

## *Liagora valida* HARVEY (Rhodophyta) from Sand Key, Florida<sup>1)</sup>

Isabella A. ABBOTT\* and Mokoto YOSHIZAKI\*\*

\*Hopkins Marine Station of Stanford University, Pacific Grove,  
California 93950, U. S. A.

\*\*Department of Biology, Toho University, Miyama, Funabashi,  
Chiba Pref., 274 Japan

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Taxonomic discrimination of *Liagora valida* Harvey (Nemaliales) is based on vegetative features that are known to vary in all species of the genus, and are therefore of little value. An ontogenetic study of the female reproductive system, based on a specimen from Sand Key, Florida, the toptype locality of *L. valida* is given, and offers three features of the reproductive system which may be more helpful for taxonomy. The young carposogonial branch is relatively straight and arises from the shoulder of the bearing cell; the cystocarp is covered by an involucre of sterile filaments whose cell shapes and sizes are similar to those of vegetative filaments; carposporangia are liberated from one to several terminal cells of the carposporophyte one or more at a time. *L. valida* is the type species of Section Validae YAMADA of the genus *Liagora*. This section contains most of the common species occurring in the warm Pacific.

*Key Index Words:* Cystocarp formation; *Liagora valida*; Nemaliales; morphology; Rhodophyta.

*Liagora valida* HARVEY (Helminthocladiaceae, Nemaliales) must be considered to be the type species for the section Validae of YAMADA (1938b, d) although not designated by that worker, probably owing to the fact that he was uncertain of its features since the species does not occur in Japan. YAMADA (1938a) mentioned examining a co-type specimen of *L. valida* (UC) but having observed only young females and spermatangia could not come to any taxonomic conclusions. Furthermore, an earlier report (OKAMURA 1935) of the occurrence of *L. valida* from outlying islands of Japan was never substantiated by YAMADA (1938a-d; 1944). The type specimen of *L. valida* from Sand key, Florida (HARVEY, 1965, p. 138) and pieces of the specimen to be considered as part of

the lectotype may be found in the Harvey herbarium (Trinity College, Dublin) and "co-types" (designated by Setchell in herbaria) are in the University of California (UC) herbarium and in the British Museum (Nat. Hist.) (BM). YAMADA (1938b, p. 4) circumscribed this section to include three groups (Decussata, Distenta and Validae). *L. boergesenii* YAMADA and *L. setchellii* YAMADA placed in section Validae by YAMADA were interpreted by ABBOTT (1945) to be larger specimens with stronger calcification from the entity previously described from the Caribbean by BØRGESEN (1915-20) and from Bermuda by HOWE (1918) as *L. valida*.

Though collections of *Liagora* from the Caribbean (ABBOTT, personal observations) contain some *Liagora valida* types of plants, i.e., thalli 40-50 mm tall, fronds cylindrical, calcification mostly continuous and relatively thick, such specimens are far more common in collections from the Pacific. At this time,

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such specimens constitute the largest group of unnamed *Liagora* specimens in any of the world's large herbaria (ABBOTT personal observations).

When YAMADA (1937; 1938a-d) published upon the Japanese taxa, he tried in every case to include descriptions and illustrations of all reproductive stages, following the example of BØRGESEN (1915-20) from the Caribbean. This was a considerable improvement over the essentially vegetatively oriented features selected by workers of the preceding century. DESIKACHARY and BALAKRISHNAN (1957) focused attention on pre- and post-fertilization events in the genus, a point of view held and practiced by the first author of this paper (ABBOTT 1945, 1970, 1976). However, such stages are difficult to observe from dried material and we prefer to work on thalli preserved in liquid, using dried material only when type or other authentic material is involved. The gift of liquid preserved material from Sand Key made possible the observations included in this paper. From external appearances and shapes of the cells of the assimilatory filaments, this specimen resembles *L. valida*, but in the details of the development of the female reproductive structures, it is uncertain what the similarities may be to the type specimen inasmuch as the variation in development shown by this and other species in the genus is poorly understood.

