

Gracilaria mixta, sp. nov. and Other Western Pacific Species of the Genus (Rhodophyta: Gracilariaceae)¹

ISABELLA A. ABBOTT,^{2,3} ZHANG JUNFU,⁴ AND XIA BANGMEI⁴

ABSTRACT: *Gracilaria mixta* from South China is one of several terete species of *Gracilaria* that requires critical microscopic examination for identification. This new species demonstrates a mixture of spermatangial types that recently have been used to separate genera in the Gracilariaceae: the simple, pitlike *Verrucosa* type and the multicavities *Polycavernosa* type arrangements. The first type is seen in the youngest branch portions, gradually changing to the second type in older parts. Both types of arrangements occasionally may be seen in the same cross section. Reexamination of male plants of the western Pacific taxa placed in *Polycavernosa* (= *Hydropuntia*) also shows both types of configurations in the same thalli. However, some species of *Gracilaria* with *Verrucosa*-type spermatangia maintain that type throughout the plants. These observations require a transfer of names from *Hydropuntia* (= *Polycavernosa*) to *Gracilaria*. From 16 taxa, 4 are retained in *Gracilaria*, 2 receive new names because of earlier homonyms, and 10 become new combinations within *Gracilaria*.

MANY STUDIES IN RECENT YEARS have been directed toward the discrimination of taxa in the red algal genus *Gracilaria* (s.l.), owing in large part to the potential commercial uses of the colloid agar that may be extracted from the cell walls. Moreover, it has been found that various properties of agars, as well as the proportion of agarose to agar fractions, vary with the species (Santos and Doty 1983), thus affecting the market value of the dried seaweed and the subsequently extracted colloid.

Recent papers on species of *Gracilaria* and *Polycavernosa* have dealt with some western Pacific species: keys to Chinese and Japanese species (Xia and Yamamoto 1985), Chinese species (Xia 1985), Japanese species (Yamamoto 1985), Taiwanese species (Chiang 1985), Hawaiian and Philippines species (Abbott 1985), and Micronesian species (Tsuda 1985), as well as a few species from elsewhere. A

comparison of *Polycavernosa* with *Gracilaria* was also made (Xia and Abbott 1985). More recent studies reported on two new taxa from South China (Zhang and Xia 1988), eight taxa from Thailand (Abbott 1988b), and six from Indonesia and adjacent areas visited by the Siboga Expedition (Abbott 1988c).

Other papers since 1985 include those by Xia (1986) on *Gracilaria salicornia*, a common Pacific and Indian Ocean species; Meneses and Abbott (1987) on *Gracilaria* and *Polycavernosa* from Guam and Micronesia; and Xia and Abbott (1987) on species of both genera from Malaysia, Thailand, and the Philippines.

Those studies had several objectives: (1) to seek features among the taxa that might clarify generic limits, (2) to elucidate the features of both previously described and new taxa and establish characters by which species could be recognized, and (3) to provide information on the distribution of previously poorly known species.

In 1989, three papers appeared that affect the status of the western Pacific *Gracilaria*-like species (as well as taxa elsewhere that are outside of the focus of this paper). First,

¹ Manuscript accepted 1 May 1990.

² Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii 96822.

³ To whom correspondence should be sent.

⁴ Institute of Oceanology, Academia Sinica, 7 Nan Hai Road, Qingdao, People's Republic of China.

Fredericq and Hommersand (1989a) proposed the order Gracilariales, based upon a study of *Gracilaria verrucosa*, the genotype; second, Fredericq & Hommersand (1989b) restored the genus *Gracilariopsis* for four species previously placed in *Gracilaria*; and third, Wynne (1989) transferred 14 species of *Polycavernosa* and two species of *Gracilaria* to *Hydropuntia*. *Hydropuntia*, based upon *H. urvillei* (Montagne, 1842), is a name that has priority over *Polycavernosa* Chang & Xia (1963).

The genus *Gracilaria* has a number of embryological features, as demonstrated by Fredericq & Hommersand (1989a), that make it different from the other taxa that are included in the Gigartinales (s.l.) (Kraft and Robins 1985). However, we do not have wide experience in working on other genera in this order, nor ultrastructural or biochemical experience that would enable us to evaluate some of the features that are used to suggest that the Gracilariales, Ahnfeltiales, and Gelidiales are more closely related to one another than they are to any of the taxa remaining in the Gigartinales (s.l.). For lack of such experience, we do not express an opinion at this time on the status of the Gracilariales or the nearest relatives of the Gracilariaceae.

With respect to the restoration of *Gracilariopsis* by Fredericq and Hommersand (1989b), the genus is now based upon very different features than those named by Dawson (1949) when he segregated it from *Gracilaria*. The primary embryological feature shown by Fredericq and Hommersand (1989b) for distinguishing *Gracilariopsis* was the transformation of cells in the floor of the cystocarp into nutritive tissue, whereas in *Gracilaria* there was no transformation. Instead, there is secondary fusion by nutritive cells to the pericarp and the floor of the cystocarp, the latter a feature shared in common with *Hydropuntia* (= *Polycavernosa*). Dawson (1949), in selecting the absence of "nutritive filaments" in the cystocarps of *Gracilariopsis* as the main characteristic distinguishing species assigned to this genus from *Gracilaria*, thus saw the outward manifestation of these internal embryological features.

However, Papenfuss (1966) noted that some specimens of *G. verrucosa* did not show nutritive filaments, while others did. Subsequently, Fredericq and Hommersand (1989a), using different material, claimed that British collections contain both *G. verrucosa* (with tubular nutritive filaments) and *Gracilariopsis lemaneiformis* (without such filaments).

The method of formation of the spermatangia, which arise on outer cortical cells, was also selected as an important feature that separated *Gracilariopsis* from *Gracilaria*. Spermatangia of *Gracilariopsis* are cut off from outermost cortical cells; this type was the basis for *Gracilaria* subgenus *Gracilariella* of Yamamoto (1978). In the western Pacific, both *Gracilariopsis chorda* (Holmes) Ohmi and *G. lemaneiformis* (Bory) Daws., Acleto & Foldvik have been reported, the first from China and Japan, the second from Indonesia and northeastern China (as *G. sjoestedtii*).

The location and occurrence of spermatangia were also features emphasized when *Polycavernosa* (Chang and Xia 1963) was first described, as occurring in large, internal, compound cavities. Also, conspicuous, darkly staining, irregularly shaped basal "nutritive filaments" emerged from the bottom and sides of the gonimoblasts, as opposed to being directed to the outer pericarp, as in *G. verrucosa*. Yamamoto (1984), the current student of gracilarioids in Japan, suggested that *Polycavernosa* might warrant subgeneric rank within *Gracilaria*, but having had no experience with these taxa, he made no formal proposals.

