

## A Taxonomic Review of Hawaiian Gelidiales (Rhodophyta)<sup>1</sup>

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**ABSTRACT:** The present study reviews most collections of Gelidiales known from Hawaii. Three genera, each one including four species, are recognized among nearly 350 specimens examined. The genus *Gelidiella* is represented in Hawaii by *G. acerosa* (Forsskål) Feldmann et Hamel, *G. adnata* Dawson, *G. macbrisiana* Dawson, and *G. myrioclada* Børgesen. The genus *Gelidium* includes *G. crinale* (Turner) Lamouroux, *G. pluma* Loomis, *G. pusillum* (Lamouroux) Le Jolis, and *G. reediae* Loomis. The genus *Pterocladia* is represented in Hawaii by *P. bulbosa* Loomis, *P. caloglossoides* (Howe) Dawson, *P. caerulescens* (Kützinger) Santelices, and *P. capillacea* (Gmelin) Bornet et Thuret.

Only six of the 21 species of Gelidiales previously reported for Hawaii were found to be represented in the material studied. There is evidence of misidentification in at least eight cases, and two specific epithets based on Hawaiian specimens are considered to be synonymous with other species. Five species previously reported from Hawaii are still unchecked due to their absence from the material studied. Seven previously unreported species of Gelidiales were added as new records for the Hawaiian flora. A key is given that identifies the Hawaiian Gelidiales, and this is followed by a description, with illustrations and a discussion, of each of the 12 species found.

TWENTY-ONE SPECIES of the red algal order Gelidiales have been so far reported for the Hawaiian Islands. The first eight were published by Chamberlain (1860), all of them lacking descriptions and exact indications of locality, and several with nonvalid specific epithets. Eight other species were listed later by Reed (1907), these also without descriptions and more than half of them with tentative determinations only. Two more were added by Neal (1930) from her ecological study at Waikiki. The species were identified as *Gelidium* sp. 1 and *Gelidium* sp. 2, with descriptions so general that they cannot be identified now. In 1960, Loomis described and illustrated five new species from Hawaii. Loomis stated that the Hawaiian specimens were collected by Reed and distinguished them with Reed's number. Regrettably, Reed gave no numbers in her publication and it is now unclear

if any or all the new species described by Loomis correspond to any of the forms originally listed by Reed with tentative names.

The present study was started in order that the taxonomy of the Hawaiian members of the group might be clarified. It was expected that such a review would reduce to less than 21 the number of species recognized for Hawaii, independent of the possibility that new records for the islands might be added later. Special emphasis was placed on studying the herbarium collections on which the previous identifications had been based, as well as on examining new collections present at various institutions. The herbarium of the Allan Hancock Foundation provided the type specimens of three species of *Gelidium* described from Hawaii; the herbarium of the University of California had the type specimens of three species of *Pterocladia* together with almost 120 mostly unidentified specimens of gelidioid algae collected in Hawaii by E. Y. Dawson, M. Reed, W. A. Setchell, and J. Tilden. The Bernice P. Bishop Museum lent close to 80 specimens collected by M. S. Doty, M. Reed, J. F. Rock, W. A. Setchell,

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and J. Tilden, and a few by J. E. Chamberlain. The personal herbarium of Dr. M. S. Doty provided close to 150 specimens collected on the several islands of the archipelago. In the

following text are frequent references to these herbarium specimens. The abbreviations AHF, UC, BPBM and DORY are used to indicate the origin of the material discussed.