### Materials and Methods

A single specimen was collected at 2-5 ft depth off Sand Key, Florida (near Key West), 4 June 1978 by John G. SCHWEDE, and is

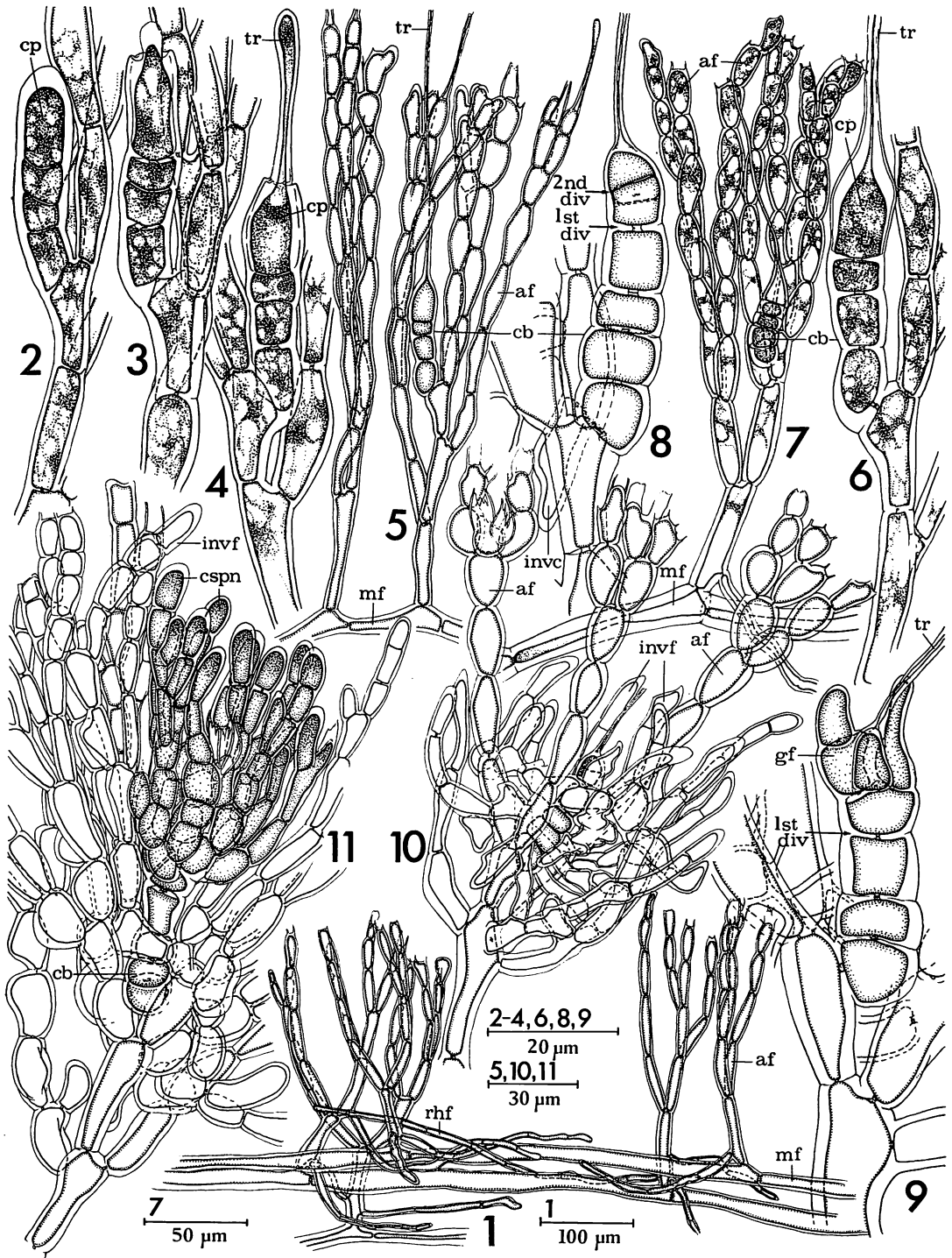
numbered ABBOTT 14836a in the first author's herbarium. Preserved material and slides made from it have been divided between the two authors. Slides were made by decalcifying in weak acid, staining with 1% aniline blue with a drop of 1% HCl, and mounted in 70% glucose syrup. Further material from the same place, numbered ABBOTT 13766, was collected at 0.5 to 2 m depth, 20 IV, 1980, leg. J.G. SCHWEDE.

