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Liagora tsengii sp. nov. (Liagoraceae, Nemaliales) from the Lesser Antilles, West Indies*

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*This paper is dedicated to Professor C. K. Tseng on the occasion of his 90th birthday
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Liagora tsengii sp. nov. (Liagoraceae, Rhodophyta) is described from St Kitts and Guadeloupe, Lesser Antilles, West Indies. Mature thalli are to 7–10 cm in height, pinkish grey, moderately to heavily calcified, mucilaginous, and dichotomously branched (often with numerous short proliferous lateral branches in older portions). Carpogonial branches are 4–5 celled and borne on the mid- or distal region of a mid-cortical supporting cell. Following presumed fertilization the zygote divides transversely and gonimoblast initials arise laterally from the distal daughter cell. A moderately diffuse gonimoblast is produced, although it does not intermingle with vegetative filaments. The lower gonimoblast cells and distal cells of the carpogonial branch coalesce and form a fusion cell. Post-fertilization sterile filaments arise from the basal cell of the carpogonial branch and occasionally from the supporting cell, and adjacent vegetative cells. Spermatangia are borne in clusters on spermatangial mother cells that arise from apical and subapical cells of assimilatory filaments. The new species differs from those previously included in the genus by its moderately diffuse gonimoblast and by the position of the post-fertilization sterile filaments. The former feature relates the new species to *Liagora indica* V. Krishn. *et* Sundararajan. *Liagora tsengii* differs from that species in the production of post-fertilization filaments from the carpogonial branch.

Introduction

The red algal genus *Liagora* J. V. Lamour. (1812) is widespread in tropical and, to a lesser extent, warm-temperate seas worldwide. Defining features of the genus include: a calcified thallus that is structurally multiaxial with a central core of longitudinal medullary filaments and anticlinal assimilatory filaments forming a loose cortex; a lateral, moderately to strongly curved, carpogonial branch; post-fertilization production of the gonimoblast directly from the zygote; and the production of sterile, post-fertilization filaments from vegetative cells in the vicinity of the carpogonial branch and supporting cell. Over 60 species are presently credited to the genus, many of which are poorly defined. Abbott (1945, 1970, 1990 a, 1990 b), Abbott and Yoshizaki (1982), Huisman and Kraft (1994), Kvaternik and Afonso-Carrillo (1995) and others have re-examined many of the recognised species and reduced a large number to synonymy. In the process the characteristic features of at least some of the accepted species have been more precisely defined. Nevertheless, there remains a significant number of poorly known species, and most herbarium collections include unidentified specimens.

The present account includes the description of a new species, *Liagora tsengii*, recently collected from shallow subtidal waters of the Lesser Antilles, Caribbean Sea.

Materials and Methods

Specimens were both dried as herbarium material and preserved in 5% Formalin/seawater. Materials for microscopic examination were later decalcified in a solution of dilute acetic acid. Slide material was stained in a mixture of 1 g aniline blue powder, 70 mL Karo®, 30 mL distilled water, and 5 mL acetic acid and slides have been deposited in MICH and MURU. Line-drawings were prepared using a camera lucida mounted on a Leitz microscope, while macro-photographs and photomicrographs were made using Kodak Technical Pan black and white film. Author abbreviations follow Brummitt and Powell (1992). Herbarium abbreviations follow Holmgren *et al.* (1990); MURU designates the Herbarium of Murdoch University.

Results

Liagora tsengii Huisman *et* Wynne sp. nov.