In describing a new species, *Gracilaria mixta*, in this paper, we demonstrate that within the same branchlet and frond the *Verrucosa*-type (oval, pit-, or conceptaclelike) spermatangial arrangement may grade into *Polycavernosa* type (multicavitated conceptacles). Those observations resulted in a re-examination of described western Pacific specimens of *Polycavernosa*. Although every spermatangial plant does not show continuous change from *Verrucosa* type to *Polycavernosa* type in the same branchlet, we have examined enough material in other taxa, including the type species of *Polycavernosa*,

P. fastigiata, to substantiate our primary observations.

MATERIALS AND METHODS

Slides prepared for microscope observation were made from material preserved in 4–5% formalin-seawater or from dried material. Sections were cut by hand, using a razor blade, stained in 1% aniline blue, fixed with 1% HCl, rinsed in distilled water, and mounted in dilute glucose syrup.

Herbarium specimens are principally found in two locations: Institute of Oceanology, Academia Sinica, Qingdao, China (abbreviated AST) and the Herbarium of the B. P. Bishop Museum, Honolulu (abbreviated BISH). Other herbaria from which specimens were borrowed are the Kützing herbarium in Leiden, The Netherlands, and the Agardh herbarium in Lund, Sweden.

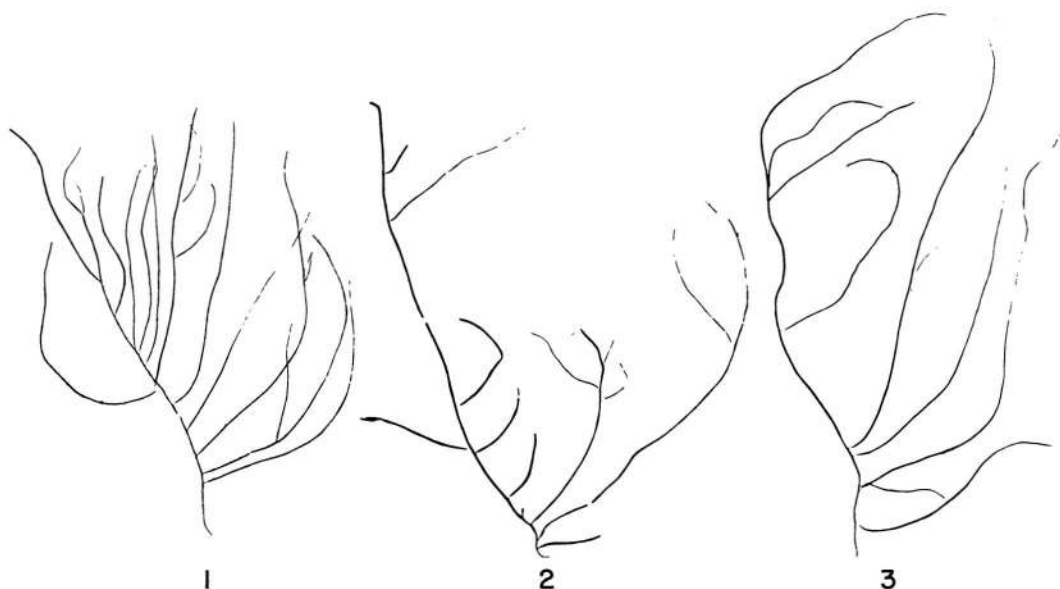
RESULTS

Gracilaria mixta Abbott, Zhang & Xia, sp. nov.

Figures 1–4, 6–7, 10–11, 12–15, 20, 23–25.

Planta erecta, solitaria vel caespitosa; axes plus minusve percurrentes, 15–45 cm longi, haptero discoidea parvo. Axes et rami teretes, 2–3 mm diam.; rami usque 35 cm longi, constricti abrupte basibus suis, attenuati ad apicem tenuem; ramificatio 1–3 ordinum, sparsa aut irregularis vel alterna vel secunda. Collocatio spermatangiorum bififormis: (1) “*Verrucosa*-typus” conceptaculis elongato-ovalibus, et (2) “*Polycavernosa*-typus” 2–7 cavitatibus. Cystocarpia protrudentia manifeste, hemisphaerica, non rostrata, non constricta basi; gonimoblastus ramosus, pseudoparenchymatus; superna fila absorbentia multa, basalia fila absorbentia multa, basalia fila absorbentia pauca, lateralia. Tetrasporangia in strato externo dispersa, cruciatim divisa, cellulis corticalibus normalibus circumfusa.

HOLOTYPE: AST 88-0234 (Figure 1), cystocarpic, growing on gravel and shells in the lower littoral, Zhanjiang, Guangdong Province, China, collected by Liu Sijian and Jie Zhenying, 2 May 1988. Other specimens (from the same collection as the holotype): AST



FIGURES 1–3. *Gracilaria mixta*. 1, Holotype: cystocarpic plant from South China (AST 880234). 2, Tetrasporophyte (AST 880234). 3, Spermatangial plant (AST 880234). All $\times \frac{1}{2}$.

88-0234a (Figure 2), spermatangial; AST 88-0234b (Figure 3), tetrasporangial. An additional specimen was collected by Jane Lewis (Lewis 3838a) from Haian, Xuwen County, Guangdong Province, 21 April 1987.

ETYMOLOGY: *Mixta* or mixed, named for the mixture of two kinds of spermatangial configurations in the same branchlets.

Plants erect, solitary or caespitose; axes more or less percurrent, 15–45 cm long, with a small discoid holdfast. Plants purplish brown, cartilaginous, and adhere imperfectly to paper on drying. Axes and branches terete, 2–3 mm diam., branches generally simple, up to 35 cm long, abruptly constricted at their bases and distally attenuate to a fine apex. Branching pattern consists of 1–3 orders, the branches sparse or irregular, alternate or secund. In transverse section (Figure 4) the fronds consist of a medulla of large parenchymatous cells 232–598 μm diam., with walls 13–23 μm thick, that are surrounded by 2–3 layers of small cortical cells, 13–20 μm diam., the outermost layer of cells ovoid and elongate-spherical, 10–17 by 7–10 μm , and pigmented. The transition from medulla to cortex is strikingly abrupt.

Spermatangial arrangements are scattered over the surface of the frond in well-separated oblong groups with irregularly lobed margins in surface view (Figure 15), the conceptacles appearing as elongate ovals to nearly elliptical forms (Figure 12) of the *Verrucosa* type in transection, or conceptacles are of the *Polycavernosa* type, appearing in globular form in surface view, with transections showing 2–7 cavities (Figures 13–14), each cavity 66–73 by 33–40 μm or taken together 83–109 by 43–83 μm . Cystocarps (Figure 16) are prominently protruding, 864–997 by 1260–1294 μm , and are hemispherical without a beaked ostiole and not constricted at the base. The gonimoblast consists of branched, pseudoparenchymatous filaments that develop from a fusion cell; there are many upper absorbing cells (traversing filaments) that connect the gonimoblast to the pericarp; the basal absorbing filaments are few and laterally placed. The carposporangia are rounded or ovoid in shape, 23–26 by 13–23 μm . The pericarp (Figure 7) is 165–191 μm thick, consisting of

