Gracilaria and *Polycavernosa* (Rhodophyta) from Micronesia

ISABEL MENESES and ISABELLA A. ABBOTT

Department of Botany, University of Hawaii, Honolulu, Hawaii 96822 U.S.A.

Abstract.—Three species of the red algal genus *Gracilaria* (Gracilariaceae) and four entities, one a new species, of the closely related genus *Polycavernosa* are recognized from material deposited in the University of Guam herbarium. *Gracilaria salicornia*, widely reported under a variety of names from throughout the warm Pacific and Indian Ocean is recognized as morphologically variable, and includes several taxa previously thought to be independent. On the other hand, a specimen from Saipan which might have been identified as *G. salicornia* on account of its habit shows superficial (Chorda-type) spermatangia which would place it in a different species. Among the four different groups of specimens that are identified with *Polycavernosa* on account of spermatangial or cystocarpic features, a new species, *P. tsudae* is described. Taking into account the numerous islands of Micronesia (Marianas, Carolines, Marshalls, western Kiribati, Tavalu) from which few or no algal collections have been made, the seven taxa show a remarkable diversity when compared to the Ryukyus, for example, where repeated collections show 11 species of *Gracilaria*, and no species of *Polycavernosa*.

Introduction

Species of *Gracilaria* and the closely related *Polycavernosa* are widely distributed geographically in warm seas, and also inhabit a variety of habitats such as lagoons, coral reefs, eroded limestone and rock tidal pools. Many of the species are economically useful and as a consequence the correct names for the species have become important. At a workshop held in Guam in 1984 and sponsored by the U.S. Sea Grant College programs bordering the Pacific, several students of these genera met and studied specimens that were brought by each investigator. In concert, it could be seen that previously held notions of species were sometimes wholly incorrect, and in other cases that boundaries of species were too narrow and were in need of restatement. Some of the conclusions appeared in the Workshop results (Abbott and Norris, 1985), others in separate papers (Zhang and Xia, 1985; Xia, 1986), and this paper is also an offshoot of the Workshop.

As Xia (1986) has shown, features chosen to distinguish *Gracilaria salicornia* are not constant, and furthermore these same features transgress boundaries that were supposed to identify *G. crassa*, *G. cacalia*, *G. minor* and *G. canaliculata*. Independently, on examining Guam and other material, we concur with her opinion that all of these species should be placed under *G. salicornia*, the oldest available name.

On the other hand, the interpretation of other authors e.g., Yamamoto (1978, pl. 49, fig. 5) and Trono and Ganzon-Fortes (1980, p. 91) of *Gracilaria eucheumoides* shows that the plants from Micronesia are not nearly as compressed, nor coarse as those from the Ryukyu Islands and the Philippines, thus broadening the description of the species. The internal anatomy of this species, whatever the external morphology, seems unusually stable, the cortex being more than 3 cells in thickness and the medullary cells appearing fairly uniform in size and shape.

Of the 10 species of *Gracilaria* recognized by Tsuda (1985) for Micronesia, *G. eucheumoides* is confirmed, as is *G. salicornia* (including *G. cacalia, G. crassa,* and *G. minor*), *G. edulis, G. coronopifolia* and *G. arcuata* are removed from the flora. The materials of the recorded *G. radicans* and *G. "verrucosa"* were not seen.

KEY TO THE SPECIES OF *GRACILARIA* FROM MICRONESIA

1. Plants decumbent. not matted, with groups of 3–4 flattened axes arising from a common disc; branches with opposite club-shaped or spinous branchlets; plants with no constrictions .... *G. eucheumoides*
1. Plants usually forming a matted, entangled mass of branches with free ends erect; axes and branches terete, branching irregular; cylindrical axes constricted or not, those with constrictions showing truncated terminal apices, and those without constrictions with acute terminal tips 2
    2. Branching pattern irregular, dichotomous or trichotomous, alternate or unilateral, the intervals between points of branching irregular also; constrictions throughout thallus, or occasionally present in main axes but not branches, or altogether absent .... *G. salicornia*
    2. Branching pattern regular, each branch with 3 to 4 nodes, the intervals (internodes) regular; branches conspicuous and strongly constricted .... *Gracilaria* sp. #1

Gracilaria salicornia (C. Agardh) Dawson. (Figs. 1–5).

Dawson, Bull. So. Calif. Acad. Sci. 53: 4, 1954a; Ohmi, Bull. Fac. Fish., Hokk. Univ., 6: 27, 1958; Trono, Micronesica 5: 64, 1969; Yamamoto, Mem. Fac. Fish., Hokk. Univ. 25: 135, 1978; Trono and Ganzon-Fortes, Illus. Seaweed Flora, p. 93, 1980; Trono *et al.*, Kalikasan Phil. J. Biol. 12: 23, 1983; Tsuda, Tax. Econ. Seaweeds, p. 91, 1985; Xia Bangmei (1986).

Synonyms: *Gracilaria cacalia* (J. Agardh) Dawson, Bull. So. Calif. Acad. Sci. 53: 5, 1954a [basionym: *Corallopsis cacalia* J. Agardh Sp. gen. et ord. alg., p. 583 (403 by error) 1852]; *Gracilaria crassa* Harvey ex J. Agardh, Sp. gen. et ord. alg., p. 417, 1876; *Gracilaria minor* (Sonder) Durairatnam, Ceylon Dept. Fish. Res. Station Bull. 10: 12, 1961 [basionym: *Corallopsis salicornia* var. *minor* Sonder, Alg. Trop. Austral, p. 24, 1871]; *Gracilaria canaliculata* (Kützing) Sonder, Alg. Trop. Austral., p. 56, 1871 [basionym: *Sphaerococcus canaliculatus* Kützing Tab. Phyc. 18: 29, 1868]; *Corallopsis opuntia* J. Agardh, Sp. gen. ord. algarum, p. 409, 1876.