Diagnosis: *Thalli ad 10 cm alti; subrosacei-grisei, moderate – grave calcarei; dichotome ramosi, ad intervalla 3–7 mm, saepe ramis brevibus lateralibus. Axes teretes, 1.5–2.0 mm diam. prope basem, ad 0.1 mm diam. prope apices contracti. Fila medullosa 10–45 μm diam. Fila assimilantes 320–500 μm longa, di-trichotome ramosa; cellulae infernae cylindraceae, 6–7 μm*

diam., cellulae superae ovoideae, 10−16 mm diam.; cellulae apicales subsphaericae, 8−12 μm diam. Dioici. Rami carpogonales 4−5 cellulares, curvi leviter, laterales. Divisio post-fecundationem zygotae transversalis, cellula distalis initia lateralia gonimoblastorum producentes. Gonimoblastus moderate diffusus, 330−450 mm diam., filis ramosis 1−3 carposporangia terminaliter et lateraliter ferentibus. Carposporangia obovoidea-ovoidea, 10−15 × 15−25 μm. Conjunctio-cellula formata, cellulas gonimoblastas infernas et cellulas rami carpogonialis includens. Fila sterilia post-fecundationem ex cellula basale rami carpogoniales, cellula sustinenti et ejus cellulis propinquis, et cellulis filorum assimilantium propinquis, filis gonimoblastis intermixta sed debiliter effecta et involucrum non facientia. Cellula materna 2−3 spermatangia ferens in cellulis apicalibus et subapicalibus filorum assimilantium.

Thalli to 10 cm high, pinkish grey, moderately to heavily calcified, dichotomously branched every 3−7 mm, often with short lateral branches. Axes terete, 1.5−2.0 mm diam. near base, tapering to 0.1 mm diam. near apices. Medullary filaments 10−45 μm diam. Assimilatory filaments 320−500 μm long, di-trichotomously branched; lower cells cylindrical, 6−7 μm diam, upper cells ovoid, 10−16 μm diam., apical cells subspherical, 8−12 μm diam. Dioecious. Carpogonial branches 4−5 celled, slightly curved, lateral. Post-fertilization division of zygote transverse, the distal cell producing lateral gonimoblast initials. Gonimoblast moderately diffuse, 330−450 μm diam., with branched filaments bearing 1−3 carposporangia terminally and laterally. Carposporangia obovoid to ovoid, 10−15 × 15−25 μm. Fusion cell formed, incorporating lower gonimoblast cells and carpogonial branch cells. Post-fertilization sterile filaments from basal cell of carpogonial branch, supporting cell and its adjacent cells, and cells of nearby assimilatory filaments, intermingling with gonimoblast filaments but poorly developed and not forming an involucre. Spermatangia 2−3 per mother cell, on apical and subapical cells of assimilatory filaments.

Etymology: The specific epithet honours Professor C. K. Tseng of the Institute of Oceanology, Academia Sinica, Qingdao, China, for his numerous contributions to phycology, including his study of Chinese species of *Liagora* (Tseng 1941).

Holotype and type locality: Timothy Beach, St Kitts, Lesser Antilles (M. Edlund and M. J. Wynne 10663, 27.xi.1995; MICH) (Fig. 1).

Specimens examined: Timothy Beach, St Kitts, Lesser Antilles (M. Edlund and M. J. Wynne 10663, 10665, 10679, 27.xi.1995; MICH). South Friar's Bay, St Kitts, Lesser Antilles (M. Edlund and M. J. Wynne 10701, 10742, 10743, 10746, 10757, 10759, 23.xi.1995; MICH). Petit Havre, between Gosier and Ste.-Anne, Grande-Terre, Guadeloupe. In drift (M. J. Wynne 8173, 25.ii.1987; MICH)

