Cryptogamie, Algol., 2002, 23 (3): 237-249

A re-assessment of the genus *Izziella* Doty (Liagoraceae, Rhodophyta)[1]

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(Received 21 January 2002, accepted 18 June 2002)

Abstract – The genus *Izziella* Doty is reassessed based on an examination of a specimen of *Liagora orientalis* J. Agardh (the species into which *Izziella abbottiae* Doty has been subsumed) from the Socotra Archipelago, Yemen. This species shows marked differences from the type species of *Liagora* [*L. viscida* (Forsskål) C. Agardh], *Ganonema* [*G. farinosum* (Lamouroux) Fan et Wang], and *Trichogloea* [*T. requienii* (Montagne) Kützing] and we therefore propose that *Izziella* be restored as an independent genus. It is our contention that *Liagora*, as presently constituted, displays considerable variation in reproductive morphology and should probably be divided into several smaller genera.

Arabian Sea / *Ganonema* / Indian Ocean / *Izziella* / *Liagora* / Liagoraceae / marine red algae / Nemaliales / Rhodophyta

Résumé – Une redéfinition du genre *Izziella* Doty (Liagoraceae, Rhodophyta). Le genre *Izziella* Doty est redéfini sur la base de l'examen d'un spécimen de *Liagora orientalis* J. Agardh (espèce dans laquelle *Izziella abbottiae* a été incluse) provenant de l'Archipel Socotra, Yémen. Cette espèce montre des différences marquées avec l'espèce type des genres *Liagora* [*L. viscida* (Forsskål) C. Agardh], *Ganonema* [*G. farinosum* (Lamouroux) Fan et Wang], et *Trichogloea* [*T. requienii* (Montagne) Kützing] et nous proposons donc que *Izziella* redevienne un genre indépendant. Nous pensons que le genre *Liagora*, tel qu'il est actuellement constitué présente une variation considérable dans la morphologie de la reproduction et qu'il devrait probablement être divisé en plusieurs genres plus petits. (Traduit par la Rédaction)

algues rouges marines / *Ganonema* / *Izziella* / *Liagora* / Liagoraceae / Mer arabique / Nemaliales / océan Indien / Rhodophyta

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

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INTRODUCTION

The genus *Izziella*, with the single species *I. abbottiae*, was described by Doty in 1978 for specimens collected from Oahu, Hawaiian Islands. The genus was thought to be closely related to *Liagora* but differing primarily in the cluster of sterile filaments radiating from the infra-supporting cell proximal to the developing gonimoblast. Doty (1978) gave a detailed description of the post-fertilization events in the new genus, which he felt were clearly unlike those of *Liagora viscida* (Forsskål) C. Agardh, the type of the genus *Liagora*. Subsequent to the description of *Izziella*, the genus was subsumed into *Liagora* (Abbott, 1990), who regarded its type species as synonymous with *L. orientalis* J. Agardh. *Liagora orientalis*, originally described from Sri Lanka, is a widespread species that has been reported from numerous localities in the tropical Indian and Pacific Oceans and the Caribbean Sea (Abbott, 1990).

Several authors have recently remarked on the variety of morphology and cystocarp types presently included in *Liagora* (Kraft, 1989; Huisman & Kraft, 1994; Huisman, 2002), suggesting that the differences are too great to be accommodated within a single genus. As a result, Huisman & Kraft (1994) resurrected the previously rejected (Abbott, 1984) *Ganonema* for *Ganonema farinosum* (Lamouroux) Fan et Wang, and subsequent authors have made further combinations in the genus (Huisman, 2002).

The present paper re-assesses the genus *Izziella* (= *Liagora orientalis*) in light of these suggestions, concluding that the genus is worthy of recognition in a taxonomic scheme in which *Liagora* is more narrowly defined. The eventual further subdivision of the latter genus is also foreshadowed. This study is based primarily on a collection made by the second author from the Socotra Archipelago, Yemen, in addition to type and authentic specimens of *Izziella abbottiae* from Oahu, Hawaiian Islands.