The specimens are more or less prostrate with an entangled mass of irregularly disposed branches with their free ends erect, axes and branches adhering to the substratum by means of many small discs. Specimens show different degrees of branch constriction, these varying among plants and within axes and branches of the same plants. Plants range from nodes not constricted through slightly to more constricted, or the constrictions are so prominent that they affect the appearance of the whole thallus, where the nodes are extremely narrow at their bases while strongly thickened in their upper extremities. Main axis inconspicuous to completely absent, the thallus width variable ranging from 0.8 mm to 4.0 mm, reaching up to 5.0 mm where the axes give rise to 3 or more branches. Branching pattern irregular, dichotomous or trichotomous in most plants, or alternate or unilateral; 3 to 5 orders of branching; branches highly variable in length; last orders of branching giving rise to 2 to 5 terminal branches ranging from 3 mm to 10 mm long; acute tips in most of non-constricted branches and truncated tips in most of the plants with constrictions.

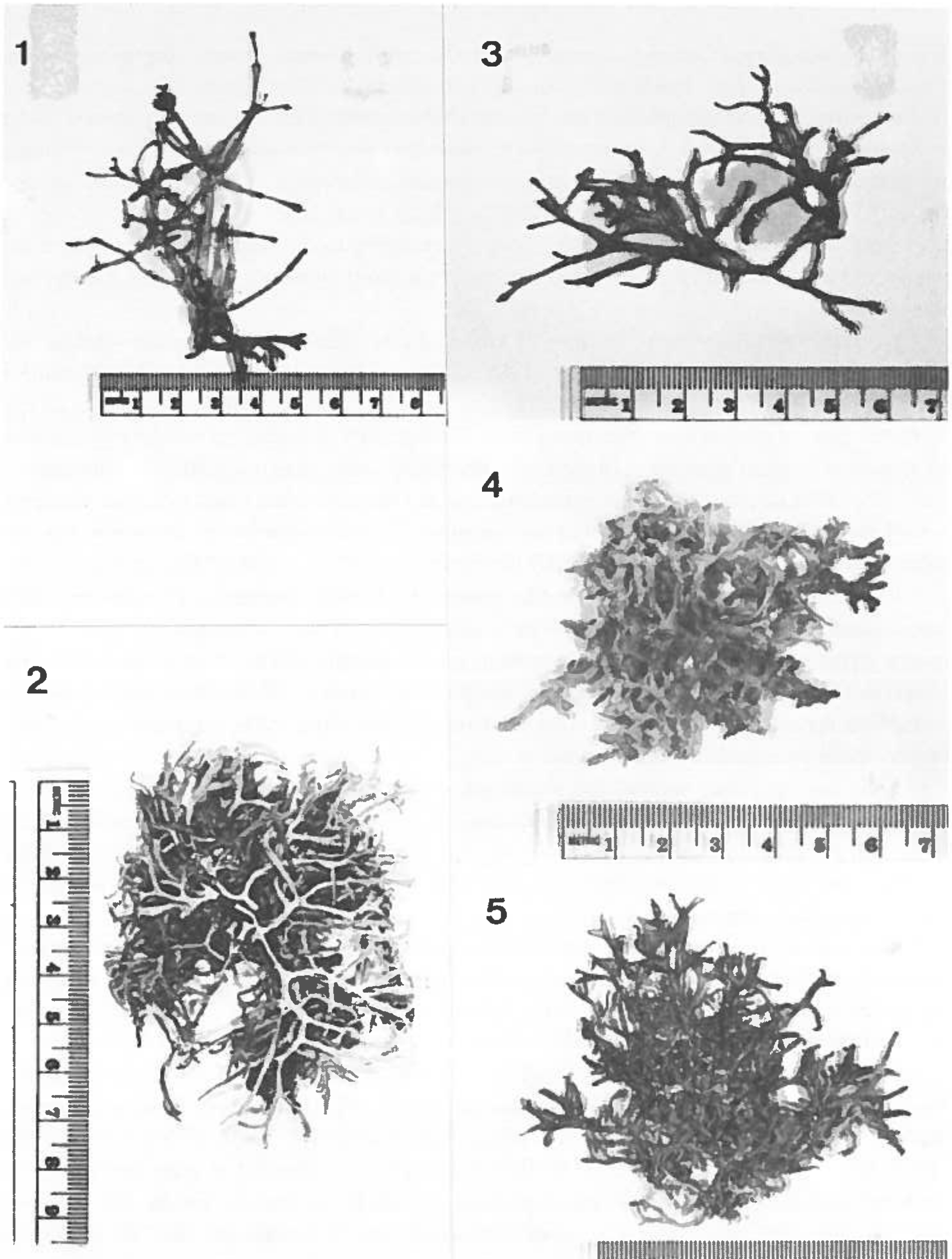
Cortical layer consisting of one or two rows of elongated or slightly compressed cells, (3.5)4.5–11.1(13.5) μm long and (2.2)3.5–7.0(11.1) μm wide. The transition from cortex to medulla is abrupt. The medullary cells increase more or less gradually in diameter toward the center, the outermost cells show, in some cases, a large content of floridean starch granules. Innermost medullary cells reach (170)220–450 μm $\times$ (230)320–600 μm and show no apparent cellular contents. Hair basal cells are scattered among the cortical cells in some but not all plants, usually elongated, intensely staining with aniline blue; (20)22.5–35.0(40.0) μm long and (5)7.5–15.0(20.0) μm wide.

Only one cystocarpic specimen was found. It showed rounded, non-rostrate cystocarps, gonimoblasts made of large, slightly elongated and highly vacuolated cells, carpospores terminal, absorbing filaments present and abundant, borne from central cells and often connected to the pericarp cells. Pericarp of two kinds of tissue, that nearest and gonimoblast arranged in several horizontal rows of bricklike cells, and distal of these, smaller cells arranged in anticlinal rows.

Only one specimen among the plants was male. The plant showed conspicuous constrictions along its branches. The spermatangial conceptacles (Verrucosa-type) are scattered along the entire surface of the frond and are deep, obovate, surrounded by three cortical layers of modified cells, occasionally laterally fused, 67.5–87.5 μm deep; 35.0–67.5(82.5) μm wide.