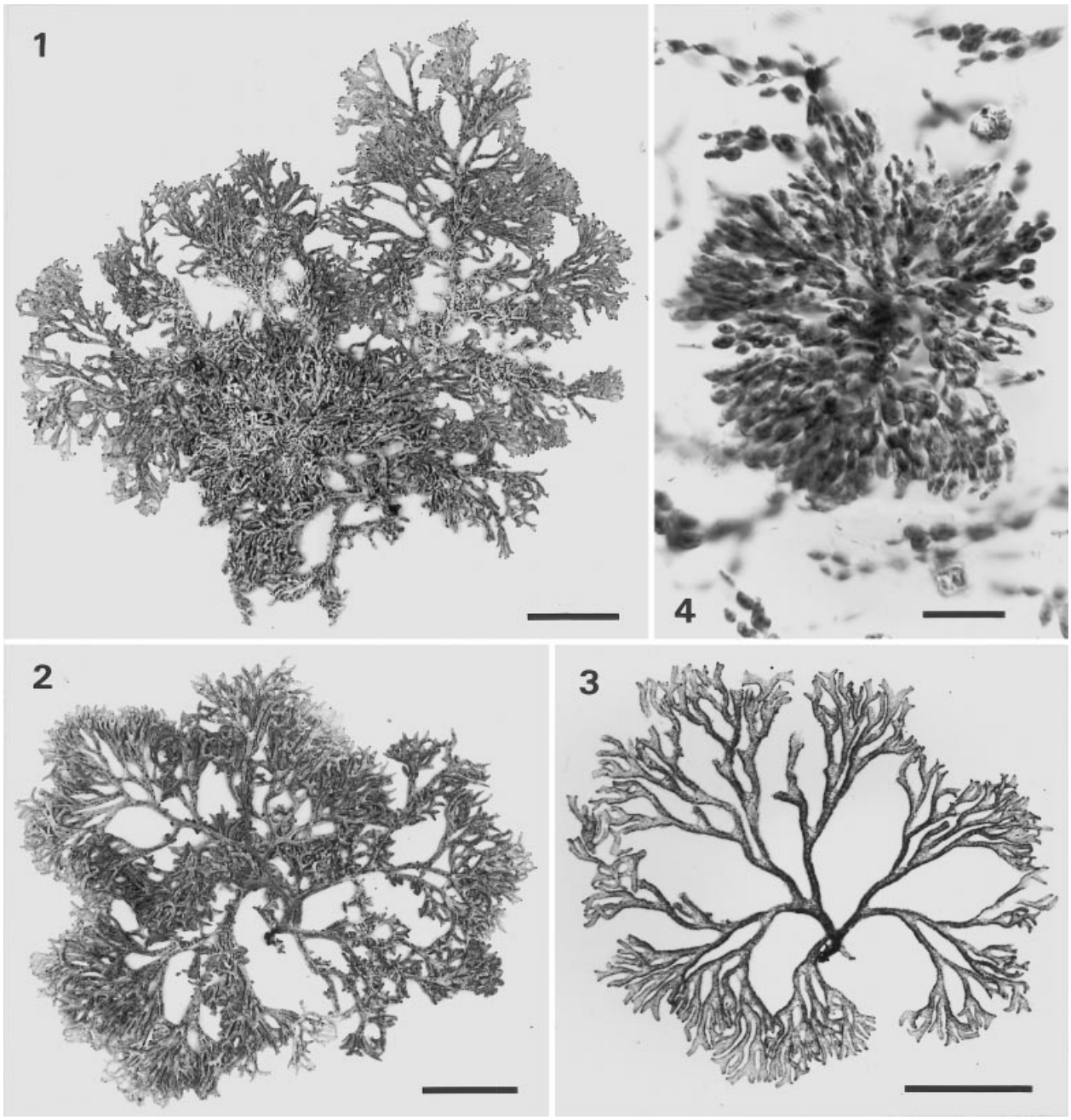
Habitat: *Liagora tsengii* occurs in the shallow sublittoral (at approximately 1−3 m depths) on reef platforms in moderately exposed sites.