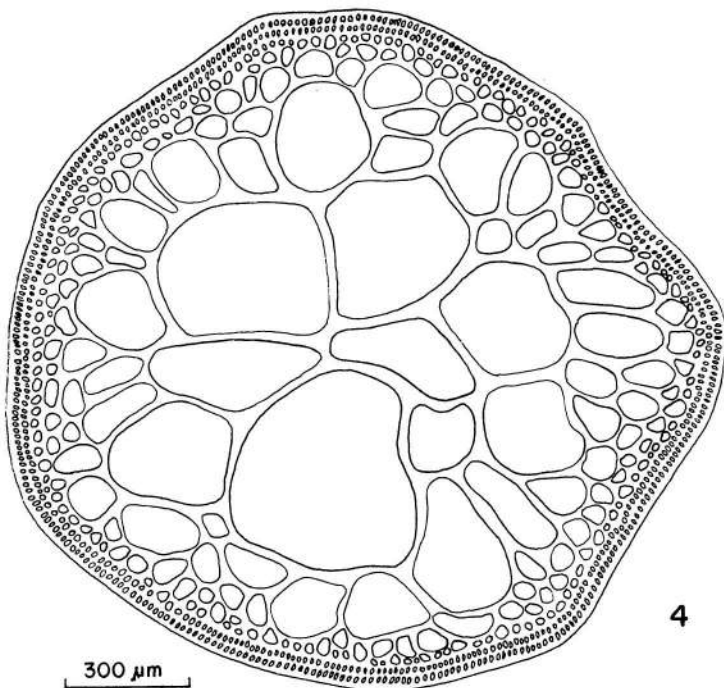
8–12 layers of cells, of which the 2 outermost layers are pigmented; the 4–5 inner ones are rounded and with secondary pit-connections; the innermost layer consists of 2–3 rows of cells that are smaller in size than other pericarpic cells.

The tetrasporangia (Figures 10–11) are scattered over the surface of frond in the external layer, cruciately divided, 26–33 by 19–26 μm in surface view, or oblong-ovoid in transection, 36–63 by 17–26 μm , and are surrounded by unmodified cortical cells.

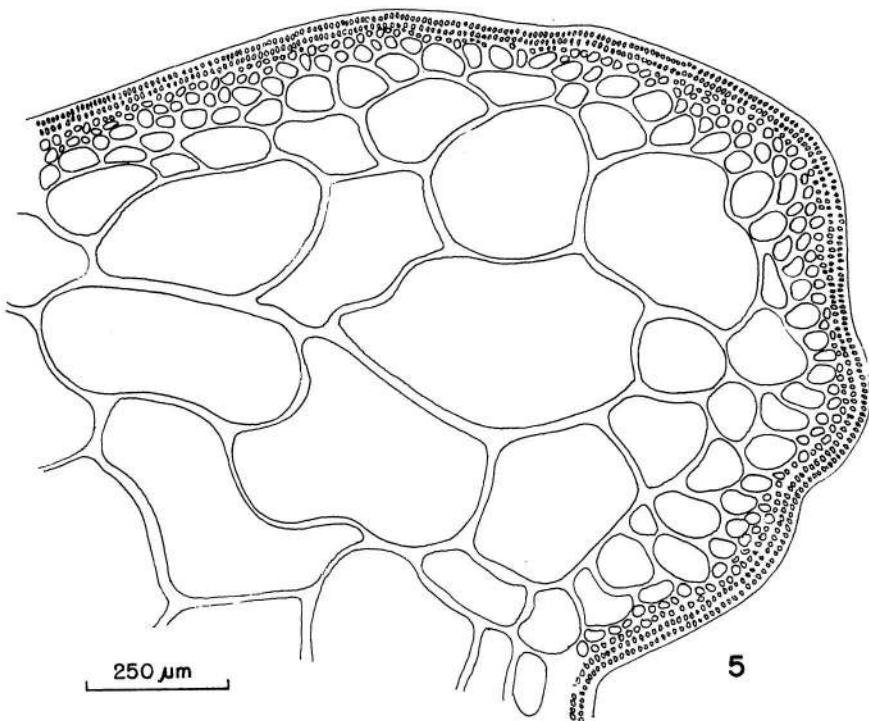
DISCUSSION

Among the Chinese species of *Gracilaria* (s.s.), *G. mixta* resembles *G. rubra* Chang & Xia most in branching pattern, and to a lesser degree *G. tenuistipitata* Chang & Xia and *G. hainanensis* Chang & Xia. From the first two, it differs in not having a strongly percurrent axis, and from the third in not being bifurcate. The second flagelliform branches of *G. mixta* are further different from those of the three other species in that they are basally constricted at their point of attachment. *G. rubra* and *G. hainanensis* have *Verrucosa*-type spermatangia; *G. tenuistipitata* shows *Textorii* type (shallow saucerlike superficial arrangements). In comparison with other Asiatic species of *Polycavernosa*, vegetative and reproductive differences and similarities are shown for *P. changii* (Figures 5, 8–9, 16–19, 21) and *P. fisheri* (Figure 22).

The occurrence of *Verrucosa*-type and *Polycavernosa*-type spermatangia in the same thallus raises several issues: (1) How were the *Verrucosa* type that were originally named by Yamamoto (1975) interpreted, and how were the *Polycavernosa* type segregated from the first? (2) How different are the two types in ontogenetic development as compared to what is published of them by Fredericq and Norris (1985) and Xia and Abbott (1985)? (3) Do all species that have *Verrucosa*-type spermatangia form *Polycavernosa* type when they mature? (4) How do these observations affect the standing of *Hydropuntia*, which now includes (Wynne 1989) all species formerly placed in *Polycavernosa*?

