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

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Abstract — The genus *Izziella* Doty is reassessed based on an examination of a specimen of *Liagora orientalis* J. A. gardh (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. A. gardh (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. A. gardh], *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. abbottiæ, 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 visciða (Forsskål) C. A gardh, 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. A gardh. 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 abbottiæ 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 Herbarium, Krijgslaan 281 – S8, 9000 Ghent, Belgium).

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. A gardh) Huisman et Schils, comb. nov. from Yemen (SMM 183). Scale = 2 cm. Fig. 2. Authentic specimen of Izziella abbottiæ (= I. orientalis) from Oahu, Hawaiian Is. (A D A 26006). Scale = 2 cm.
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 3-6. Fig. 3. Three-celled carpogonial branch borne on an assimilatory filament. (SM M 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 (SM M 183). Scale = 20 µm. Fig. 5. Later stage showing several divisions of the distal cell and initiation of lateral gonimoblast filaments. (SM M 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 (SM M 183). Scale = 20 µm.


**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.

**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. (A D 24190). Scale = 20 µm.
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.
Re-assessment of Izziella (Liagoraceae, Rhodophyta)
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 L. abbottiae (MELU A 037729, A 037730; 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. viscidia (Huisman, 2002), we feel that L. orientalis is incorrectly placed in L. orientalis and we have undertaken a comparative morphological examination of potentially related genera. Four genera are considered: Liagora (type species Liagora viscidia), 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. viscidia 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 L. orientalis. A comparison of the mature cystocarps of L. orientalis (Fig. 9) and L. viscidia (Fig. 10) shows differences in morphology sufficient to warrant placement in separate genera. The cystocarp of Liagora viscidia 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 L. orientalis is generically distinct from L. orientalis. Since I. abbottiae Doty (1978) was based on this taxon (as L. 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.

<table>
<thead>
<tr>
<th></th>
<th>Liagora</th>
<th>Ganonema</th>
<th>Izziella</th>
<th>Trichogloea</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Assimilatory filaments</strong></td>
<td>Di/tri/polychotomously branched, mostly near periphery</td>
<td>Dichotomously branched, often with unbranched periphery</td>
<td>Dichotomously branched, often with unbranched periphery</td>
<td>Dichotomously branched, often with unbranched periphery</td>
</tr>
<tr>
<td><strong>Medullary filaments</strong></td>
<td>5-40 µm diam.</td>
<td>25-150 µm diam.</td>
<td>15-50 µm diam.</td>
<td>15-45 µm diam.</td>
</tr>
<tr>
<td><strong>Carpogonial branch</strong></td>
<td>3-6 celled, strongly to moderately curved.</td>
<td>4-5 celled, straight or slightly curved</td>
<td>3-4 celled, curved</td>
<td>6-9 celled, straight, basal 3-6 cells unmodified</td>
</tr>
<tr>
<td><strong>Sterile (or involucral) filaments</strong></td>
<td>Intermingling with gonimoblast filaments</td>
<td>Surrounding gonimoblast forming a separate cluster, derived from cells above and below the supporting cell</td>
<td>Subtending gonimoblast, forming a separate cluster, derived from mid-cells of carpogonial branch</td>
<td></td>
</tr>
<tr>
<td><strong>Stalk cell (large elongate fusion cell subtending the gonimoblast)</strong></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td><strong>Fusion cell</strong></td>
<td>Present</td>
<td>Absent</td>
<td>Present, involving the cells of the carpogonial branch and the subtending assimilatory filament.</td>
<td>Present, involving the cells of the carpogonial branch and the subtending assimilatory filament.</td>
</tr>
<tr>
<td><strong>Gonimoblast</strong></td>
<td>Somewhat diffuse, with radiating filaments</td>
<td>Compact, with radiating filaments</td>
<td>Compact, with filaments whorled around a central spine</td>
<td>Compact, with radiating filaments</td>
</tr>
<tr>
<td><strong>Spermatangia</strong></td>
<td>On spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments</td>
<td>On terminal, subterminal or lateral spermatangial branches, often forming heads of assimilatory filaments</td>
<td>On spermatangial mother cells borne on terminal and subterminal cells of assimilatory filaments</td>
<td>On spermatangial mother cells whorled on mid cells of assimilatory filaments</td>
</tr>
</tbody>
</table>
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. A gardh) Huisman et Schils, comb. nov.

**Basionym:** Liagora orientalis J. A gardh. A necta algologica, p. 99 (1896).

**Lectotype:** From S r Lanka, W. Ferguson (L D 32252). n.v., fide A bbott, 1990: fig. 7.

**Synonyms** (fide A bbott, 1990; A bbott, 1995; A bbott, 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 
- Liagora visakhapatnamensis U mamaheswara R ao, Hydrobiologia 33: 201 

As a further consequence of our observations, we feel that Liagora 
should be restricted to species with much-divided cortical filaments, lateral car-
pogonial branches, cystocarps with somewhat diffuse gonimoblasts wherein the 
sterile filaments intermingle or loosely envelop, and spermatangia borne on ter-
mal or subterminal spermatangial branches. Izziella, in contrast, has cortical fil-
aments that are often distally simple, compact gonimoblasts, and sterile filaments 
that form a separate cluster below the gonimoblast. This latter feature is superfi-
cially 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 car-
pogonial 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 demon-
strate 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 in involucr that envelopes the gonimoblast 
(Huisman, 2002) and in lacking a large stalk cell. It is our contention that 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.

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