Morphology and vegetative anatomy: Thalli are to 10 cm in height, pinkish grey, and are attached by a single discoid holdfast. Thalli are dichotomously branched every 3−7 mm (Figs 1, 2). Short lateral proliferations are usually present, generally on the lower half of thallus and are more prevalent in female specimens (Figure 3 shows a male specimen lacking lateral proliferations). Calcification is moderate to heavy and is conspicuously pitted. Axes are terete, from 1.5−2.0 mm diam. near the base, tapering to 0.1 mm diam. near the apices. Medullary filaments are composed of elongate cells, to 45μm diam. but mostly 10−35 μm diam. Assimilatory filaments are dichotomously or trichotomously branched (Fig. 5), to 320−500 μm long; lower cells are cylindrical, 6−7 μm diam, grading to ovoid upper cells, 10−16 μm diam. The outermost cells are subspherical and 8−12 μm diam. Cells of assimilatory filaments have a prominent, central pyrenoid. Hairs and glandular cells are often present on apical cells. Rhizoidal filaments are commonly produced on lower cells of the assimilatory filaments and form secondary medullary and assimilatory filaments. The latter are generally more sparsely branched than the primary filaments.

Reproduction: The species is dioecious. Carpogonial branches are 4−5 celled, slightly curved, and are borne laterally on the mid-to upper region of a mid-to upper cell of an assimilatory filament (Fig. 5). Following presumed fertilization the zygote divides transversely, with the lower cell not dividing further. The distal cell produces lateral gonimoblast initials that elongate and branch frequently (Figs 6, 7). Mature gonimoblasts are moderately diffuse (Fig. 4), 330−450 μm diam., with branched filaments bearing terminally or laterally 1−3 separate carposporangia (Fig. 9). Carposporangia are obovoid to ovoid, 10−15 × 15−25 μm. Fusion cells are formed (Fig. 8), incorporating the lower gonimoblast cells and cells of the carpogonial branch, although the basal cell of the carpogonial branch generally remains discernible. Sterile filaments arise from the basal cell of the carpogonial branch, occasionally from the supporting cell, and cells above, below and adjacent to the supporting cell. They intermingle with the gonimoblast filaments but are generally poorly developed and do not form an involucre. Spermatangia are spherical to ovoid, 4−5 × 3−4 μm and borne in clusters of 2−3 on spermatangial mother cells that arise from apical and subapical cells of assimilatory filaments (Fig. 10).