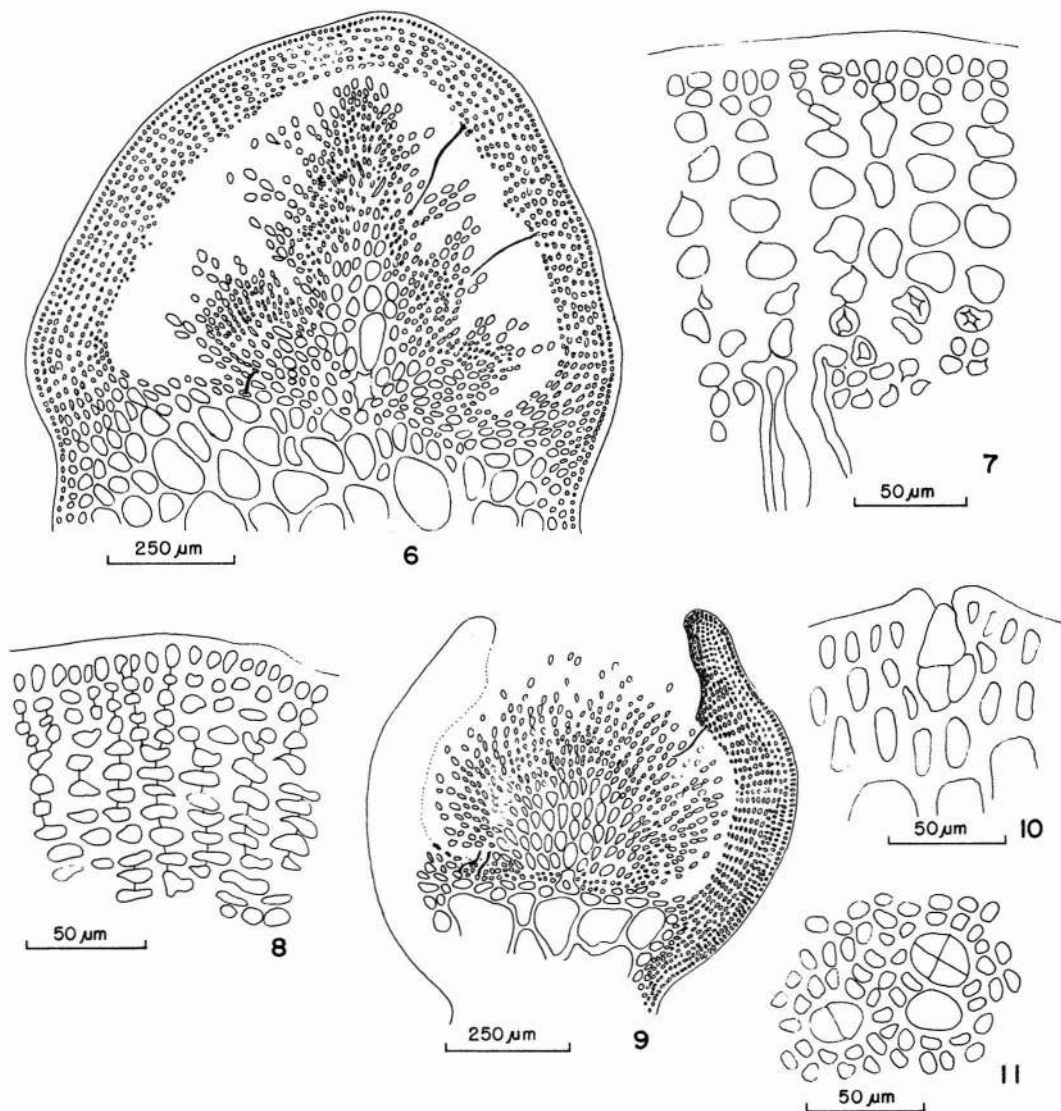


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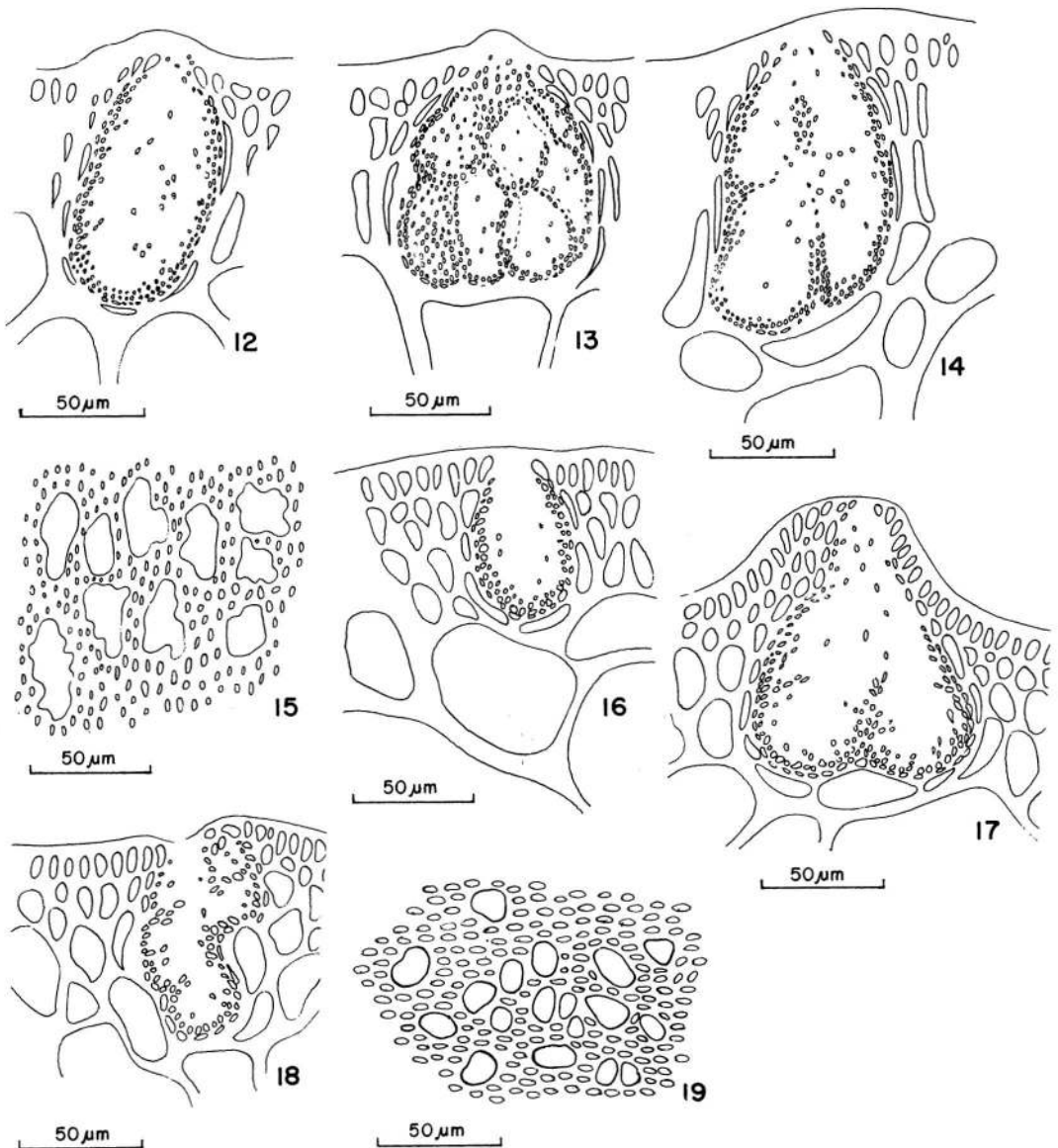
FIGURES 4–5. *Gracilaria mixta* and *G. changii*. 4, *G. mixta*, transection of part of main axis showing relationships of cortical to medullary cells (AST 880234). 5, *G. changii*, transection of part of main axis showing relationships of cortical to medullary cells (Doty 28549 from Malaysia).



FIGURES 6–11. *Gracilaria mixta* and *G. changii*. 6–7, *G. mixta* (AST 880234): 6, Longitudinal section of cystocarp showing traversing filaments. 7, Longitudinal section of pericarpial tissue. 8–9, *G. changii* (Doty 28549): 8, Longitudinal section of pericarp. 9, Longitudinal section of cystocarp showing few traversing filaments. 10–11, *G. mixta* (AST 880234b): 10, Transection of part of cortex with tetrasporangium. 11, Surface view of tetrasporangia.