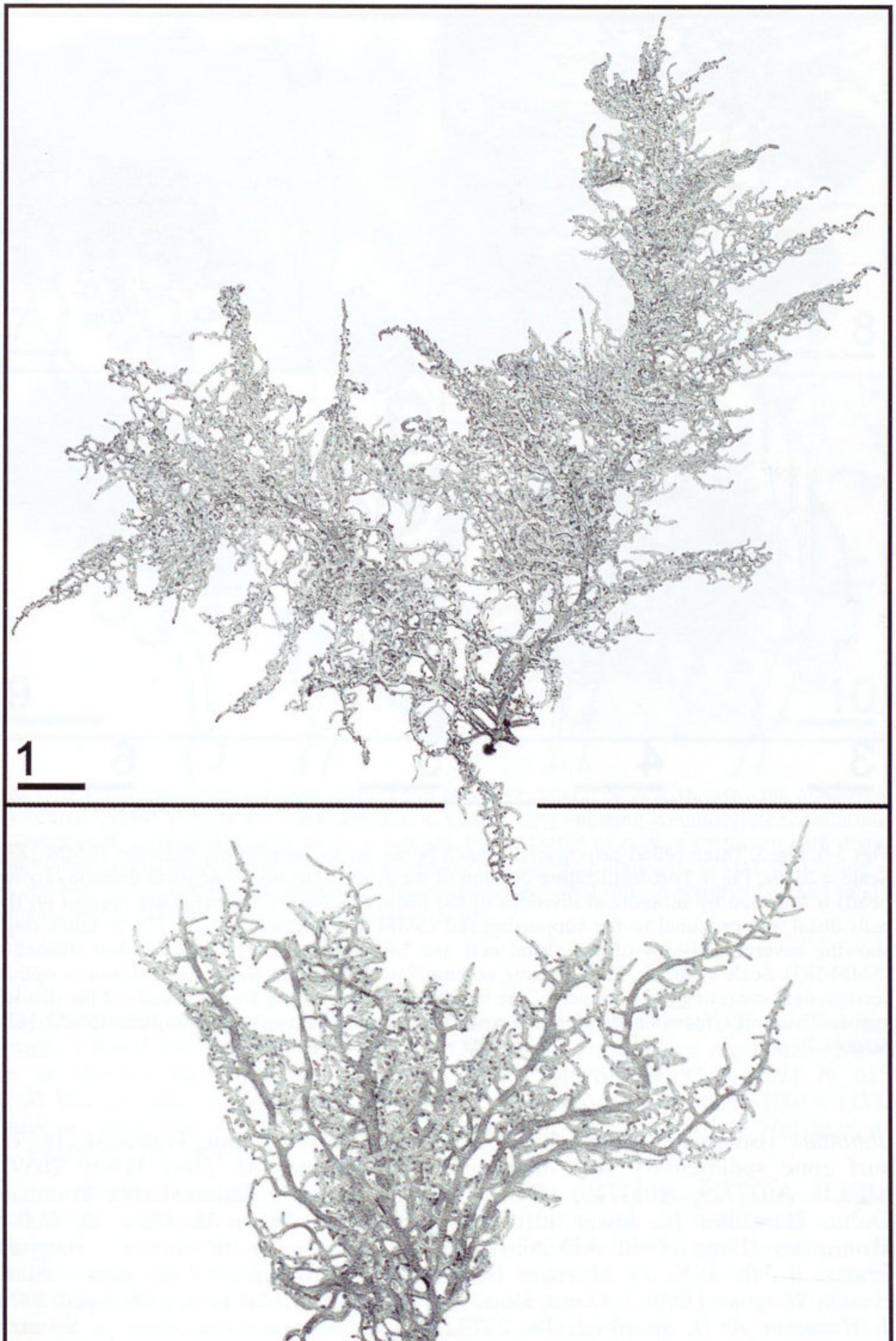
MATERIALS AND METHODS

Specimens were collected while snorkeling and preserved in approximately 5% formalin/seawater. Portions of plants for microscopical examination were decalcified in 1N HCl under a fume hood, washed in seawater, stained in 1% aniline blue, washed again in seawater, then mounted in a 50% Karo® (CPC International) corn syrup solution and macerated or lightly squashed to separate the filaments. Herbarium specimens and slide preparations are held in GENT (Ghent University Herbariumor the Botany Departement, University of Hawaii at Manoa).

OBSERVATIONS

Specimens examined. (1) *Liagora orientalis* – East Coast of Samha Island, Socotra Archipelago, Yemen (ALG-19: 12° 09.72 N, 35° 05.08 E), subtidal at 1.5 m depth, 7 April 2000, *T. Schils* (SMM 183) (Fig. 1). (2). *Izziella*