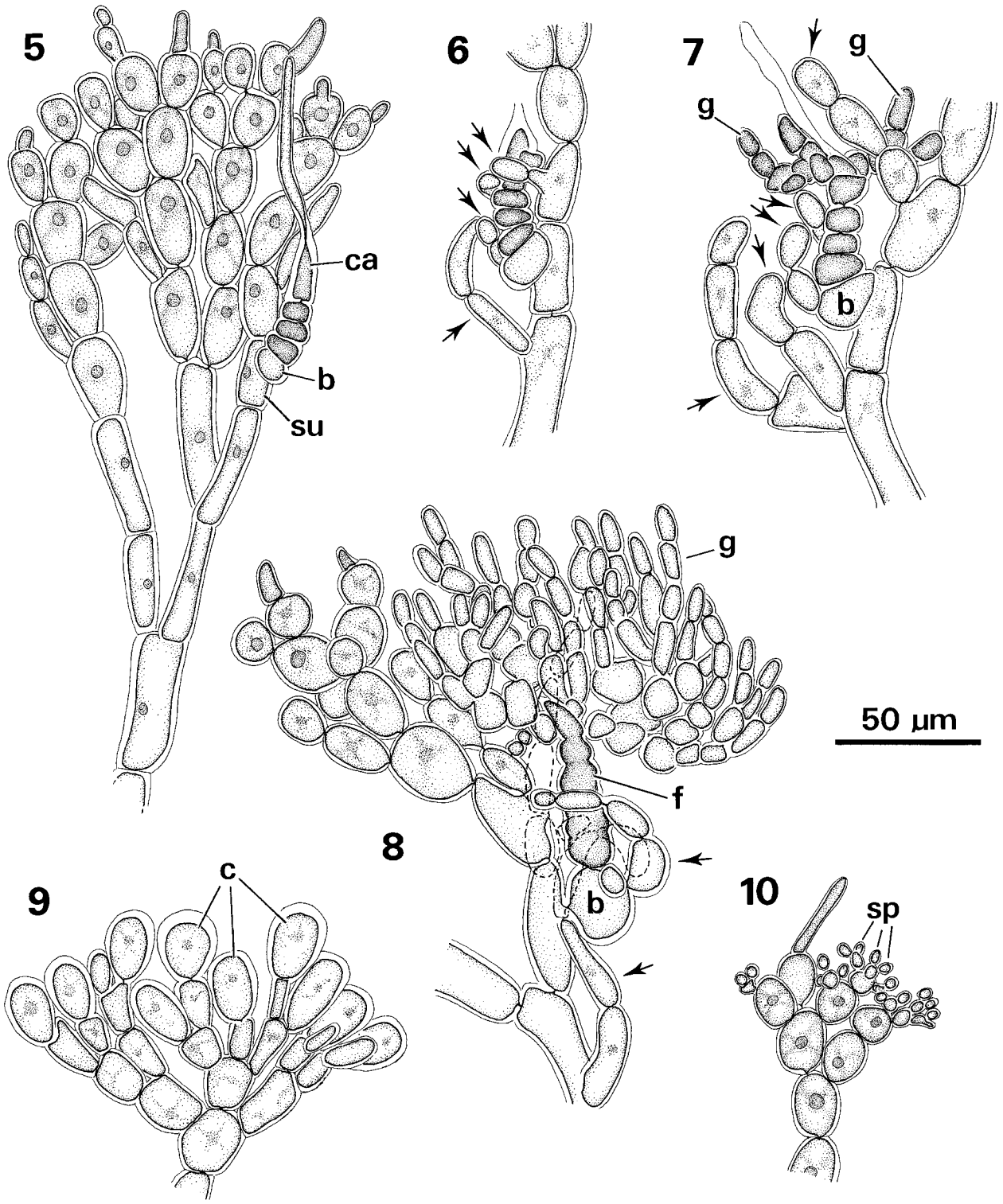
Discussion

The majority of the morphological and reproductive features of *Liagora tsengii* (including its calcified, di-



Figs 1–4. *Liagora tsengii* sp. nov.
Fig. 1. The holotype specimen (MICH 10663). Scale = 2 mm. Fig. 2. Female specimen showing proliferous lateral branches (MICH 10759). Scale = 2 mm. Fig. 3. A male specimen, lacking proliferous lateral branches (MICH 10701). Scale = 2 mm. Fig. 4. Cystocarp with somewhat diffuse gonimoblast filaments. (MICH 10663). Scale = 50 μm.

chotomously branched thallus, lateral carpogonial branches, and production of sterile post-fertilization filaments during the development of the cystocarp) suggests that the new species is appropriately placed in *Liagora*. Unfortunately the genus also includes a large number of only vaguely delineated species and, despite the excellent recent studies by Abbott (1990 a, 1990 b) that reduced many species to synonymy, we are still some way from a satisfactory understanding of the genus in its entirety. Thus any speculation as to the relationships of *L. tsengii* must also recognise the need for considerable further study of the many poorly known species. Despite this, we are confident that *Liagora tsengii* is unique within the genus due to the production of a moderately diffuse gonimoblast and short post-fertilization filaments from the basal cell of the carpogonial branch. Although this latter feature clearly distinguishes the new species, a comparison with possibly closely related species is warranted. We should stress that the moderately diffuse gonimoblasts in *Liagora* are unlike the diffuse gonimoblasts characteristic of some closely related genera