KEY TO THE SPECIES OF GELIDIALES IN HAWAII

1. Internal hyphae absent ..... 2 (*Gelidiella*)
1. Internal hyphae present ..... 5
2. Thalli more than 2 cm high. Erect axes cylindrical, arcuate, 500–600  $\mu\text{m}$  in diameter ..... *Gelidiella acerosa*
2. Thalli smaller than 2 cm high. Erect axes less than 250  $\mu\text{m}$  in diameter ..... 3
3. Thalli less than 1 mm high. Attached by prostrate filaments with unicellular rhizoids through most of their undersurface. Erect axes up to 75  $\mu\text{m}$  in diameter ..... *Gelidiella adnata*
3. Thalli 1–2 cm high ..... 4
4. Erect axes cylindrical, up to 180  $\mu\text{m}$  in diameter, congenitally fused near the base, irregularly branched above. All axes ending in conically attenuated apices .... *Gelidiella myrioclada*
4. Erect axes flattened, up to 260  $\mu\text{m}$  broad and 160  $\mu\text{m}$  thick, unbranched in their most basal half, alternately and subdistichously branched above. Branches contracted near the base, slightly clavate ..... *Gelidiella machrisiana*
5. Cystocarps bilocular, with one or more ostioles on each surface. Carposporangia not in short chains ..... 6 (*Gelidium*)
5. Cystocarps unilocular, with one or more ostioles on only one surface. Carposporangia usually in short chains ..... 9 (*Pterocladia*)
6. Thalli 3 to 20 cm high, plumosely or pinnately branched ..... 7
6. Thalli 0.5 to 7 cm high, irregularly branched ..... 8
7. Thalli plumosely branched at their apical half, with margins subentire or dentate below. Axes up to 20 cm high and 1.5 mm broad. Tetrasporangia and cystocarps on pinnately compound, somewhat twisted, and densely congested branches ..... *Gelidium pluma*
7. Thalli pinnately branched up to 5 orders, sometimes pyramidal in appearance. Axes to 5 cm high, and up to 1.0 mm broad. Tetrasporangia and cystocarps on ultimate portions of enlarged, flat branches ..... *Gelidium reediae*
8. Axes cylindrical or slightly flattened, up to 350  $\mu\text{m}$  broad and up to 7 cm high. Scarcely branched. Branches appearing rather as dichotomies. Tetrasporangia on expanded sori at the end of axes and branches ..... *Gelidium crinale*
8. Axes flat, compressed, up to 3 cm high and 2 mm broad. Simple or irregularly branched along the margins or with lanceolate proliferations from the truncate upper end of the erect axes. Branches lanceolate or spatulate, contracted at their bases. Tetrasporangia in rounded sori on ovoid or rounded fertile branches ..... *Gelidium pusillum*
9. Thalli small, repent, up to 1.5 cm high and composed of creeping axes, with holdfasts and 2–5 simple branches at each node. Younger cells in oblique rows. Young tetrasporangia in V-shaped rows ..... *Pterocladia caloglossoides*
9. Thalli with erect fronds, above 2 cm high ..... 10
10. Thalli with pectinate branching. Erect axes up to 5 cm high with short, cylindrical or slightly clavate branches along the margins. Tetrasporangia in sori at the terminal swollen portions of branches, resembling bulbous stichidia ..... *Pterocladia bulbosa*
10. Thalli pinnately branched ..... 11
11. Thalli light or dark green, sometimes almost blackish; up to 7 cm high, regularly or irregularly branched. Cystocarps elongated, up to 2 mm long, without prominent peristome but with evident sterile margins ..... *Pterocladia caerulescens*
11. Thalli red, typically with pyramidal outlook, up to 200 cm high and pinnately branched in the upper half of the erect fronds. Cystocarps rounded, up to 600  $\mu\text{m}$  in diameter, with protruding peristome ..... *Pterocladia capillacea*

SPECIES OF GELIDIALES IN HAWAII  
GELIDIELLA*Gelidiella acerosa* (Forsskål) Feldmann et Hamel*Synonyms*

Feldmann and Hamel 1934, p. 533. *Fucus acerosus* Forsskål 1775, p. 190 (obligate synonym). Facultative synonyms: *Echinocaulon acerosus* (Forsskål) Børgesen 1932, p. 5, pl. 1, fig. 3; *Fucus rigidum* Vahl 1802, p. 46; *Gelidium rigidum* (Vahl) Greville in Montagne 1842, p. 45; *Gelidiopsis rigida* (Vahl) Weber van Bosse 1904, p. 104; *Echinocaulon spinellum* Kützing 1843, p. 40; *Echinocaulon ramelliferum* Kützing 1868, p. 14, pl. 39; *Echinocaulon rigidum* Kützing 1868, pl. 40, fig. a, d.