Figs 1, 2. Fig. 1. Specimen of *Izziella orientalis* (J. Agardh) Huisman *et* Schils, comb. nov. from Yemen (SMM 183). Scale = 2 cm. Fig. 2. Authentic specimen of *Izziella abbottiae* (= *I. orientalis*) from Oahu, Hawaiian Is. (AD A26006). Scale = 2 cm.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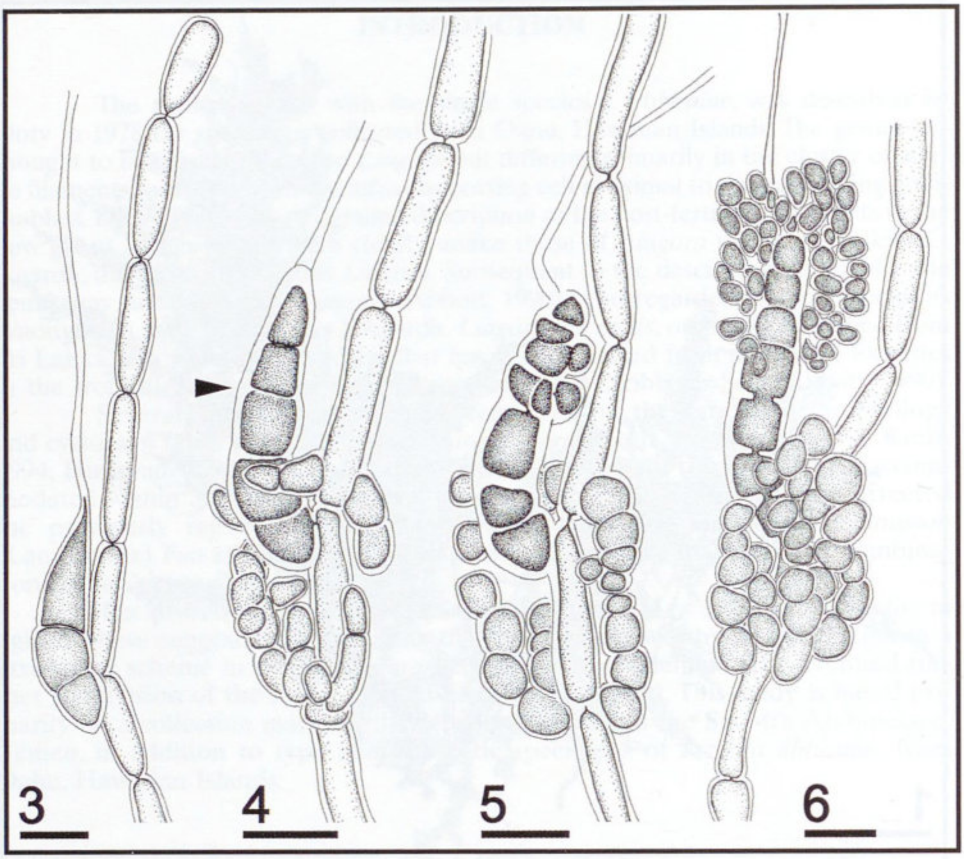
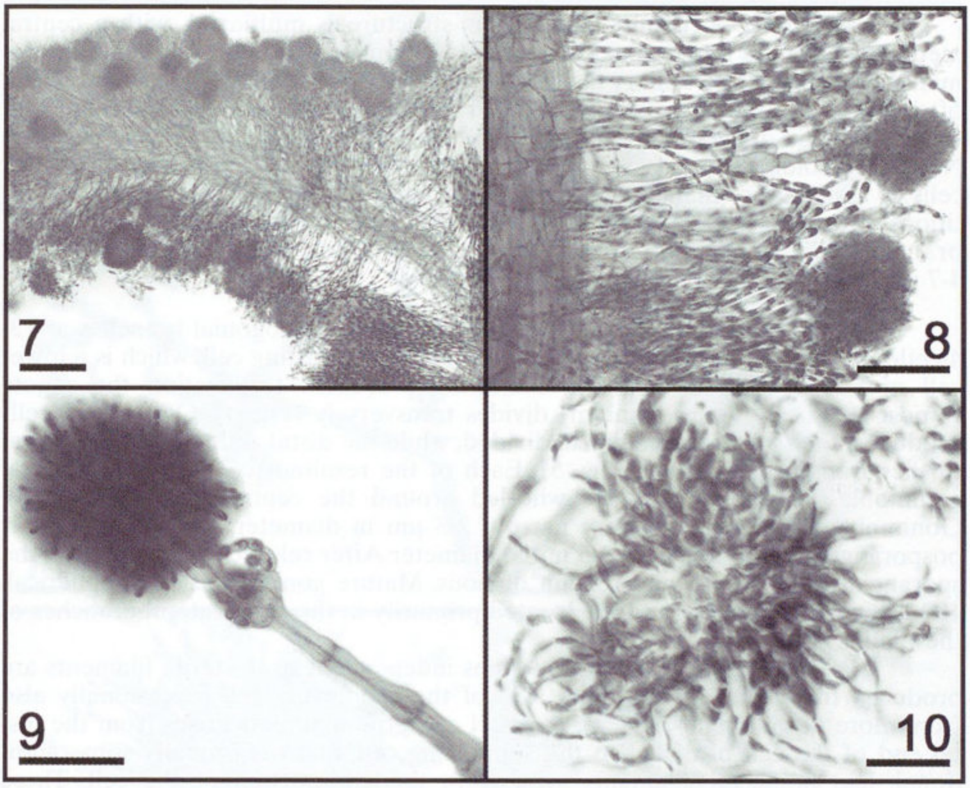


Figs 3-6. Fig. 3. Three-celled carpogonial branch borne on an assimilatory filament. (SMM 183). Scale = 20 µm. Fig. 4. Post-fertilization division of the zygote. The first transverse division (arrowhead) is followed by subsequent divisions of the distal cell. Sterile filaments are present on the cells distal and proximal to the supporting cell (SMM 183). Scale = 20 µm. Fig. 5. Later stage showing several divisions of the distal cell and initiation of lateral gonimoblast filaments. (SMM 183). Scale = 20 µm. Fig. 6. Young gonimoblast. The sporangial mass is shown in optical section, demonstrating the presence of the longitudinal core arising from the cells of the divided zygote. The sterile filaments are forming a separate cluster below the gonimoblast (SMM 183). Scale = 20 µm.