Figs 5–10. *Liagora tsengii* sp. nov.
Fig. 5. Detail of an assimilatory filament with a lateral, 5-celled, carpogonial branch (MICH 10663). Fig. 6. Immediate post-fertilization development showing the initiation of sterile filaments (arrows). A gonimoblast initial (partly obscured) is present on the carpogonium (MICH 10663). Fig. 7. Later post-fertilization development with gonimoblast initials arising laterally from the distal cell of the transversely divided zygote. Note the sterile filament on the basal cell of the carpogonial branch. Arrows indicate post-fertilization sterile filaments (MICH 10663). Fig. 8. Later stage showing diffuse gonimoblast filaments, formation of a fusion cell and persistent sterile filaments on the basal cell of the carpogonial branch. Some post-fertilization filaments are shown as hatched lines to avoid obscuring the fusion cell (MICH 10663). Fig. 9. Spermatangia borne on spermatangial mother cells arising from the apical and subapical cells of assimilatory filaments (MICH 10746). Fig. 10. Gonimoblast filaments with terminal carposporangia. (MICH 10663)
Abbreviations: b = basal cell of carpogonial branch; ca = carpogonium; f = fusion cell; g = gonimoblast filaments; sp = spermatangia; su = supporting cell; Arrows indicate post-fertilization sterile filaments.

such as *Yamadaella* I. A. Abbott (Abbott 1970), in which the gonimoblast filaments are seemingly indeterminate and intermingle with the assimilatory filaments. Those of *Liagora tsengii* do not intermingle with the assimilatory filaments and are herein regarded as moderately diffuse due to the presence of clear spaces between the gonimoblast filaments (see Fig. 4). In contrast, compact gonimoblasts, such as those present in species such as *L. ceranoides* J. V. Lamour., have no spaces between gonimoblast filaments. Thus in summary we recognise (at least) three gonimoblast morphologies in the Liagoraceae: diffuse, moderately diffuse, and compact. The presence in *L. tsengii* of a moderately diffuse gonimoblast in which sterile post-fertilization filaments are intermingled relates the new species to the generitype, *L. viscida* (Forssk.) C. Agardh (as described by Kylin 1930 and Kvaternik and Afonso-Carrillo 1995, but see below). It is therefore unlike the majority of the species presently attributed to the genus, in which gonimoblasts are mostly compact, or, if diffuse, do not intermingle with the involucral filaments. Of the species for which post-fertilization development is well-documented (or can be reasonably inferred from published illustrations), only *L. brachyclada* Decne. (Levring 1941: fig. 11: I), *L. papenfussii* I. A. Abbott (Abbott 1945: fig. 16. Desikachary 1956: fig. 5 e, f, g), *L. perennis* I. A. Abbott (Abbott 1995: fig. 1: 5), *L. tetrasporifera* Børgesen (Kvaternik and Afonso-Carrillo 1995: 460, fig. 52), *L. indica* V. Krishnam. *et* Sundrarajan (Krishnamurthy and Sundararajan 1985: 59), *L. viscida* (Kvaternik and Afonso-Carrillo 1995: 450, fig. 8), *L. mauritiana* Børgesen (Børgesen 1951: fig. 12 b) and *L. divaricata* C. K. Tseng (Tseng 1941: fig. 4) appear to have moderately diffuse gonimoblasts. Unpublished studies by the first author on other *Liagora* species adds *L. harveyana* Zeh, *L. galaxauroides* Dickie and *L. howensis* A. H. S Lucas to that list. Features of the species with moderately diffuse gonimoblasts are given in Table I. Based on the included features, *L. tsengii* appears to be most closely related to *L. viscida* and *L. indica.*

Table 1: Comparison of possibly related *Liagora* species.