The cruciately divided sporangia are scattered over the entire surface of the frond, immersed in slightly modified cortical layers where the cells are elongated anticlinally and the cortex consists of 3–4 rows of cells. Sporangia ranged from 30 μm to 52.5 μm long ($X = 40.66\ \mu m$, $S_d = 6.06\ \mu m$) and 15.0 to 32.5 μm wide ($X = 21.5\ \mu m$, $S_d = 4.8\ \mu m$).

DISTRIBUTION: *Mariana Islands: Anatahan,* RT 4886; *Saipan,* Tanapag Harbor, RT 3130; Garapan Lagoon, RT 5358; Chalan Kanoa, RT 1946; *Rota,* near Afuefuniyao Pt., RT 2756; *Guam,* Tamuning, RT 1807; Agana Bay, RT 5070, 5059, MVCF 792; Cocos Lagoon, s.n., 200 m east of Bobbi Island; s.n. leeward barrier reef, leg. R. Rechebei and R. Tsuda; s.n. on patch reef leg. R. Rechebei and R. Tsuda; RR 12; Pago Bay, on inner reef, RT 2027; s.n. inner reef southwest of marine lab, leg. R. Rechebei; V. P. P.#23; Agat Bay, s.n. south of boat channel, leg. S. G. Nelson; RT 5361; Umatac, RT 1896; Tumon Bay, RT 1740; 2139; 2093; 2097; outer reef flat near Fujita Hotel, leg. R. Rechebei and R. Tsuda; M. R. Carlson #2; B. C. Stone 5053; R. H. Randall 57; R. S. Sanders #17; B. C. Stone 5072; Saupon Pt., RT 1861; Inarajan, leg. Fletcher #21; Asanite Pt., B. C. Stone 4879; Ipan, RT 2110; Toguan Bay, R. Randall 155; Tanguisson, intertidal near power plant, leg. R. Rechebei; Asan Beach, leg. J. Taitano. *Caroline Islands: Yap:* Colonia, RT 5351. *Belau:* Babelthuap, RT 4048; Aurepushekam Island, RT



Gracilaria salicornia. Fig. 1. Specimen with very narrow segments and inconspicuous constrictions from San Vitores Beach, Tumon Bay, Guam (Tsuda 2139). Fig. 2. From leeward barrier reef at reef margin, Cocos Lagoon, Guam, leg. R. Rechebei and R. T. Tsuda. Fig. 3. Specimen from the same collection as Figure 1 showing different branching pattern. Fig. 4. From the same collection as Figure 2 showing different branching pattern and marginal proliferations. Fig. 5. From outer reef flat near Fujita Hotel, Tumon Bay, Guam, leg. R. Rechebei.

4053; Airai channel, Pa-68-5; s.n. leg. Halsted and Mote; Koror, P. Lansing #93; s.n. on dead coral between Koror and Babelthuap. *Pohnpei:* RT 2370.

The above material includes the records (Tsuda 1985) upon which *G. arcuata, G. cacalia, G. crassa,* and *G. salicornia* were identified for Micronesia.

The species is abundant in inshore locations near the Marine Laboratory of the University of Guam.

Other distribution: Widely distributed in the Old World tropics from the Red Sea (Newton, 1953); Indian Ocean (Durairatnam, 1961; Rao, 1972); South China (Chang and Xia, 1976); southern Japan and Ryukyu Is. (Ohmi, 1958; Yamamoto, 1978); Australia (Withell, unpublished, 1985); Philippines (Manila Bay, type locality), and throughout the Philippines (Trono and Ganzon-Fortes, 1980; Trono et al., 1983; Abbott, 1985), Hawaiian Islands (Xia, 1986; Abbott, 1985).

DISCUSSION: Cell sizes (cellular area) versus cell position in a vertical cell row (from cortex to medulla) were compared for those Micronesian plants previously identified as *G. arcuata* Zanardini, *G. salicornia* (C. Agardh) Dawson, and *G. crassa* Harvey ex J. Agardh. Gradation of cell size from outermost cell to medulla was determined using the method developed by Yamamoto (1978). Values of cell size versus cell position for the three species fit a semilogarithmic curve without significant deviations ($P < 0.005$), suggesting that there are no significant differences in the cellular size patterns of the three groups of specimens. The Japanese species showed no significant differences in their cellular pattern excepting *G. eucheumioides* Harv. (Yamamoto, 1978). The gradation of cell size in Micronesian specimens showed an abrupt change from cortex to medulla, as well as among the three outer-most medullary layers, but a rather gradual increase among the central medullary cells. For each cell position (point of the curve) 115 cells of 23 specimens were measured, their area evaluated by multiplying the minor and major diameters.

In addition to the similarities in the internal structure, *G. salicornia* shows a close resemblance to *G. crassa* in external characters, both species in Guam showing variable degrees of constrictions. Ohmi (1958) mentioned the degree of constriction as the only clear distinction between the two species from Japan, but this character is as highly variable in the Guam specimens as in the Japanese specimens (Yamamoto, 1978). Great variability in any character that is used for discriminating taxa is reason for its abandonment, and calls for substitution of other features that are more stable. Since some habitat differences are correlated with branching patterns and constrictions (Trono and Ganzon-Fortes, 1980) and Xia (1986), it is suggested that external vegetative features are unreliable for this group of taxa, and that they should be merged and recognized as one variable species with stable reproductive features. Moreover, anatomical details of gametophytes and sporophytes are similar in all of these specimens, whether externally constricted or not. In RT 2097 and MRC 2, some branches are constricted and others lack constrictions.

Cystocarpic and tetrasporangial plants of salicornia-type specimens from this Micronesian material are very similar to those described from China (Chang and Xia, 1976), Japan (Ohmi, 1958; Yamamoto, 1978) and from the type locality in the Philippines (Trono et al., 1983). The large, vacuolated gonimoblastic cells and abundant absorbing filaments of the Guam material is identical with the description of cystocarps of *G. arcuata* as identified from Japan by Ohmi (1958). Furthermore, spermatangial conceptacles of "arcuata" and "salicornia" from Japan are similar in shape and sizes to the Guam material, but the Guam material has smaller conceptacles than those reported for *G. arcuata* var. *arcuata* from India by Rao (1972). However, these comparisons are not based upon type or topotype material from the Red Sea and *G. arcuata* of Rao (1972), Ohmi (1958), Chang and Xia (1976) and Yamamoto (1978) are not thought to represent Zanardini's *G. arcuata* as clearly implied by Børgesen's (1934) illustration of plants from India which he claimed matched Zanardini's description. A search in the Paris, Copenhagen and British Museum collections of *Gracilaria* specimens did not reveal any Red Sea material of *G. arcuata.*

Gracilaria eucheumoides Harvey. (Fig. 6).