abbottiae (isotypes) – Kahanahaiki, Waianae District, Oahu, Hawaiian Is., on surf zone sedimentary rock bench, 23 March 1969, *M. Doty* (Doty 20591; MELU A037729, A037730). (3) *Izziella abbottiae* – Kahanahaiki, Waianae, Oahu, Hawaiian Is., lower littoral, 10 February 1962, *M. Doty & H.B.S. Womersley* (Doty 19630; AD A26006) (Fig. 2). (4) *Liagora viscida* – Banyuls, France, 7 July 1937, *G. Mazoyer* (AD A24190). (5). *Liagora perennis* – Maili Beach, Waianae District, Oahu, Hawaiian Is., on intertidal bench, 26 April 2002, *J. Huisman & D. Spafford* (IA 28727). (6) *Ganonema farinosum* – Swanzy, Oahu, Hawaiian Is., 12 April 2002, *J. Huisman & D. Spafford* (IA 28712). (7) *Ganonema farinosum* – Hanauma Bay, Oahu, Hawaiian Is. (IA 13871). (8)



Figs 7-10. Fig. 7. Decalcified squash preparation of a short lateral branch, showing the numerous cystocarps. (SMM 183). Scale = 200 µm. Fig. 8. Closer view, showing gonimoblasts terminating elongate stalk cells. (SMM 183). Scale = 100 µm. Fig. 9. Detail of mature cystocarp with distal gonimoblast mass, small cluster of sterile filaments, and elongate stalk cell. (SMM 183). Scale = 50 µm. Fig. 10 *Liagora viscida*. Mature cystocarp with somewhat diffuse gonimoblast and intermingled sterile filaments. (AD 24190). Scale = 20 µm.

Liagora orientalis – Nanakuli, Oahu, Hawaiian Is., on intertidal limestone bench, 5 April 1985, *M. Cannon* (IA 17183). (9, 10) *Trichogloea requienii* – SSW tip of Rocher du Diamant (Diamond Rock), Martinique (14° 26.94 N, 61° 02.41 W), 14 June 1995 (Littler 30916). No data recorded (Littler 42001). (11). *Liagora ceranoides* – Kaaawa, Oahu, Hawaiian Is., 12 April 2002, *J. Huisman & D. Spafford* (IA 28703).

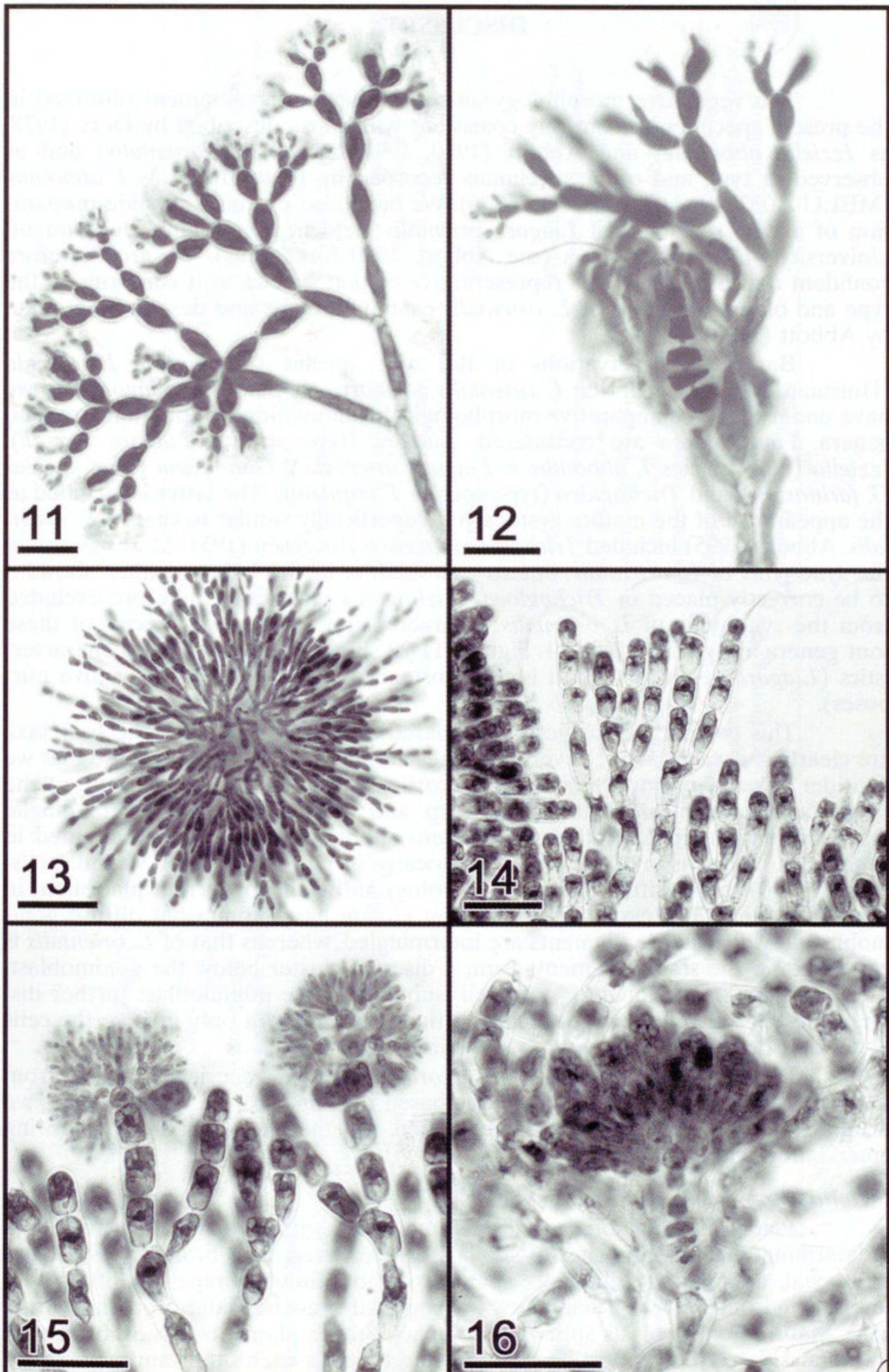
Habit. The Yemen plant (Fig. 1) is 22 cm in height, greyish/light green (when dried), mucilaginous, and arises from a discoid holdfast 3 mm in diameter. Percurrent primary axes bear indeterminate lateral branches of similar form, both in turn bearing a further order of numerous short lateral branches. Primary axes and major lateral branches are 1-2.5 mm in diameter, broader at the base and tapering gradually towards the apex. Secondary and short lateral branches are 0.5-1 mm in diameter Calcification is moderate and farinose.

