: *Helminthora dendroidea* P. Crouan et H. Crouan in Mazé et Schramm 1878: 178.

Synonym: *Liagora dendroidea* P. Crouan et H. Crouan in Mazé et Schramm.

Heterotypic synonym: *Liagora mucosa* M. Howe 1920, The Bahama Flora, pp. 556-557.

The assignment of *Liagora mucosa* to *Ganonema* provides support to Kraft's (1989) and Huisman & Kraft's (1994) speculation that *Liagora* species of the section *Mucosae* are all probably referable to *Ganonema*. We await transfer of those species pending their examination. As more detailed morphological and reproductive information becomes available for further Liagoraceae species, it is likely that further generic boundaries will require change. The Liagoraceae represents a fertile area for molecular systematics in the future.

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