Most, if not all, recent students of gracilarioids have relied too heavily on the diagrams of Yamamoto (1975) of the development of several types of spermatangia. From such illustrations, Yamamoto and others concluded that the spermatangia in the *Verrucosa* type were initially derived from outer cortical cells.

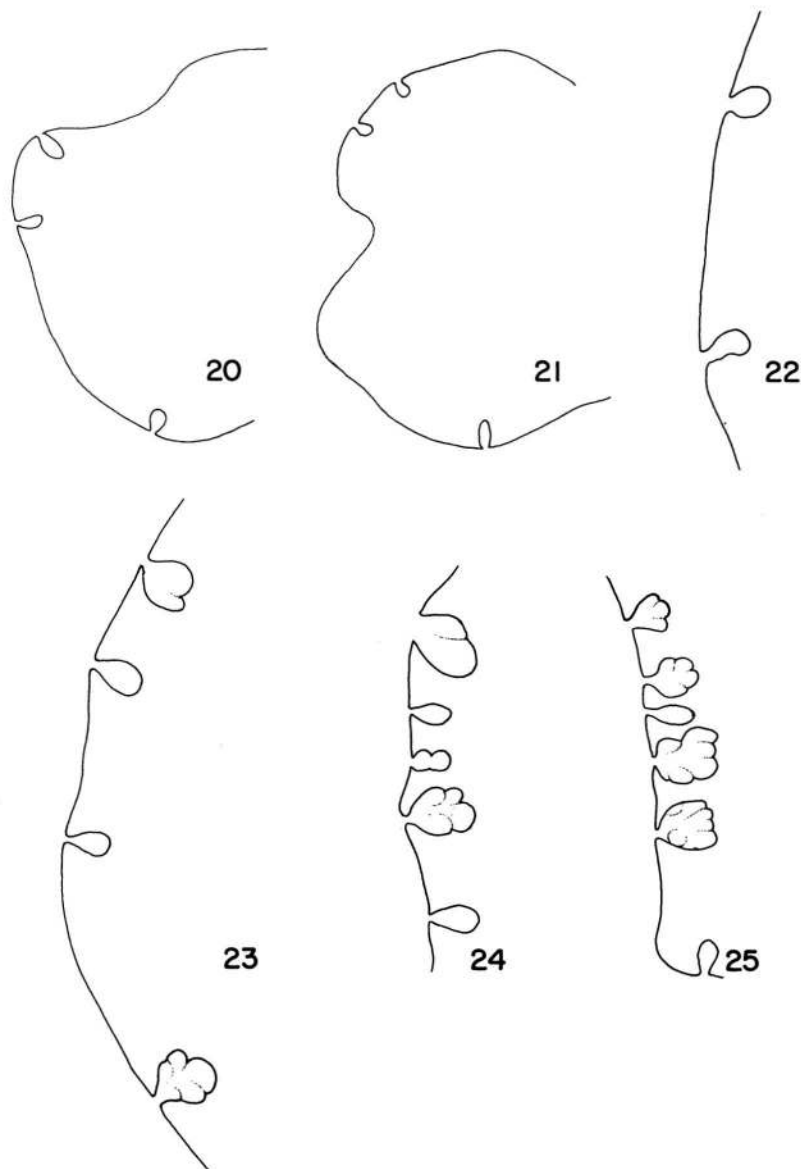
This derivation has been found to be incorrect upon examination of the ontogenetic sequences in Irish specimens of *Gracilaria verrucosa* by Fredericq and Hommersand (1989a). These workers found that “parent” cells of spermatangia in the *Verrucosa* type were intercalary (i.e., subsurface cortical



FIGURES 12–19. *Gracilaria mixta* and *G. changii*. 12–15, *G. mixta* (AST 880234a): 12, *Verrucosa*-type spermatangia. 13–14, *Polycavernosa*-type spermatangia. 15, Surface view of spermatangial arrangements. 16–19, *G. changii* (Fisher 1022 from Malaysia): 16, *Verrucosa*-type spermatangia. 17–18, Multi-cavitated *Polycavernosa*-type spermatangia. 19, Surface view of spermatangial arrangements.

cells), and they illustrated (Fredericq and Hommersand, 1989b, figs. 49–54) the development of both spermatangia and spermatangial conceptacles. Earlier, *Polycavernosa*-type spermatangial branch systems were

stated to be derived from internal cortical or outer medullary cells (Fredericq and Norris 1985) or subcortical cells (Xia and Abbott 1985). By divisions at right angles to, or thallus inward of, the original cortical cell,



FIGURES 20–25. Diagrams of transections of branches showing *Verrucosa* and *Polycavernosa* types of spermatangia. 20–22, Diagrams ca. 1 cm from apex of young branchlet showing only *Verrucosa*-type spermatangia. 20, *G. mixta* (AST 880234); 21, *G. changii* (Fisher 1022). 22, *G. fisheri* (Fisher 1087), respectively. 23–25, *G. mixta* (AST 880234): Diagrams showing *Verrucosa*-type and *Polycavernosa*-type spermatangial arrangements mixed in the same transection ca. 3 cm from apex of young branchlet.

small clusters of spermatangial mother cells and spermatangia result, filling the internal spaces at some width and depth and greatly disrupting the inner cortex or outer medullary

cells. Until now, it has been thought that this type of spermatangial development was different from *Verrucosa* type, but our present interpretation is that ontogenetically the

Polycavernosa type is a variation of the *Verrucosa* type. Both can occur together in the same thallus, or the *Verrucosa* type can stand alone.

In reexamining a specimen (AST 80-2236) of the generitype of *Polycavernosa*, *P. fastigiata* (a thallus 9.5 cm tall), an entire 1-cm-long segment at the apex of the plant contained, toward its lower end, a few *Verrucosa*-type spermatangial conceptacles: at 3 to 3.5 cm from the apex, *Verrucosa* type and *Polycavernosa* type were mixed; whereas at 4.5 cm from the apex, and below, only *Polycavernosa* type were present. Zhang (unpublished data) examined a specimen of *P. fastigiata* also (AST 80-2335) and observed a few *Verrucosa*-type conceptacles 0.25 cm from the apex, mixed *Verrucosa* and *Polycavernosa* types at 1 cm, and only *Polycavernosa* type lower than 3.5 cm from the apex of a 7-cm-tall thallus.

In our newly described species, *Gracilaria mixta*, the penultimate cortical cell and the next one proximal to it form short filaments of one to three cells (called basal cells), each of which ultimately bears one to two spermatangial mother cells, each producing one to two spermatangia. Spermatangia are ca 1.0 μm diam.; because of their abundance, they give the impression of being able to be formed sequentially from the same mother cells. In the *Polycavernosa*-type arrangement, the basal cells also appear to be able to form more mother cells in spaces left by collapsing cortical cells. Fredericq (1988:209) reported a diagnostic character for *Polycavernosa* in attributing the fusion of spermatangial "parent" cells with vegetative cells, an ability she believed accounted for the clustered occurrence of male conceptacles derived from different intercalary initials.