Vegetative Structure. The thallus structure is multiaxial, with a central medulla of hyaline longitudinal filaments 15-50 μm in diameter. Assimilatory filaments are borne on medullary filaments and are sparsely dichotomously branched, often with lengthy unbranched sections. The filaments are 450-600 μm long, with cells 7-16 μm in diameter, lower cells cylindrical, upper cells ellipsoidal or obovoid. Narrow rhizoidal filaments, 6-10 μm in diameter, commonly arise from the lower cells of assimilatory filaments and course through the medulla, producing adventitious secondary assimilatory filaments that are generally simple or rarely branched. Cells of assimilatory filaments have a prominent central pyrenoid, 4-7 μm in diameter.

Carpogonial Branch and Carposporophyte. Carpogonial branches are 3-4-celled (Fig. 3) and arise on the distal half of the supporting cell, which is a lower cell of an assimilatory filament. Following presumed fertilization the zygote (= post-fertilization carpogonium) divides transversely (Fig. 4). Of the two cells produced, the proximal remains undivided, while the distal cell undergoes several further transverse divisions (Fig. 5). Each of the resultant cells produces lateral gonimoblast filaments that are whorled around the central cells (Figs 5, 6). Gonimoblast filaments are very narrow, 2-3 μm in diameter, with terminal carposporangia 5-7 μm long and 3-5 μm in diameter After release of carpospores, the sporangial walls persist and remain obvious. Mature gonimoblasts are spherical, 100-220 μm in diameter, and are located primarily in the short lateral branches of the thallus (Fig. 7).

Prior to fertilization, and perhaps independent to it, sterile filaments are produced from the cells to either side of the supporting cell (occasionally also from more distant cells) (Fig. 4). A whorl of sterile filaments arises from the distal end of the cell proximal to the supporting cell, and occasionally some additional, less branched, filaments arise from the mid-portion of the cell. These latter filaments are frequently reduced to only a single globose cell. The sterile filaments (from the cells distal and proximal to the supporting cell) grow towards each other and eventually envelop the supporting cell, producing a cluster of filaments that appear as a second cell mass below the gonimoblast (Figs 6, 9). After fertilization an extensive fusion cell is formed that encompasses the cells of the carpogonial branch, the supporting cell, and the majority of cells of the assimilatory filament subtending the supporting cell (Fig. 9). This fusion cell increases in length and girth and becomes hyaline, eventually appearing as a 'stalk' bearing the gonimoblast (Figs 8, 9). The fused cells of the carpogonial branch can be seen as a core within the gonimoblast. The lengthening stalk raises the gonimoblast to the level of the outer margin of the assimilatory filaments.