Species	Branching	Carpogonial branch.	Fusion cell	C. sporangia	Gonimoblast	Reference
L. albicans	With percurrent axes or dichotomous	2−4 celled	Yes	Undivided	Compact	Abbott 1990 a
L. brachyclada	Dichotomous	4 celled	Yes?	Quadripartite	Moderately diffuse	Levring 1941
L. divaricata	Dichotomous w. proliferations	4−6 celled,	No	Undivided	Moderately diffuse	Tseng 1941
L. galaxauroides	Dichotomous	4 celled	No	Undivided	Moderately diffuse	Pers obs.
L. howensis	Various	4−5 celled	Yes	Quadripartite	Moderately diffuse	Pers. obs.
L. harveyana	Dichotomous with proliferations	3−5 celled	Yes	Quadripartite	Moderately diffuse	Pers. obs.
L. indica	Dichotomous	4−5 celled	Yes	Undivided	Moderately diffuse	Krishnamurthy and Sundararajan 1985
L. mauritiana	Dichotomous/ irregular	4 celled	No	Undivided	Moderately diffuse	Børgesen 1951
L. orientalis	Irregular	3−4 celled	No	Undivided	Compact	Abbott 1967, as *L. tanakai*
L. papenfussii	Pinnate	3−4 celled,	No	Quadripartite	Moderately diffuse	Abbott 1945; Desikachary 1956
L. perennis	Dichotomous	3−4 celled	No	Quadripartite	Moderately diffuse	Abbott 1995
L. tetrasporifera	Dichotomous	3 celled	Yes	Quadripartite	Moderately diffuse	Kvaternik and Afonso-Carrillo 1995
L. viscida	Dichotomous	4 celled	Yes	Undivided	Moderately diffuse	Kvaternik and Afonso-Carrillo 1995
L. tsengii	Dichotomous with proliferations	4−5 celled	Yes	Undivided	Moderately diffuse	This paper

Carpogonial branch morphology in the Liagoraceae varies considerably and is open to interpretation. We follow Kraft (1989, p. 294), who defines the carpogonial branch as 'the structure, however long and containing however many unmodified cells, which subtends the carpogonium and which itself is either unbranched or bears only subsidiary laterals'. Species of *Liagora* in which sterile filaments have been reported to arise from the supporting cell or from the cells of the carpogonial branch include *Liagora orientalis* J. Agardh (as *L. tanakai* I. A. Abbott; Abbott 1967: 33), *Liagora albicans* J. V. Lamour. (as *L. maxima* Butters; Abbott 1945: 148), *L. viscida* (Hamel 1930: 76, Kvaternik and Afonso-Carrillo 1995: our inference from fig. 5), and *L. indica* (Krishnamurthy and Sundararajan 1985: 57). With the exception of *L. indica*, these observations have been largely refuted by Abbott (1990 a, b), Desikachary (1956), and Desikachary and Balakrishnan (1957). Kvaternik and Afonso-Carrillo (1995) apparently illustrate a sterile filament arising from the supporting cell (their fig. 5) but do not describe this process in the text. It would appear that, in most cases at least, these observations were incorrect. In fact, Desikachary and Balakrishnan (1957) state 'It can be safely said that all reports of their [involucral filaments] formation from the sterile cells of the carpogonial branch or the supporting cells can be discounted'. Given both conditions occur in *L. tsengii* we would be hesitant to dismiss their occurrence in other species, despite the comments of Desikachary and Balakrishnan (1957). Thus the species mentioned above are also included in Table I for comparison. Alternatively we can accept that all reports of such filaments are inaccurate, leading us to question whether *L. tsengii* should be included in *Liagora* at all. At the moment we believe it should be included in *Liagora*. The vegetative and reproductive characters shared between *L. viscida* and *L. tsengii* point to a single genus, perhaps more so than the similarities between *L. viscida* and the majority of other species presently included in the genus.

From the above it appears that *L. tsengii* is most closely related to *L. indica* as described by Krishnamurthy and Sundararajan (1985). The two species share moderately diffuse gonimoblasts, sterile filaments arising from the supporting cell in addition to other vegetative cells, and the lateral initiation of early gonimoblast filaments. The species differ in their habit (proliferous lateral branches generally present in *L. tsengii* and absent in *L. indica*) size and shape of their carposporangia (obovoid to ovoid, $10-15 \times 15-25$ μm in *L. tsengii*; spherical to ovoid, 7×10 μm in *L. indica*) and size of cystocarps (330−450 μm diam. in *L. tsengii,* 'about 168 μm' diam. in *L. indica*). *Liagora tsengii* also appears closely related to *L. viscida* as described by Kvaternik and Afonso-Carrillo (1995), differing in habit (proliferous lateral branches generally present in *L. tsengii* and absent in *L. viscida*) and length and form of assimilatory filaments ('to 144 μm long' with regular trichotomous divisions in *L. viscida*, to 500 μm long and rarely with trichotomous divisions in *L. tsengii*).