### Observations

Fronds cylindrical, up to 35 mm high, 1.5 mm in widest diameter, 5-8 times dichotomously branched, fastigiate, and heavily calcified throughout. Construction of multi-axial medullary filaments and cortical (assimilatory) filaments. The medulla is composed of two kinds of strand cells which are intermixed: 1) filaments 5-10  $\mu\text{m}$  in diameter which arise from the basal cells (Fig. 1) of assimilatory filaments and are rhizoidal in nature, and 2) medullary filaments 12-35  $\mu\text{m}$  in diam. The assimilatory filaments are usually 4-6 times furcate. The lower cells of the assimilatory filament are cylindrical, becoming oval to moniliform in appearance in the upper portion and the cells increasing in length away from the apex. Each cell of the assimilatory filaments contains a centrally located stellate plastid with a single pyrenoid. In the youngest apices, assimilatory filaments are irregularly dichotomously branched, the filaments rather straight and upper cells mostly oval (Fig. 4); frequent unicellular hairs occur on the ultimate cells. In slightly older sections where, for example, unfertilized carpogonial branches are

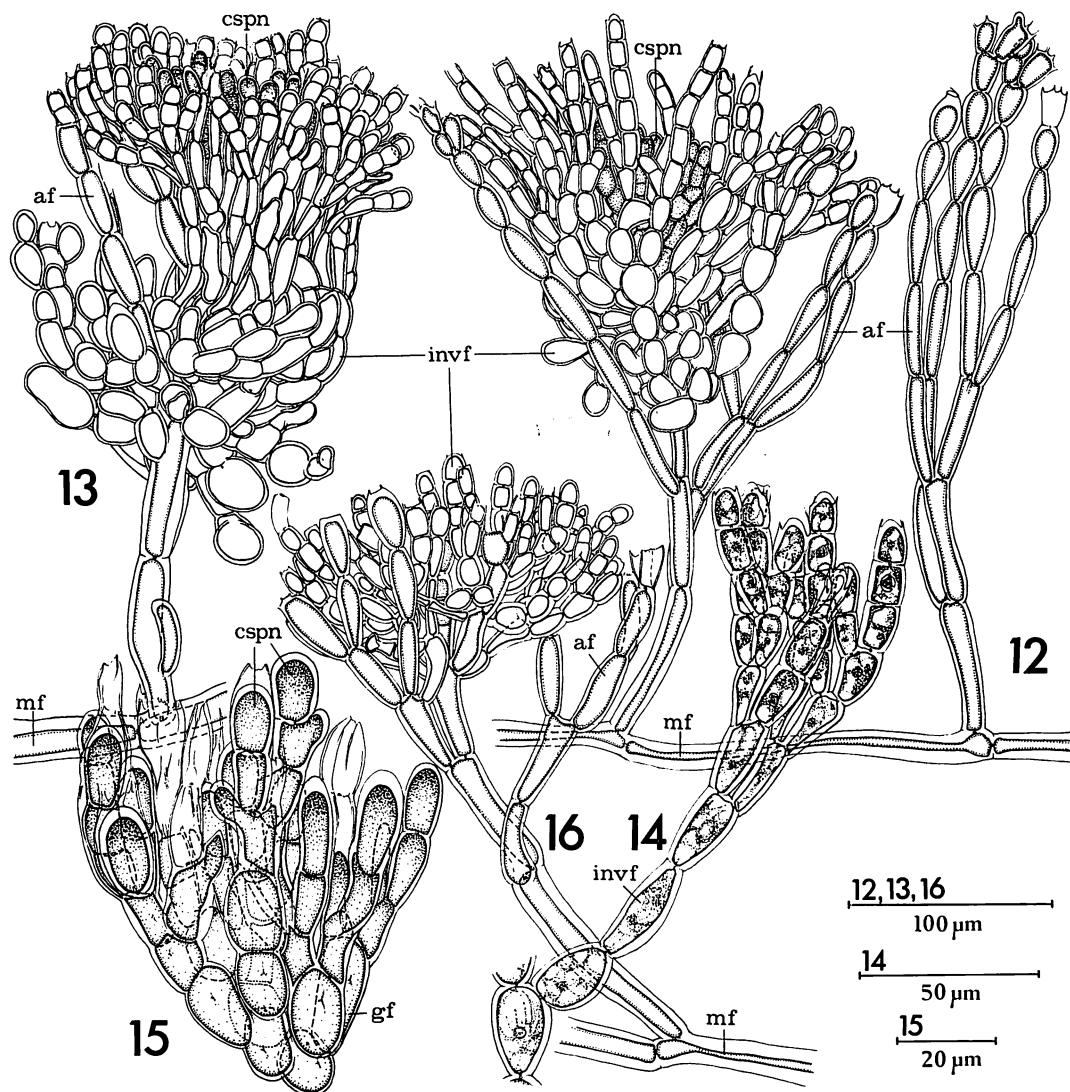
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Figs. 1-11. *Liagora valida*. 1. Relationship of assimilatory filaments (af) to medullary filaments (mf), showing rhizoids (rhf) that are produced by the lower cells of the assimilatory filaments. 2, 3, 4. Details of young carpogonial branches being formed from the shoulders of bearing cells. 5. Young carpogonial branch borne on lower cells of assimilatory filaments, indicating new and deliquescing unicellular hairs in terminal vegetative portions. 6. Young carpogonial branch with carpogonium (cp) ready for fertilization. 7. Young carpogonial branch and details of cells of assimilatory filaments (af) cluster. This carpogonium was not fertilized. 8. Carpogonium after fertilization showing first and second divisions. 9. Immediate post-fertilization events in the carpogonium area, including first division after fertilization, and initiation of gonimoblast (gf) cells. The trichogyne (tr) is still attached. 10, 11. Various stages in the development of the gonimoblast showing carposporangia (cspn), involucre of sterile filaments (invf), and relationship to assimilatory filaments (af).