Figs 11-16. Figs 11-13. *Liagora perennis* Abbott (all IA 28727). Fig. 11. Cortical filaments and spermatangia, showing much-divided filaments and apical/subapical spermatangial branches. Scale = 20 μm. Fig. 12. Lateral carpogonial branch. Scale = 20 μm. Fig. 13. Mature cystocarp with somewhat diffuse gonimoblast and intermingled sterile filaments. Scale = 50 μm. Figs 14-16. *Ganonema farinosum* (Lamouroux) Fan *et* Wang. Fig. 14. Cortical filaments, showing undivided filaments of the outer cortex. (IA 28712). Scale = 100 μm. Fig. 15. Spermatangial branches in dense heads. (IA 28712). Scale = 100 μm. Fig. 16. Cystocarp with compact gonimoblast mass and sterile filaments forming an involucre. (IA 13871). Scale = 50 μm. ▶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DISCUSSION

The vegetative morphology and reproductive development observed in the present specimen are entirely consistent with those described by Doty (1978, as *Izziella abbottiae*) and Abbott (1990, 1999, as *Liagora orientalis*) and as observed in type and other specimens recorded by Doty (1978) as *I. abbottiae* (MELU A037729, A037730; AD 26006). We have also examined a slide preparation of a type specimen of *Liagora orientalis*, held in the Botany Department, University of Hawaii, Manoa (see Abbott, 1990 for details). We are therefore confident that our material is representative of that species as it conforms to the type and other specimens of *L. orientalis* examined by us and described in detail by Abbott (1990).

Based on observations of the type species of *Liagora*, *L. viscida* (Huisman, 2002), we feel that *L. orientalis* is incorrectly placed in *Liagora* and we have undertaken a comparative morphological examination of potentially related genera. Four genera are considered: *Liagora* (type species *Liagora viscida*), *Izziella* (type species *I. abbottiae* = *Liagora orientalis*), *Ganonema* (type species *G. farinosum*), and *Trichogloea* (type species *T. requienii*). The latter is included as the appearance of the mature cystocarp is superficially similar to that of *L. orientalis*. Abbott (1995) included *Trichogloea javensis* Børgesen (1951: 22-26) as one of the synonyms of *L. orientalis*, but an examination of the type specimen shows it to be correctly placed in *Trichogloea*. *Trichogloea javensis* is therefore excluded from the synonymy of *L. orientalis*. Characteristics of the type species of these four genera are given in Table 1. Figures 11-22 show examples of these characteristics (*Liagora perennis* Abbott is used instead of *L. viscida* for illustrative purposes).

This comparison suggests that, based on the type species, the four taxa are clearly separable. While several features are included in Table 1, those that we consider of primary importance are the cortical structure, the architecture of the carpogonial branch and mature cystocarp, and the derivation of spermatangia. Our observations indicate that *L. orientalis* should no longer be maintained in *Liagora*. A comparison of the mature cystocarps of *L. orientalis* (Fig. 9) and *L. viscida* (Fig. 10) shows differences in morphology sufficient to warrant placement in separate genera. The cystocarp of *Liagora viscida* has a somewhat diffuse gonimoblast in which sterile filaments are intermingled, whereas that of *L. orientalis* is compact and the sterile filaments form a discrete cluster below the gonimoblast. The presence of an elongate 'stalk cell' subtending the gonimoblast further distinguishes *L. orientalis*, as fusion cells in the genus *Liagora* only involve the cells of the carpogonial branch and are small in comparison.