Liagora tsengii is possibly identical to an undescribed taxon from Florida reported as '*Liagora* aff. *ceranoides*' by Brodie and Norris (1992, 1996). Whilst those authors did not formally name this entity, they did provide a detailed discussion of the differences between it and previously described species. All distinctive features of *L. tsengii* considered important by us are either described or illustrated for *L.* aff. *ceranoides* by Brodie and Norris (1992), including the presence of short, post-fertilization sterile filaments on the basal cell of the carpogonial branch and occasionally the supporting cell (Brodie and Norris 1992: figs 18, 20, 22) and a diffuse gonimoblast (their figs 21, 25). Brodie (pers. comm. 1998) expressed the opinion that *L.* aff. *ceranoides* probably represented a new species, but was reluctant to describe it given the imperfect knowledge of many of the existing species of *Liagora.*

Characterization of genera in the Liagoraceae is based almost entirely on features of the carpogonial branch and cystocarp. It is therefore unfortunate that there has been a significant disagreement regarding the post-fertilization development in the generitype of *Liagora*, *L. viscida*. The species' reproductive development was first described by Kylin (1930), who described a gonimoblast with diffuse filaments that lacked an involucre. His illustration suggests that sterile filaments are present, but that they are intermingled with the gonimoblast filaments. Desikachary and Balakrishnan (1957), however, described material in which a distinct involucre is present, although their illustrations depicted only immature cystocarps. Abbott (1990 b) described *L. viscida* as having 'a substantial involucre…and consists of specially formed post-fertilization filaments'. Recently Kvaternik and Afonso-Carrillo (1995) examined material from the Canary Islands referable to *L. viscida* and reported its gonimoblast filaments to intermingle with the involucral filaments. Clearly there remains some confusion regarding the post-fertilization development in *Liagora viscida*. Unfortunately the type material is lost, but the species has been neotypified by Abbott (1990 b) on a collection from Anse du Troc, east of Banyuls-sur-Mer, France (T. Christensen No. 6107, June 1954). Mounted on the neotype sheet in C are six specimens, of which none are fertile (Huisman, unpublished observations), an unsatisfactory situation that further hampers the characterization of the genus. In the present study the structure and post-fertilization development of *Liagora viscida* were examined in specimens from near the type locality [Banyuls, France, *G. Mazoyer*, 7.vii.1937; AD, A24,190. 15.ix.1949; AD, A15,831. Adriatic, *F. Krasser*, iv; NSW 399014] and found to be identical to that illustrated by Kylin (1930) and described by Kvaternik and Afonso-Carrillo (1995), i. e. with sterile filaments

intermingling with the gonimoblast filaments. If we accept this development as typical of *L. viscida*, then very few of the species of *Liagora* for which post-fertilization developmental stages are known conform to the process as it occurs in the type species (*L. tsengii* being one), the majority having compact gonimoblasts that do not intermingle with the post-fertilization sterile filaments. Since many of the genera now recognised in the Liagoraceae are defined on very precise reproductive events, the variability in the species presently included in *Liagora* could well justify a subdivision of the genus. This subdivision was flagged by Kraft (1989) and in part undertaken by Huisman and Kraft (1994), who resurrected an emended *Ganonema* K. C. Fan and Yung C. Wang (now Wang Yongchan) for *G. farinosum* (J. V. Lamour.) K. C. Fan *et* Yung C. Wang and at least some of the species included in the section Mucosae of *Liagora*. Further morphological and possibly molecular studies are required, however, before any further subdivision can be proposed with confidence.

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