Dawson, Pac. Sci. 8: 438, 1954b; Trono, Micronesica 5: 63, 1969; Yamamoto, Mem. Fac. Fish. Hokk. Univ. 25: 136, 1978; Trono and Ganzon-Fortes, Illus. Seaweed Flora Philippines, p. 91, 1980; Saraya and Trono, Nat. and Appl. Sci. Bull. 34: 40, 1982.

Mostly prostrate plants attached to the substratum by a small disc from which a small number of coarse, thick, compressed branches arise. Branches provided with club-shaped or spinous opposite branchlets, the branching pattern irregular, first order usually unilateral, the next higher orders irregularly alternate; upper parts of the main axes strongly branched in twos or threes. Main axes up to 4 mm wide, moderately to strongly compressed.

Cortical layer consisting of (2) 3–4 rows of cells, 2.5–7.5 (12.5) μm wide, 4.0 – 12.5(16.5) μm long; medulla consisting of 20 to 25 layers of cells slightly increasing in diameter toward the center, from outermost to innermost cells ranging from 30 – 240 μm × 50 – 290 μm, innermost cells range from 130 to 210 μm × 160 to 290 μm. Hairs deciduous, hair basal cells scattered among the cortical cells, elongated or somewhat bottle-shaped, 25.0 – 35.0(37.5) μm long and 10 – 12.5(17.5) μm wide.

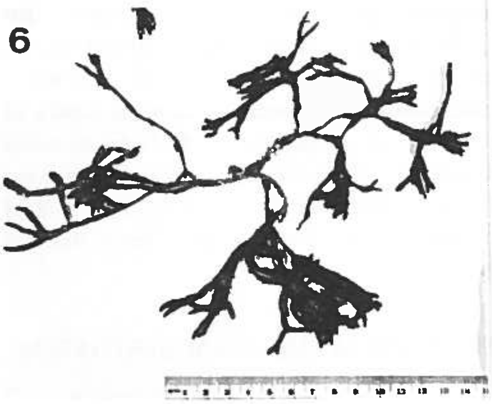
Except for one tetrasporangial specimen reported by Yamamoto (1978), specimens assigned to this species are usually sterile.

The four specimens identified with this species are from Yap and Belau: on sandy bottom near shore between Pelak and Goffen entrance, Yap (RT 5370); in inner lagoon reef in *Enhalus* bed, at 1–2 m deep at Pelak, Yap (RT 3976); and growing on dead coral, 0.4 m deep, off bridge between Koror and Babelthuap, Belau. These are new records not previously reported by Tsuda (1985).

Among the species examined in this study, only this one shows a 3-layered cortex and a central medulla with cells of rather uniform shape and size. The specimens agree with the internal and external characteristics of *G. eucheumoides* described by Yamamoto (1978) but the medullary cells in the Micronesia material are smaller than those reported from Japan. A comparison with the description of the Philippines material (Trono *et al.*(1983) shows that there are certain differences in the number of cortical layers, the Micronesian material having 2 to 3 layers while the plants reported by Trono *et al.* (1983) have up to 4 cortical layers and their cells are larger (20 to 30 μm diameter).

Gracilaria sp. #1. (Fig. 7).

Plant regularly branched, consisting of long internodes constricted at their ends and each giving rise to 2–4 branches with noticeable narrow bases. Approximately 12 cm tall, terete axes ranging from 1 to 2 mm wide.



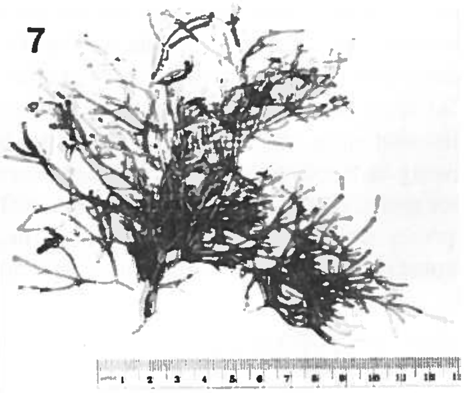


Fig. 6. *Gracilaria eucheumoides* from between Pelak and Gofenu entrance, Yap, Western Caroline Islands (Tsuda 5370). Fig. 7. *Gracilaria* species with Chorda-type spermatangia, from Susupe, Saipan, leg. R. Rechebei.

Cortex of 1–2 layers of anticlinally elongated cells, disposed uniformly close together; change from cortex to medulla rather abrupt, outermost medullary cells small, increasing gradually toward the center of the axis. Cortical cells 7.5–10.0(12.5) μm long and 2.5–5.0 μm wide, the cells full of floridean starch granules. Central medullary cells 260–460 μm diameter, almost isodiametric.

Only one specimen (spermatangial) collected on a sandy reef at about 1 m depth at Susupe, Saipan, leg. R. Rechebei.

DISCUSSION: Although superficially resembling *G. salicornia* in the occasional constrictions that are present, the specimen is more erect than prostrate. Spermatangia are cut off by outermost cells of the cortical layer and on the surface are continuous as is typical of the Chorda-type spermatangia (Yamamoto, 1978). Spermatangia of *G. salicornia* occur in conceptacles (Verrucosa-type spermatangia).

Since this specimen resembles *G. salicornia* in its "typical" constricted axes and branches (found to be rather atypical in specimens examined in this paper), each specimen must be examined carefully in order to clearly distinguish these two taxa. Perhaps cystocarpic plants will show some distinction between the two species.