seen (Figs. 2, 3), the upper cells of the filaments become more moniliform and in still older portions where cystocarps are being formed in adjacent branch systems, shorter

more densely branched cortical systems appear (Fig. 5) with corymbose outline. They are formed in part by broadening cells and in part by upper cells deliquescing (Fig. 5),



Figs. 12-15. 12, 13. Various stages in the development of the gonimoblast showing carposporangia, involucre of sterile filaments, and relationship to assimilatory filaments. Fig. 12 also shows the shape of older assimilatory filaments clusters where terminal cells have dropped off. 14. Detail of a cluster of involucral (sterile) cells showing plastids and other cellular details. 15. Detail of mature terminal portions of cystocarp showing sporangial walls from emptied carpospores, illustrating 2-celled chains of carposporangia before discharge or dissolution. 16. An old cystocarp with both assimilatory and gonimoblast filaments showing terminal loss of cells, thus becoming shorter and smaller than younger gonimoblasts (cf figs. 12 and 13). Abbreviations used in figures: af, assimilatory filaments; cb, carpo gonial branch; cp, carpo gonium; cspn, carpo rangium; 1st div, first division of zygote; gf, gonimoblast filament; invc, involucral cell; invf, involucral filament; mf, medullary filament; rhf, rhizoidal filament; 2nd div, second division of zygote; tr, trichogyne.

leaving shortened filaments of similar shaped cells.

Carpogonial branches are first formed (Fig. 2) in abundance in the younger terminal branches. The carpogonial branch is formed (Fig. 6) in an upper lateral position (near the shoulder of the bearing cell) on the second to fourth cell situated above the basal cell of an assimilatory filament. The carpogonial branch is slightly curved and is normally composed of four cells (Fig. 8) sometimes three or five (Fig. 7) cells. The carpogonium produces a trichogyne from the distal end. In trichogyne initiation, the trichogyne base may be pinched in (Fig. 6), or gradually tapered (Fig. 4). Mature carpogonial branches are 10  $\mu\text{m}$  in widest diameter. The trichogyne is up to 150  $\mu\text{m}$  long, and 3-4  $\mu\text{m}$  in diam. Trichogynes develop almost directly toward the surface of the thallus, ultimately projecting beyond the surface. Frequent curved carpogonial branches with clear contents (empty) are seen; they become thick walled but do not develop further.