Because of the three-dimensionality of the maturing cavities, appearing like small baskets inside larger baskets, it is difficult to definitely follow developmental processes in either longitudinal or paradermal sections. However, at the apex and to about 1 cm below it, no conceptacles can be seen in surface view, but gradually a few small pores are seen, and by 3.0 to 4.0 mm, distinct clear spots are seen in surface view, which will become larger in diameter further away from the apex. As Xia

and Abbott (1987:415) observed, the number of conceptacles is large and their arrangement crowded, the pores rounded to spherical in surface view of the *Verrucosa*-type arrangement. In *G. mixta*, by 3 cm from the apex, a lateral coalescence of spermatangial conceptacular walls shows two to three, up to four conceptacles together. It is only after this phase has been reached that laterally confluent pockets or cavities are found at the base and midsections of the conceptacles (the smaller baskets within the larger ones). In surface view, the conceptacles look "lumpy," their margins lobed. This description does not differ substantially from that given by Xia and Abbott (1985:158–160). The interpretation is different, however, in light of observations of both *Verrucosa*-type and *Polycavernosa*-type spermatangia in the same branches. We must assume that in certain species, *Polycavernosa*-type spermatangial arrangements are the mature manifestations of the *Verrucosa* type. In other taxa such as *Gracilaria coronopifolia* J. Agardh and *G. papenfussii* Abbott, however, *Verrucosa*-type spermatangia are observed throughout the fronds, from near the apices of branches to near the basal portion of axes (Abbott, unpublished data). These observations also apply to *G. asiatica* Chang & Xia, *G. rubra*, *G. hainanensis*, *G. articulata* Chang & Xia, *G. coronopifolia* J. Agardh, and *G. salicornia* (C. Agardh) Dawson from China (Zhang, unpublished data).

These observations affect the boundaries of the genus *Gracilaria*, some of its subgenera, and the genus *Hydropuntia* (= *Polycavernosa*).

The subgenera of *Gracilaria* that were proposed by Yamamoto (1975) were mainly based upon the location and development of spermatangial arrangements. They were (1) the subgenus *Gracilaria*, with *Verrucosa*-type spermatangia; (2) the subgenus *Textoriella*, with *Textorii*-type spermatangia; and (3) the subgenus *Gracilariella*, with *Chorda*-type spermatangia (superficial spermatangia). Yamamoto (1984) later mentioned two more types of spermatangial patterns but proposed no new subgenera. *Textorii*-type spermatangia (in saucerlike depressions) grading into *Verrucosa*-type conceptacles were described by Zhang and Xia (1984) in material from

TABLE 1
DIAGNOSTIC FEATURES OF *Gracilaria*, *Gracilariopsis* AND *Hydropuntia* (*Polycavernosa*)

TAXON	TUBULAR NUTRITIVE CELLS (TRAVERSING FILAMENTS)	SPERMATANGIAL INITIALS	TETRASPORANGIA	CARPOSPORANGIA
<i>Gracilaria</i> Fredericq & Hommersand (1989a)	Present; no transformation of gametophytic cells in floor of cystocarp	Intercalary cortical cells	Basal only	In chains
<i>Gracilariopsis</i> Fredericq & Hommersand (1989b)	Absent; cells in floor of cystocarp transformed cytologically into nutritive tissue	Superficial	Terminal cells	Clusters or chains
<i>Hydropuntia</i> (= <i>Polycavernosa</i>) Fredericq & Norris (1985) Xia & Abbott (1985)	Present/absent; secondary fusions by tubular nutritive cells fusing to floor of cystocarp	Subcortical (intercalary)	Lateral or basal	Rows or chains

China, and Reading and Schneider (1986) reported a similar condition from North Carolina. Although the material from such widely separated geographic areas was identified as *Gracilaria blodgettii*, no comment is made upon the accuracy of the determination by S. Fredericq and J. Norris (unpublished data). Abbott has examined specimens from both studies and does not think that they are the same species; in other words, the mixture of spermatangial types may be more common than realized.

S. Fredericq and J. Norris (unpublished data) conclude their examination of *Textorii*-type spermatangia in *G. blodgettii* (including *G. cylindrica*) with the statement that since surface cortical (*Textorii*) and intercalary (*Verrucosa*) cells both divide by concavo-convex walls to form spermatangial mother cells, either spermatangial arrangement could be found on a given plant. The observations (above) of *Polycavernosa*-type spermatangia being derived from *Verrucosa*-type arrangements, in addition, seem to demonstrate that there may be a continuum of spermatangial types within the genus.

From the species that have been examined from very disparate geographic locations in the past few years, the range of variability of

spermatangial configurations seems now to be understood and the data are before us to make some new assessments. Table 1 gives a comparison of critical features of the cystocarpic and spermatangial development of *Gracilaria* and two genera (*Gracilariopsis* and *Hydropuntia*) recently segregated from *Gracilaria*. Although information provided in such a table is synoptic and omits details that may seem to be important to some students of this group, the results show very little that would warrant continued recognition of two genera, *Hydropuntia* (= *Polycavernosa*) and *Gracilariopsis*. Two features previously have been used to define these latter two genera: first, the presence or absence of "tubular nutritive cells" of Fredericq and Hommersand (1989a) that occur between the gonimoblast and pericarp, differentiating *Gracilaria*, as shown by its type species, *G. verrucosa*, and *Gracilariopsis* as shown by its type species, *G. lemaneiformis*, respectively. (The term "tubular nutritive cells" used by Fredericq and Hommersand [1989a] refers to the same structures called "absorbing filaments" by Xia and Abbott [1985, 1987] in consonance with its first use by Mikami [1965], when he proposed the term for postfertilization connection between the gonimoblast and sterile gameto-

phytic medullary cells in *Iridaea* [Gigartinales]. In fact, these sterile filaments form an inner [internal] pericarp around the developing gonimoblast in *Iridaea* species and appear to represent a homologous development of sterile [external] pericarpic filaments in gracilarioids. In Abbott's opinion, the concept of *absorbing filaments* is better applied to those filaments [called "upper absorbing filaments" by Xia and Abbott 1987] than is the term "nutritive filaments" [applied by Dawson 1949] or "tubular nutritive cells" [applied by Fredericq and Hommersand 1989a,b]. Better than these because of its neutrality is the term *traversing filaments*, offered by Kraft [1977]. The actual nutritive cells or filaments have never been demonstrated to be nutritive in function; the term itself is already applied to a totally different filament that connects the products of carpogonial fusion with an auxiliary cell in the Gigartinales [s.l.]. Such filaments are tubular [i.e., there are no other kinds of nutritive filaments under the above definitions.] There is some question about the usefulness of "nutritive" cells or filaments as a feature of prime importance in the delimitation of genera. As used by Fredericq and Hommersand (1989b), this character comes second only to that of spermatangial formation in *Gracilariopsis*, yet earlier it was implied by Bird and McLachlan (1984) that at least in *Gracilaria foliifera* such filaments appear in aging cystocarps, but not in younger ones in the same thallus. In other taxa, for example, traversing filaments are seen in the cystocarps of *G. rubra*, with *Verrucosa*-type spermatangia (Chang and Xia 1976: 101, figs. 1, 4, 5), thus similar to *G. verrucosa* (Fredericq and Hommersand 1989a), but are lacking in cystocarps of *G. tenuistipitata*, thus similar to *Gracilariopsis* (Fredericq and Hommersand 1989b), but with *Textorii*-type spermatangia (Chang and Xia 1976: 104, figs. 1, 3). In many species of what had been segregated as *Polycavernosa*, some species have traversing filaments, and some lack them. Within the same species there can be no absolute designation of male type since individual plants of given species in many cases show an intergrading series of spermatangial types.