Polycavernosa

The genus *Polycavernosa* was described by Chang and Xia (1963) to include those species that develop spermatangial conceptacles with internal cavities or diverticula, and that possess absorbing filaments at the base of the gonimoblast, lying in the cortical layers, or as later modified by Xia and Abbott (1985) also along the lateral regions of the pericarp. These are different from absorbing filaments (=nutritive filaments) that commonly occur in some species of *Gracilaria* where gonimoblast tissue is frequently connected to the pericarp, a feature previously used (Dawson, 1949) to distinguish *Gracilaria* species from *Gracilariopsis* species. Although these unique spermatangial configurations and basal absorbing filaments are not yet universally accepted as definitive features that segregate two genera (Bird and McLachlan, 1982), Fredericq and Norris (1985) furnish features of post-fertilization events that further support the generic distinctions. The material from Micronesia, possibly outliers for the genus that appears to have its center of distribution in Malaysia, spreading to the Indian Ocean, is identified with *Polycavernosa* owing to the distinctive spermatangial arrangements. However, cystocarpic plants were not collected for several of the recognized taxa and they are necessary to be certain of species identification. We are dividing the specimens into three groups. This is the first report of the genus for the northern Mariannas.

KEY TO THE SPECIES OF *POLYCAVERNOSA* FROM THE GUAM HERBARIUM

1. Plants no more than 2.5 cm tall, branches compressed, axes somewhat arcuate . . . 2
1. Plants more than 3 cm tall, up to 17 cm, branches subdichotomous to irregularly divided; axes not arcuate . . . 3
2. Frond segments wide, penultimate segments spreading, apices blunt . . . *Polycavernosa* species #2
2. Frond segments narrow, penultimate segments abruptly giving rise to short branchlets with acute apices . . . *Polycavernosa* species #3
3. Axes of main branches tapering at base, fronds with irregular distant branches . . . *Polycavernosa* species #1
3. Axes of main branches not tapering at base, fronds subdichotomously divided; plants 10–17 cm tall, terete to somewhat compressed, with 1–4 orders of branching, 0.5 to 1.0 mm diam . . . *Polycavernosa tsudae*

Polycavernosa species #1 (Fig. 8).

Plants up to 10 cm tall, with an irregular unilateral branching habit, branching to 3–4 orders, the main branches frequently tapering to the axis, the ultimate orders frequently spinelike; fronds drying compressed though surface wrinkled and indicating a previously fleshy condition. Cortex 2-celled, cells 10–15 μm diam, cells abruptly changing size into the medulla. Spermatangial conceptacles crowded, the cortical cells between them elongated, in younger parts of the thallus ovate to obovate, becoming lobulated in later stages of development, 60–100 μm deep and 50–90 μm wide. These two specimens (from 200 m east of Bobbi Islands, Cocos Lagoon, Guam) were identified by Xia Bangmei and H. Yamamoto at the Workshop as *G. arcuata* Zanardini.

Polycavernosa species #2, #3. (Fig. 9).

Fronds of species #2 no more than 2.5 cm tall, attached by means of a small disc from which several erect axes arise, dichotomously or fastigiately branched into short, broad branchlets; apices acute, rounded, or flat. Cortex 1–2 rows of cells, cells rounded 9(10)–11(13.5) μm long and 4.5(5)–7(8) μm wide. In portions of the frond bearing spermatangial conceptacles the cortex is modified to 3–4 rows, and elongated anticlinally when located next to the conceptacles. The change from cortex to medulla is abrupt; medullary cells increase in size inwardly, the innermost cells range from 200 to 400(600) μm diameter. Occasionally floridean starch granules are present in the medullary cells.

No cystocarpic or tetrasporangial plants were found among the Guam material. This plant was collected at 1 m deep on reef flat at Saupon Pt., Tamuning (RT 1884), and has spermatangial conceptacles profusely lobulated in early stages of development, larger than those of *Polycavernosa* species #1, 100 to 150 μm deep, 70 to 180 μm maximum diameter. It was identified by Xia Bangmei as *G. salicornia*. The third plant (collected 20 m south of Cocos Island, Cocos Lagoon) exhibits immature spermatangial conceptacles grouped in patches over most of the frond that resemble ovate conceptacles of Verrucosa-type (Yamamoto, 1978), but when larger and more mature show clear diverticula. This last specimen (*Polycavernosa* #3) shows the largest cortical cells of the three plants, which may be correlated with the pattern of distribution of the spermatangial conceptacles in the frond. It was identified by Xia Bangmei and H. Yamamoto as *G. arcuata* Zanardini.

The material allows identification to the genus *Polycavernosa* but prevents species identification which at this time (Xia and Abbott, 1985) relies on habit, nature of cystocarp details and spermatangial details of which this material only offers the last. Because of overall similarities in spermatangial conceptacle structure, all three specimens are tentatively grouped as one species. Since the spermatangia in these three specimens show different degrees of development of the conceptacles, it is suggested that this feature should be carefully examined since some of the young conceptacles could be thought to be those of Verrucosa-type in the genus *Gracilaria*.

Polycavernosa tsudae Abbott and Meneses, sp. nov. (Figs. 10–13).

Plants 12–17 cm tall, from a short main axis with several leading branches; second order branches subdichotomous, branchlets irregularly alternate, frequently unilateral or flagellate, last order frequently short and proliferous or if terminal, branchlets elongate and tapering. Branches up to 0.5 mm diam. with rounded apices. Tetrasporangial plants with more numerous branching orders and branchlets than cystocarpic plants; the single male specimen with fewer orders of branching than the female and sporic plants and more elongated than either.

Cortex of 1 row (occasionally 2), formed of small, darkly staining, irregularly shaped cells, mostly rounded, 3.0 to 10 μm long (n = 148 cells) and 3.0 to 12.5 μm wide (n = 243 cells). Medullary cells rows 6–11, the cell sizes changing abruptly, a few large central cells irregularly shaped, 90–240 × 130–360 μm diameter.