After fertilization, most of the trichogyne breaks down except for the basal portion. The first division (Figs. 8, 9) of the fertilized carpogonium is transverse, followed by slightly oblique divisions of the upper daughter cell (Fig. 9) which alone initiates further divisions that form the gonimoblast. The next divisions are longitudinal. A sterile involucre of filaments is produced immediately after fertilization. These filaments are initiated by cells adjacent (especially directly above and below) to the cell on which the carpogonial branch is borne, and are very prominently developed. The bearing cell of the carpogonial branch never produces sterile cells. From their initiation (Figs. 10, 11) the involucreal filaments branch rapidly and tightly surround the carpogonial branch. As the carposporophyte grows upward the involucreal filaments also grow in an upward direction (Fig. 12). The gonimoblast filaments are compact; the cells of the lower part of the gonimoblast broaden and develop a dense, rich protoplast. The upper part of the gonimoblast filaments remain fairly slender (Fig. 13) and produce carposporangia termi-

nally. Carposporangia are sometimes observed (Fig. 13) in 2-celled chains, both spores being discharged from the terminal pore, or one develops ahead of the proximal one (Fig. 15). The mature carposporangia are obovoid to dome-shaped, measuring 15-18 by 8-12  $\mu\text{m}$ . The wall of a mature carposporangium ruptures at the distal end, releasing the carpospore. The empty carposporangial wall remains. The upper lateral portion (Fig. 15) of the first proximal cell swells upward to one side, initiating a new carposporangium. In old and senescent cystocarps, gonimoblast filaments and the upper cells of the involucre have disappeared (fig. 16).

### Discussion

Though often characterized (AGARDH 1896; BØRGESSEN 1915-20) as having assimilatory filaments that describe a corymbose (Fig. 5), this shape is only evident in areas that bear developing cystocarps, for regions where young carpogonial branches are developing (Figs. 2-6) show a different kind of arrangement of cortical filaments, being more regularly branched throughout and having cells more elongate. In the oldest portions, where terminal cells are being shed (Fig. 12), again the assimilatory filaments are not corymbose. In the developing carpogonial branches (Figs. 2, 3, 6) the branch is cut off from the shoulder of the bearing cells and are thus different from the formation of the carpogonial branches of *Liagora viscida* (KYLIN 1930, Fig. 3, A-C) the type species for the genus where the carpogonial branch is borne laterally in mid-portions of lower cortical cells.

BØRGESSEN (1915-20) was the first to show that rhizoids from the basal cells of the anticlinally directed assimilatory filaments join with the axial filaments to make up the medulla. Our observations illustrated in Fig. 1 substantiate this.

AGARDH (1896) and BØRGESSEN (1915-20) emphasize that the cystocarps are borne above the layer of calcium carbonate. This was not clearly seen in the Sand Key specimens of *L. valida*, and is a feature that is

shared with other species of *Liagora* such as *L. boergesenii* (ABBOTT 1945). Its importance cannot be assessed at this time.

Finally, BØRGESEN (1949) illustrated spermatangia from thalli occurring in Mauritius. These are ultimate cells that are smaller than those bearing them and are not formed on stalks. Male reproductive organs should be re-examined from Florida or the Caribbean to check this point, as most spermatangia of *Liagora* are stalked.

Our observations that the Sand Key cystocarps possess involuclral (sterile) filaments that are of the size and shape of vegetative filaments demonstrate an unusual feature for *Liagora* species, where the involucre is usually of more slender dimensions and conspicuously different from vegetative cells. Should this be a constant feature of *L. valida*, it would be a very useful one for taxonomic distinction. Our observations on numbers of terminal cells of the gonimoblast that are involved in forming carposporangia are new for the genus.

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### イサベラ A. アボット\*・吉崎 誠\*\*：イシハダの雌性生殖器官と果胞子体形成過程

コナハダ属の中で最も多数の種を含むイシハダ節の基準種とみなすことのできるイシハダ *Liagora valida* HARVEY について、産地標本 (topotype specimen) を用いて雌性生殖器官と果胞子体形成過程を観察した。造果枝は同化糸細胞の肩部に生じ、通常4細胞からなる。接合子は造果枝の長軸に直角の面で2個の娘細胞に分割し、上方の娘細胞は造胞糸始源細胞、下方の娘細胞は柄細胞となる。受精後、造果枝に近接する細胞から総苞糸を生じる。総苞糸は分岐伸長し、同化糸とはほぼ同じ形態と大きさに発達し、果胞子体を密にとり囲む。総苞糸の形態は、コナハダ属の種の分類に役立つ形質であると思われる。(\* Hopkins Marine Station of Stanford University, Pacific Grove, California 93950, U. S. A., \*\*274 船橋市三山 2-2-1 東邦大学理学部生物学科)