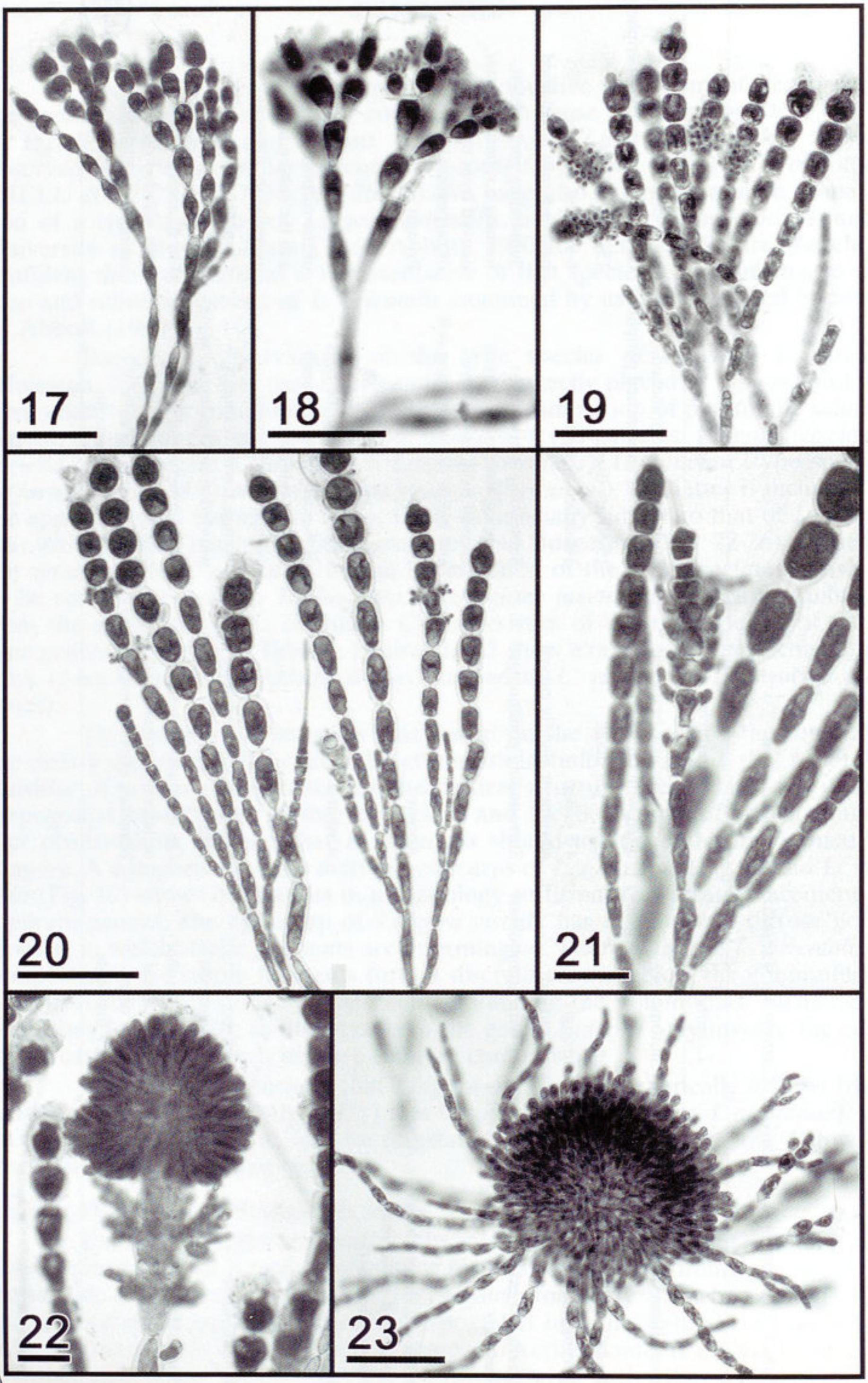
We therefore conclude that *Liagora orientalis* is generically distinct from *Liagora*. Since *Izziella* Doty (1978) was based on this taxon (as *I. abbottiae*), we propose that the genus should be reinstated. We therefore make the following emendation and combination:

Izziella Doty *emend*. Huisman *et* Schils

Plants mucilaginous, moderately calcified, with percurrent primary and indeterminate lateral branches of similar form, or irregularly branched. Structure multiaxial; assimilatory filaments sparsely dichotomously branched, often with unbranched outer cortical filaments. Carpogonial branches lateral on supporting cells. Mature gonimoblasts spherical, compact. Sterile filaments arising from cells to either side of the supporting cell, growing towards each other and enveloping

Tab. 1. Comparison of *Liagora, Ganonema, Izziella,* and *Trichogloea.*

	Liagora	*Ganonema*	*Izziella*	*Trichogloea*
Assimilatory filaments	Di/tri/polychotomously branched, mostly near periphery	Dichotomously branched, often with unbranched periphery	Dichotomously branched, often with unbranched periphery	Dichotomously branched, often with unbranched periphery
Medullary filaments	5-40 µm diam.	25-150 µm diam.	15-50 µm diam.	15-45 µm diam.
Carpogonial branch	3-6 celled, strongly to moderately curved.	4-5 celled, straight or slightly curved	3-4 celled, curved	6-9 celled, straight, basal 3-6 cells unmodified
Sterile (or involucral) filaments	Intermingling with gonimoblast filaments	Surrounding gonimoblast	Subtending gonimoblast, forming a separate cluster, derived from cells above and below the supporting cell	Subtending gonimoblast, forming a separate cluster, derived from mid-cells of carpogonial branch
Stalk cell (large elongate fusion cell subtending the gonimoblast)	Absent	Absent	Present	Present
Fusion cell	Present	Absent	Present, involving the cells of the carpogonial branch and the subtending assimilatory filament.	Present, involving the cells of the carpogonial branch and the subtending assimilatory filament.
Gonimoblast	Somewhat diffuse, with radiating filaments	Compact, with radiating filaments	Compact, with filaments whorled around a central spine	Compact, with radiating filaments
Spermatangia	On spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments	On terminal, subterminal or lateral spermatangial branches, often forming heads	On spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments	On spermatangial mother cells whorled on mid cells of assimilatory filaments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the supporting cell, eventually producing a cluster of filaments that appear as a second cell mass below the gonimoblast. Fusion cell formed encompassing the cells of the carpogonial branch, the supporting cell, and the majority of cells of the assimilatory filament subtending the supporting cell. Spermatangia borne on short spermatangial branches arising on apical or subapical cortical cells.