Cystocarps protruding, rounded, not basally constricted. Gonimoblast cells small, numerous, crowded, and slightly elongated. Absorbing filaments rare to scarce, located at the base of the gonimoblast or appearing at the upper portion of it, occasionally invading the pericarpic tissue. Pericarp of 7–11 cell layers of thin-walled periclinally elongated cells with star-shaped contents and 6–8 small islands of tissue close to the spore mass.

Tetrasporangial plants with cruciately divided tetrasporangia, 30–45 μm long and 15–30 μm wide, the cortex surrounding sporangia modified, forming 2 to 3 rows of anticlinally elongated cells.

The single spermatangial plant shows lobulated spermatangial conceptacles ranging from 40 to 70(85) μm deep and 30(35) to 50 μm diameter. Internal diverticula are present throughout all stages of development.

Frondes 11–17 cm altae, ramificatio irregularis, axes et rami teretes. Cortex unicellularis (raro bicellularis). Cystocarpia sine basali constrictione, non rostrata, cum paucis basalibus filis absorbentibus. Cellulae pericarpii cum contentis stellatis.

Holotype: Abbott 17672, collected in Saipan Lagoon by Stephen G. Nelson, May 21, 1985 (BISH); isotypes in GUAM and AST. Other specimens: *Saipan:* Tanapag Harbor, RT 3145; Garapan Lagoon, RT 5357; Pt. Arigan, RT 3220; s.n. in seagrass area off Hafa Adai Hotel; Abbott 17383, 20 m offshore from the Hyatt Hotel, common on sand-coral rubble substrate at 1–2 m depth, leg. Heather Fortner (BISH). *Guam,* Sella Bay, RT 5068; s.n. from Cetti or Sella Bay, leg. S. G. Nelson; Fouha Bay, RT 4780; Nimitz Channel, RT 5359. *Yap,* Caroline Islands, Tomil Harbor entrance, RT 3960.

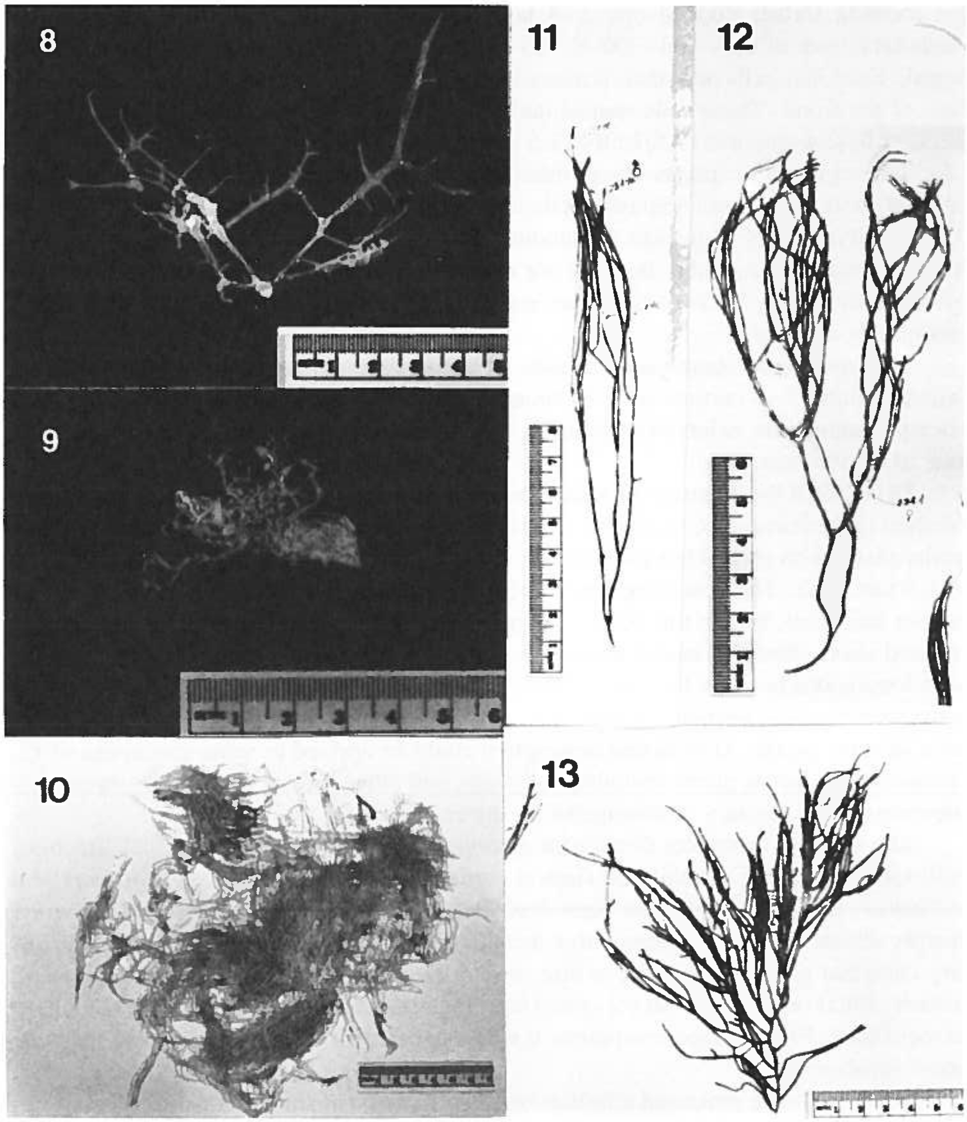
We name this species for Dr. Roy T. Tsuda, University of Guam, whose abiding interest in algae has resulted in many published papers on them and who has established a very good herbarium of algae at the University of Guam that represents an excellent collection from the warm Pacific.

The new species is closely related to *P. fisheri* Xia and Abbott (1987), described from Thailand, based upon features of the cystocarp where there is no basal constriction in both species, few absorbing filaments, and both show pericarp cells with star-shaped contents. The branching patterns of both taxa are very variable as the contrasting descriptions show. The two species differ in that the cystocarps are rostrate in *P. fisheri* and not in *P. tsudae,* the cortex is 3–4 celled in *P. fisheri* and 1–2 celled in *P. tsudae.* While the former feature has not been tested on large numbers of specimens of *Polycavernosa,* the latter feature appears to be a stable one even though a vegetative character.