The second feature concerns the place of

origin of the spermatangial mother cells. As shown in the table and explained above, this is of doubtful value, as it has been demonstrated that the *Verrucosa* type and *Textorii* type may grade into each other, as do the *Verrucosa* type and *Polycavernosa* type. Although the *Chorda* type shown by *Gracilariopsis* so far has been determined to be stable, perhaps insufficient numbers of specimens have been examined. We suggest that the genus *Gracilariopsis* be tentatively accepted until such time as more specimens are examined and the invariability of their spermatangial arrangements is better established. The four species recognized by Fredericq and Hommersand (1989b) are *G. lemaneiformis* (Bory) Daws., *Acleto* & Foldvik, *G. chorda* (Holmes) Ohmi, *G. costaricensis* Dawson, and *G. tenuifrons* (Bird & Oliveira) Fredericq & Hommersand. To these should be added *Gracilariopsis heteroclada* (Zhang & Xia) Zhang & Xia, comb. nov. (basionym: *Gracilaria heteroclada* Zhang & Xia, 1988, Taxonomy of Economic Seaweeds 2:132, figs. 10-17).

These observations indicate that although spermatangia have been very useful in identifying and separating the species of *Gracilaria*, as a result of this study they are demonstrated to be of less value than they were thought to be 15 years ago (Yamamoto 1975). To accept this stand is to admit that the taxonomy of gracilarioids has become more difficult: the feature that marked subgenera probably only can be used broadly, but not absolutely, to characterize species. The following changes are made in western Pacific taxa that we have reexamined since Zhang and Xia (in the present paper) found the mixture of *Verrucosa*-type and *Polycavernosa*-type spermatangia on the same branchlets and thalli of *G. mixta*. In these 10 species, both kinds of spermatangial arrangements are present.

1. *Gracilaria stellata* Abbott, Zhang & Xia, nom. nov.

SYNONYM: *Polycavernosa divergens* Xia & Abbott, 1987, Phycologia 26:409. *Hydropuntia divergens* (Xia & Abbott) Wynne, 1989, Taxon 38:477. Non *Gracilaria divergens* (C. Ag.) J. Agardh, 1876, Epicr., p. 420.

ETYMOLOGY: Named for the star-shaped contents of the pericarpic cells.

2. *Gracilaria changii* (Xia & Abbott) Abbott, Zhang & Xia, comb. nov. (See Figures 5, 8–9, 16–19, 21)

BASIONYM: *Polycavernosa changii* Xia & Abbott, 1987, Phycologia 26:407.

SYNONYM: *Hydropuntia changii* (Xia & Abbott) Wynne, 1989, Taxon 38:476.

3. *Gracilaria edulis* (Gmelin) Silva, 1952, Univ. Calif. Berkeley Publ. Bot. 25:293.

BASIONYM: *Fucus edulis* Gmelin, 1768, Hist. Fuc., p. 113.

SYNONYMS: *Polycavernosa fastigiata* Chang & Xia, 1963, Stud. Mar. Sin. 3:125. *Hydropuntia fastigiata* (Chang & Xia) Wynne, 1989, Taxon 38:477.

Note: Probably the most common name used for Pacific *Gracilaria* specimens from nineteenth-century collections is *Gracilaria lichenoides*, which Silva (1952) equates with *G. edulis*. Although there is no known type specimen of *G. edulis*, and only very questionable ones of Lamourouxian *lichenoides*, the identification of *G. lichenoides* from the Pacific matches those specimens that are identified as *Polycavernosa fastigiata*. When first recognized, *P. fastigiata* was of limited occurrence and the specimens expressed a relatively narrow morphology, since extended by examination of hundreds of specimens from the waters of the warm western Pacific.

4. *Gracilaria fisheri* (Xia & Abbott) Abbott, Zhang & Xia, comb. nov. (See Figure 25)

BASIONYM: *Polycavernosa fisheri* Xia & Abbott, 1987, Phycologia 26:411.

SYNONYM: *Hydropuntia fisheri* (Xia & Abbott) Wynne, 1989, Taxon 38:477.

5. *Gracilaria percurrans* (Abbott) Abbott, comb. nov.

BASIONYM: *Polycavernosa percurrans* Abbott, 1988, Taxonomy of Economic Seaweeds 2:146.

SYNONYM: *Hydropuntia percurrans* (Abbott) Wynne, 1989, Taxon 38:477.

6. *Gracilaria bangmeiana* Zhang & Abbott, nom. nov.

SYNONYMS: *Polycavernosa ramulosa* Chang

& Xia, 1963, Stud. Mar. Sin. 3:125. *Hydropuntia ramulosa* (Chang & Xia) Wynne, 1989, Taxon 38:477.

Non *Gracilaria ramulosa* J. Agardh, 1876, Epicr., p. 417.

Non *G. furcellata* f. *ramulosa* (J. Agardh) May, 1948, Aust. CSIRO Bull. 235, p. 56.

ETYMOLOGY: Named for our respected colleague, Xia Bangmei.

7. *Gracilaria subtilis* (Xia & Abbott) Xia & Abbott, comb. nov.

BASIONYM: *Polycavernosa subtilis* Xia & Abbott, 1987, Phycologia 26:413.

SYNONYM: *Hydropuntia subtilis* (Xia & Abbott) Wynne, 1989, Taxon 38:477.

8. *Gracilaria tsudae* (Abbott & Meneses) Abbott, comb. nov.

BASIONYM: *Polycavernosa tsudae* Abbott & Meneses, 1987, Micronesica 20:195.

SYNONYM: *Hydropuntia tsudae* (Abbott & Meneses) Wynne, 1989, Taxon 38:477.

9. *Gracilaria urvillei* (Montagne) Abbott, comb. nov.

BASIONYM: *Hydropuntia urvillei* Montagne, 1842, Prodromus generum, specierumque phycearum novarum . . . , p. 7.

SYNONYMS: *Corallopsis urvillei* (Montagne) J. Agardh, 1876, Sp. Gen. Ord. Alg. 3(1): 583. *Polycavernosa urvillei* (Montagne) Xia & Abbott, 1987, Phycologia 26:414.