Izziella orientalis (J. Agardh) Huisman *et* Schils, comb. nov.

Basionym: *Liagora orientalis* J. Agardh. *Analecta algologica*, p. 99 (1896).

Lectotype: From Sri Lanka, *W. Ferguson* (LD 32252). n.v., *fide* Abbott, 1990: fig. 7.

Synonyms (*fide* Abbott, 1990; Abbott, 1995; Abbott, 1999; excluding *Trichogloea javensis* Børgesen):

Liagora formosana Yamada, *Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido Imperial University* 2: 32-33 (1938).

Liagora tanakai I.A. Abbott, *Bulletin of the Japanese Society of Phycology* 15: 33 (1967).

Liagora visakhapatnamensis Umamaheswara Rao, *Hydrobiologia* 33: 201 (1969).

Izziella abbottiae Doty, *Phycologia* 17: 34 (1978).

As a further consequence of our observations, we feel that *Liagora* should be restricted to species with much-divided cortical filaments, lateral carpogonial branches, cystocarps with somewhat diffuse gonimoblasts wherein the sterile filaments intermingle or loosely envelop the fertile filaments, and spermatangia borne on terminal or subterminal spermatangial branches. *Izziella*, in contrast, has cortical filaments that are often distally simple, compact gonimoblasts, and sterile filaments that form a separate cluster below the gonimoblast. This latter feature is superficially similar to that of *Trichogloea*, but the ontogeny of these structures is entirely different. Those of *Trichogloea* are derived from mid-cells of the elongate carpogonial branch, whereas the sterile filaments of *Izziella* arise from the cells to either side of the supporting cell.

Although the characteristics shown in Table 1 outline the differences between the four genera, consideration of other species of *Liagora* does demonstrate what could be regarded as a continuum of character states. Species such as *Liagora ceranoides* Lamouroux have close affinities with *Izziella*, as both display compact gonimoblasts (Fig. 22) and fusion cells. *Liagora ceranoides* differs from *Izziella*, however, in the production of an involucre that envelopes the gonimoblast (Huisman, 2002) and in lacking a large stalk cell. It is our contention that

◀ Figs 17-23. Figs 17, 18. *Izziella orientalis* (J. Agardh) Huisman *et* Schils. Fig. 17. Cortical filaments, showing sparsely branched filaments of the outer cortex. (IA 17183). Scale = 50 µm. Fig. 18. Spermatangial branches formed on apical/subapical cells. (IA 17183). Scale = 50 µm. Figs 19-22. *Trichogloea requienii* (Montagne) Kützing. Fig. 19. Cortical filaments with spermatangia borne in whorls on lower cells. (Littler 42001). Scale = 50 µm. Fig. 20. Straight, many-celled, carpogonial branch and cortical filaments, showing undivided filaments of the outer cortex. (Littler 30916). Scale = 50 µm. Fig. 21. Post-fertilization division of the carpogonium and production of sterile filaments from lower cells of the carpogonial branch. Scale = 20 µm. Fig. 22. Mature cystocarp formed at the end of the carpogonial filament, with sterile filaments borne on the lower cells of the carpogonial filament. (Littler 30916). Scale = 20 µm. Fig. 23. *Liagora ceranoides* Lamouroux. Showing compact gonimoblast and involucral filaments. (IA 28703). Scale = 50 µm.

Liagora, as presently constituted, should be subdivided into several smaller genera. One of these segregate genera would include species with compact gonimoblasts, such as *L. ceranoides*. The subdivision of *Liagora* was also suggested by Huisman & Kraft (1994) and Huisman & Wynne (1999), although no generic boundaries were indicated. Preliminary DNA sequence studies (Huisman, Saunders & Harper, unpublished, in prep.) indicate that *Liagora* is indeed polyphyletic and support its subdivision into more precisely defined units. Further work on a range of species, however, is required before any additional taxonomic and nomenclatural revisions can be made.

Acknowledgement. John Huisman acknowledges the financial support of the 'Australian Biological Resources Study' and the 'Western Australian Department of Commerce and Trade' while at Murdoch University, where Associate Professor Michael Borowitzka hosted his research. While at the University of Hawaii, Manoa, JH was supported by a grant from the David and Lucile Packard Foundation, and sincerely thanks Dr Isabella Abbott for her support. Dave Spafford is thanked for his able diving support. Tom Schils expresses his sincere thanks to the Senckenberg Research Institute, Germany (Michael Apel, Uwe Zajonz and Fareed Krupp), for the excellent field trip preparations to the Socotra Archipelago, and is indebted to the Fund for Scientific Research Flanders (Belgium) for a research assistant grant and a travel grant to Murdoch University (Western Australia). Gerry Kraft (University of Melbourne) is thanked for his numerous suggestions that greatly improved the manuscript, and for information regarding the isotype specimen of *Izziella abbottiae* housed in MELU. Professor Bryan Womersley and the State Herbarium of South Australia are thanked for the loan of authentic *Izziella abbottiae*.

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