This new species is similar in gross aspect to *Polycavernosa subtilis,* described by Xia and Abbott (1987) from Penang, Malaysia where the branching pattern, however, is more strongly dichotomous, the cystocarps basally constricted, terminally rostrate, possessing abundant and very robust basal absorbing filaments. In *P. tsudae,* the branching pattern is irregular, frequently unilateral, the cystocarps not basally constricted, not rostrate, and possessing few or no absorbing filaments. Also, in separating from the pericarp, the spore mass is torn away, leaving islands of small cells below the pericarp proper, and in this way resembling torn *tela arachnoidea* of certain Rhodymeniales (cf. *Fauchea* of Kylin, 1930, p. 34, fig. 21c).

Cell sizes of the type material are given in ranges since neither cell length nor cell width are normally distributed (Kolmogorov test, $P < 0.01$), so values cannot be expressed as means and standard deviations. The length and width of cortical cells was compared among tetrasporangial, cystocarpic and male specimens; there is no significant difference among the cortical cell lengths of the three reproductive stages; nevertheless, the male specimen has significantly narrower cortical cells than the cystocarpic and tetrasporangial plants (Kruskal-Wallis test, $P<0.01$). This slight difference in cortical structure could well be due to the presence of spermatangial conceptacles. The statistical tests may be found in Sokal and Rohlf (1969).

In the Guam material, the cortex is of 1–2 cell rows, (5.0)7.5 to 12.5(15.0) μm long and 3.75 to 7.5(10.0) μm wide; cell sizes abruptly changing between cortex and medulla,



Polycavernosa species. Fig. 8. *P.* species #1 from 200 m east of Bobbi Island, Cocos Lagoon, Guam, leg. S. G. Nelson. Fig. 9. *Polycavernosa* #3 from 20 m south of Cocos Island sand islet, Cocos Lagoon, Guam, leg. S. G. Nelson. Fig. 10. *Polycavernosa tsudae* from reef patch off Pt. Muchot, Tanapag Harbor, Saipan (Tsuda 3145). Fig. 11. Spermatangial plant of *P. tsudae* from Saipan Lagoon, leg. S. G. Nelson, May 21, 1985 (Abbott 17672). Fig. 12. Cystocarpic plant of *P. tsudae* (Abbott 17672). Fig. 13. Tetrasporangial plant of *P. tsudae* (Abbott 17672). (Figs. 11–13 are specimens from the holotype sheet, BISH).

the medulla further divided into 3–4 layers of intermediate sized cells and an inner medullary layer of cells 100–300 × 120–330 μm in diameter. Although no hairs were found, basal hair cells persisted, scattered among the cortical layers along the entire surface of the frond. These cells stained dark blue with aniline blue, ranging from 17.5 to 22.5(30.0) μm long and (7.5)10.0–12.5 μm wide.

Two cystocarpic plants show small cystocarps neither rostrate nor basally constricted, with small gonimoblastic cells uniformly sized, carpospores terminal in short 3–4 celled filaments. In median longitudinal section, the gonimoblast is lobed. Absorbing filaments present but neither frequent nor conspicuous, mostly restricted to the basal part of the gonimoblast. Pericarp cells with star-shaped contents. No male plants were found among this material.

Tetrasporangial plants have cruciate tetrasporangia, immersed in modified cortical layers forming 3–4 cortical rows of rounded cells. The cortical cells surrounding each tetrasporangium are enlarged anticlinally. Mature tetrasporangia are 20 to 30 μm wide and 20.5–50.0 μm long.

DISCUSSION: A group of specimens that we recognize as close to *P. tsudae* are labelled (in herbario) as *Gracilaria edulis* or *G. coronopifolia* and are loosely branched or bushy plants with several branches arising directly from a basal disc and with branches up to 1.5 mm wide. The branching pattern of some plants is dichotomous, irregularly alternate or unilateral, branch tips acute. The pattern in other plants differs by irregularly distributed short, flexible, lateral branchlets, single or grouped in twos or threes, usually with long nodes between branches, ultimate orders of branching short and numerous, in some axes forming terminal groups of 4–5 small branches giving a corymbose appearance to some plants. This second description could be applied to some specimens of *G. coronopifolia*. These plants resemble *P. tsudae*, and other species of *Polycavernosa;* fertile material is necessary to distinguish the species.

The material resembles *Gracilaria coronopifolia* J. Agardh in its internal structure, both species showing variable cell sizes in cortical and medullary cells. *G. coronopifolia* in Hawaii, its type locality, has been described as having a single or two-celled cortex sharply distinct from the adjacent large medullary cells (Dawson, 1949) or having medullary cells that gradually increase in size toward the center of the axis (Yamamoto, 1978; Abbott, 1985) or, finally, with a 2-celled layer between the cortex and the large medullary tissue (Ohmi, 1958) in Japanese plants. It would appear that there might be more than one taxon involved here.

There are some structural affinities between *Gracilaria edulis* (Gmelin) Silva as described by Japanese workers and the material from Guam, although the descriptions of *G. edulis* are confused in the literature, one group of descriptions (Ohmi, 1958; Yamamoto, 1978) clearly aligning the material to the genus *Gracilaria*, and another description clearly attributing the species to *Polycavernosa* (Umameshwara Rao, 1972) as it is now delimited. Furthermore, Ohmi (1958) described abundant connective filaments (=absorbing filaments) between the gonimoblast and the pericarp, while in the Guam specimens, absorbing filaments are hardly distinguishable and infrequent. Another difference is that tetrasporangia in *G. edulis* are surrounded by slightly modified cortical cells as described by Yamamoto (1978) for the Japanese specimens, while in the specimens collected in

Guam, cortical cells are distinctly modified in the region of the tetrasporangia, being enlarged anticlinally more than the adjacent cortical cells.

A fuller description of the material is provided here since the habits of the specimens show variation and cell measurements are also somewhat variable. It is hoped that such a broad interpretation of vegetative aspect, coupled with reproductive details will aid in identification of this new species.