10. *Gracilaria vanbosseae* (Abbott) Abbott, comb. nov.

BASIONYM: *Polycavernosa vanbosseae* Abbott, 1988, Taxonomy of Economic Seaweeds 2:152.

SYNONYM: *Hydropuntia vanbosseae* (Abbott) Wynne, 1989, Taxon 38:378.

Non *Gracilaria cylindrica* of Weber van Bosse, 1928, Siboga Expedition Monograph 59a:432.

The six following species assigned to *Hydropuntia* by Wynne (1989) have not been re-examined; they are not from the western Pacific and we lack material of some of them. However, because four of them were previously in *Gracilaria*, they are restored there.

11. *Gracilaria cornea* J. Agardh, 1852, Sp. Gen. Ord. Alg. 2(2): 598.

SYNONYM: *Hydropuntia cornea* (J. Agardh) Wynne, 1989, Taxon 38:476.

12. *Gracilaria crassissima* (Crouan & Crouan) Crouan & Crouan, 1866, in Schramm & Maze, Essai . . . , p. 20.

BASIONYM: *Plocaria crassissima* Crouan & Crouan, 1866, in Schramm & Maze, Essai . . . , p. 20.

SYNONYMS: *Polycavernosa crassissima* (Crouan & Crouan) Fredericq & Norris, 1985, Taxonomy of Economic Seaweeds 1:152. *Hydropuntia crassissima* (Crouan & Crouan) Wynne, 1989, Taxon 38:477.

13. *Gracilaria rangiferina* (Kützinger) Piccone, 1886, Alg. Vettor Pisani, p. 71.

BASIONYM: *Sphaerococcus rangiferinus* Kützinger, 1849, Sp. alg., p. 779. (= *S. cervicornis* of Kützinger, 1843, Phyc. Gen. Pl. 62, fig. II.)

Non *S. cervicornis* (Turner) C. Agardh.

SYNONYMS: *Gracilaria dentata* J. Agardh, 1852, Sp. Gen. Ord. Alg. 2(2): 603. *Polycavernosa dentata* (J. Agardh) Lawson & John, 1987, Mar. Alg. Trop. Africa, p. 228. *Hydropuntia dentata* (J. Agardh) Wynne, 1989, Taxon 38:477. *Gracilaria henriquesiana* Hariot, 1908, J. Bot. Paris, ser. 2, 1:162 (as to syntype, leg. *Ribeiro*, No. 14, Paris Museum). *Polycavernosa henriquesiana* (Hariot) Chang & Xia, as to specimens reported by Ohmi, 1968, Bull. Fac. Fish., Hokkaido Univ. 19:83, pl. 2, fig. 6. *Hydropuntia henriquesiana* (Chang & Xia) Wynne, 1989, Taxon 38:477.

Note: Kützinger (1843: pl. 62, fig. II) illustrated the habit and a cross section of this alga, showing tetrasporangia in a compressed thallus, under the name *Sphaerococcus cervicornis* (Turner) C. Agardh [*Gracilaria cervicornis* (Turner) J. Agardh]. The material was said to have come from the Antilles. Later, Kützinger (1849:779) decided that this material was distinct from *S. cervicornis* and described it as a new species, *S. rangiferinus*. This time the specimen was said to have been collected at Pernambuco and given to Kützinger by Binder. Still later, Kützinger (1868: pl. 86, Figs. a,b) again illustrated the type material; the figures were essentially similar to those published in 1843.

J. Agardh (1852), in the protologue of his new species *Gracilaria dentata*, stated that this alga had been depicted by Kützinger in 1843 under the name *Sphaerococcus cervicornis* and later described by Kützinger as a new species, *S. rangiferinus*. It is clear, therefore, that *Gracilaria dentata* was initially superfluous and hence illegitimate. According to Art. 7.13 of the ICBN, *G. dentata* is automatically typified by the type of *Sphaerococcus rangiferinus* because J. Agardh did not definitely indicate a different type. We have examined a representative specimen of *Gracilaria dentata* in the Agardh herbarium (no. 29496) and have compared sections prepared from it with sections made from the type of *Sphaerococcus rangiferinus* (in Kützinger herbarium, Leiden). We conclude that J. Agardh's concept of *G. dentata* is conspecific with *G. rangiferinus*.

With respect to the several specimens of *G. henriquesiana*, which are divided between Coimbra and Paris Museum herbaria (Steen-toft 1967), *Ribeiro* No. 14 (a syntype in Paris Museum) is cystocarpic. The cystocarp does not contain any of the large "basal absorbing filaments" (or basal traversing filaments) that species of *Polycavernosa* (s.s.) show. This species was not listed as being in Ghana by Lawson & John (1987).

14. *Gracilaria multifurcata* Børgesen, 1953, Biol. Medd. K. Dan. Vidensk. Selsk. 21(9): 42.

SYNONYMS: *Polycavernosa multifurcata* (Børgesen) Chang & Xia, 1963, Stud. Mar. Sin. 3:126. *Hydropuntia multifurcata* (Børgesen) Wynne, 1989, Taxon 38:477.

15. *Gracilaria albornozi* (Rodriguez) Abbott, comb. nov.

BASIONYM: *Polycavernosa albornozi* Rodriguez, 1988, Ernstia 46:1.

SYNONYM: *Hydropuntia albornozi* (Rodriguez) Wynne, 1989, Taxon 38:477.

16. *Gracilaria corymbiata* (Rodriguez) Abbott, comb. nov.

BASIONYM: *Polycavernosa corymbiata* Rodriguez, 1986, Ernstia 38:23.

SYNONYM: *Hydropuntia corymbiata* (Rodriguez) Wynne, 1989, Taxon 38:477.

Note: *G. albornozii* and *G. corymbiata* male plants have not been examined by us; tetrasporangial plants that Professor Rodriguez sent to Abbott appear to represent distinct species.

Finally, the consequences of these observations require comments upon the subgenera of *Gracilaria* in the framework of the classification of Yamamoto (1978), which all students of the genus have followed. If *Gracilaria* is reinstated as an independent genus, the subgenus *Gracilariella* Yamamoto (1975), based upon *Chorda*-type spermatangia, is superfluous. Similarly, with the observations of Zhang and Xia (1984) and Reading & Schneider (1986) that *Verrucosa*-type and *Textorii*-type spermatangia may grade into each other, the subgenus *Textoriella* Yamamoto (1975) is compromised. The stability of the *Verrucosa* type is further questioned when the multicavitated spermatangial arrangements of *Polycavernosa* are shown to be derived from it. On the other hand, at least seven species mentioned earlier are known to show the *Verrucosa* type of arrangement and to maintain that type throughout the thallus; there are many species with *Textorii*-type spermatangia also that retain their configuration throughout the plant. Why some taxa appear to be stable in this feature and others unstable is not known. Further studies on this will be necessary, just as other features will need retesting and reevaluation.

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