Acknowledgments

We are grateful to Dr. Jack Davidson of the University of Hawaii Sea Grant Program for funds that allowed this study to be conducted; we thank Dr. Roy T. Tsuda for the loan of specimens from the University of Guam Herbarium, and Xia Bangmei for helpful discussions upon species limits in this group of red algae. We thank the Curators of Algae at the British Museum (Natural History) (BM), Botanical Museum, University of Copenhagen (C), and the Cryptogamic Herbarium, Paris (PC) for the loan of specimens. We are grateful to Karla McDermid for the Latin description of the new species of *Polycavernosa*.

This research was sponsored in part by the University of Hawaii Sea Grant College Program under Institutional Grant No. NA81AA-D-00070 from NOAA Office of Sea Grant, Department of Commerce.

References

Abbott, I. A. 1985. *Gracilaria* from the Philippines: List and distribution of the species. In: I. A. Abbott and J. N. Norris, (eds.), Taxonomy of Economic Seaweeds, pp. 89–90. Calif. Sea Grant College Program, La Jolla.

Abbott, I. A., and Norris, J. N. (Eds.). 1985. Taxonomy of Economic Seaweeds. Calif. Sea Grant College Program, La Jolla. 167 pp.

Agardh, J. G. 1852. Species gen. ord. algarum . . . Lund. 2 (2): 1–504.

———. 1876. Species gen. ord. algarum . . . Leipzig. 3(1): Epicrisis system. florid. 724 pp.

Bird, C. J., and McLachlan, J. 1982. Some underutilized taxonomic criteria in *Gracilaria* (Rhodophyta, Gigartinales). Bot. Mar. 25: 557–562.

Børgesen, F. 1934. Some Indian Rhodophyceae especially from the shores of the Presidency of Bombay: IV. Bull. Misc. Inform. Roy. Bot. Gard. Kew, 1: 1–31.

Chang, C. F., and Xia Bangmei. 1963. *Polycavernosa*, a new genus of the Gracilariaceae. Stud. Mar. Sinica 3: 119–126.

Chang, C. F., and Xia Bangmei. 1976. Studies on Chinese species of *Gracilaria*. Studia Mar. Sinica 11: 91–163 (in Chinese).

Dawson, E. Y. 1949. Studies of Northeast Pacific Gracilariaceae. A. Hancock Found. Publ., Occ. Pap. 7: 1–105.

———. 1954a. Notes on Tropical Pacific Marine algae. Bull. South. Calif. Acad. Sci. 53(1): 1–7.

———. 1954b. Marine plants in the vicinity of the Institut Oceanographique de Nha Trang, Vietnam. Pac. Sci. 8(4): 373–481.

Durairatnam, M. 1961. Contribution to the study of the marine algae of Ceylon. Fish. Res. Station, Dept. Fish., Ceylon Bull. 10: 1–181.

Fredericq, S. and Norris, J. N. 1985. Morphological studies on some tropical species of *Gracilaria* Grev. (Gracilariaceae, Rhodophyta): Taxonomic concepts based on reproductive morphology. In: I. A. Abbott and J. N. Norris (eds.) Taxonomy of Economic Seaweeds, pp. 137–155. Calif. Sea Grant College Program, La Jolla.

Kützing, F. T. 1868. Tabulae Phycologicae 18: 35, + 100 pls.
Kylin, H. 1930. Über die Entwicklungsgeschichte der Florideen. Lunds Univ. Arsskr. N. F. Avd 2. 26: 104 pp.
Newton, L. M. 1953. Marine Algae. In: Sci. Rept John Murray Exped. 1933–34, 9 (no. 5): 395–420.
Ohmi, H., 1958. The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. Mem. Fac. Fish. Hokkaido Univ. 6(1): 1–66.
Rao, M. Umamaheswara. 1972. On the *Gracilaria* of the seas around India. J. mar. biol. Ass. India 14(2): 671–696.
Saraya, A., and G. C. Trono, 1982. The marine benthic algae of Santiago Island and adjacent waters in Bolinao, Pangasinan. II. Rhodophyta. Nat. and Appl. Sci. Bull. 34(1): 1–83.
Sokal, R. R., and F. J. Rohlf, 1969. Biometry. W. H. Freeman, San Francisco. 776 pp.
Sonder, O. W. 1871. Die Algen des tropischen Australiens. Naturw. Verein Abhandl. 5(2): 35–74.
Trono, G. C. 1969. Benthic algae of the Caroline Islands. II. Phaeophyta and Rhodophyta. Micronesica 5(1): 25–119.
Trono, G. C., A. Azanza-Corrales, and D. Manuel, 1983. The genus *Gracilaria* (Gigartinales, Rhodophyta) in the Philippines. Kalikasan, Phil. J. Biol. 12(1–2): 15–41.
Trono, G. C., and E. T. Ganzon-Fortes, 1980. Illustrated Seaweed Flora of Calatagan, Batangas, Philippines. 115 pp. Univ. Phil. Mar. Sci. Center, Manila.
Tsuda, R. T. 1985. *Gracilaria* from Micronesia: Key, List and Distribution of the Species. In: I. A. Abbott, and J. N. Norris, (eds.) Taxonomy of Economic Seaweeds, pp. 91–92. Calif. Sea Grant Program, La Jolla.
Xia Bangmei (1986). On *Gracilaria salicornia* (C. Agardh) Dawson. Chin J. Oceanol. Limnol. 4: 100–105, 1. pl.
Xia Bangmei, and I. A. Abbott, 1985. The genus *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta): a comparison with *Gracilaria* Grev., and a key to the species. In: I. A. Abbott, and J. N. Norris, (eds.), Taxonomy of Economic Seaweeds, pp. 157–162. Calif. Sea Grant College Program, La Jolla.
Xia Bangmei and I. A. Abbott, (1987). New species of *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta) from the western Pacific. Phycologia 26: 405–418.
Yamamoto, H., 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25(2): 97–152.
Zhang JunFu and Xia Bangmei. 1985. Some problems in the taxonomy of Chinese species of *Gracilaria* (Rhodophyta). Proc. Int. Seaweed Symp. 11: 59–62.