*Description*

Thalli up to 5 cm high (Figure 1A) formed by several tufted, entangled, cylindrical, and sometimes arcuate erect axes rising from a creeping axis decumbent and arcuate, up to 500  $\mu\text{m}$  diameter, attached to the substratum by stoloniferous rhizoids. Erect axes cylindrical or very slightly compressed, up to 600  $\mu\text{m}$  diameter, sometimes gradually tapering toward the apices and usually with sparse, filiform, distichously arranged opposite or subopposite pinnae, up to 30 mm long, generally shorter apically and frequently incurved abaxially. External cortical cells anticlinally elongated in transection, up to 4  $\mu\text{m}$  diameter and 7  $\mu\text{m}$  long. Internal cortical cells more rounded, grading into a medulla of larger, elongated cells of about 30  $\mu\text{m}$  diameter. Tetrasporangia in the apical portion (Figure 1B) of vegetative pinnae modified into swollen branches of conical shape. Tetrasporangia oblong (Figure 1C), 40–50  $\mu\text{m}$  long by 20–30  $\mu\text{m}$  broad, cruciately divided, sparsely and irregularly disposed on the branch, the lower usually in a more advanced stage of development than those near the apex.

*Discussion*

This species was originally described by Forsskål (1775) from the Red Sea where it was collected (Børgesen 1932) "ad Mochhae littora". Later authors (Vahl, 1802 Kützing 1868, Weber van Bosse 1904, 1921, Børgesen 1936, 1938, Taylor 1942, 1960, Dawson 1944, 1954a,

Egerod 1971) have reported it from most warm seas, thus confirming a basically tropical distribution for the species. It has never been formally reported before from Hawaii, but the collections studied had nearly 40 specimens from the islands of Laysan, Kauai, Maui, Oahu, and Hawaii. They were found living on coral reefs, consolidated basalt benches, or lava shores near or slightly below low water mark. On Oahu, this is one of the commonest members of the order, living strongly attached to melobesoid algae, extending across most of the reef flats and becoming darker and larger under shaded conditions.

Sexual reproduction is unknown for the genus and asexual reproduction rarely occurs in the Hawaiian specimens studied. Tetrasporangial thalli have been gathered only once (DORY 8080) and several of the fertile branches had undivided spores (Figure 1C) like those reported by Egerod (1971) for specimens from Thailand and by Dawson (1944) for *Gelidiella* (?) *refugiensis* from the Gulf of California. In addition, the spores of the Hawaiian specimens were sparser and more irregularly distributed than has been commonly illustrated for this species.

*Gelidiella acerosa* has been known in the literature under eight different combinations. One of these names, *Gelidium rigidum*, was reported by Chamberlain (1860) and was thought to constitute the oldest record of this species for the islands. However, the only specimen identified as such among Chamberlain's material (BPBM 106482) is similar to a large thallus of *Pterocladia capillacea*. On the other hand the *Gelidium* sp. 2 of Neal (1930) very likely belongs to this species. In her description, Neal mentioned that the species has a round stem and narrow, more linear branches. At the Bernice P. Bishop Museum there is an herbarium sheet (no. 106509) named *Gelidium* sp. in Neal's writing, collected at Rabbit Island, Oahu, which is *Gelidiella acerosa*.

*Gelidiella adnata* Dawson*Reference*

Dawson 1954a, p. 423, fig. 33f.

*Description*

Thalli minute, up to 1 mm high (Figure 1D), forming a red creeping cover on top of rocks.

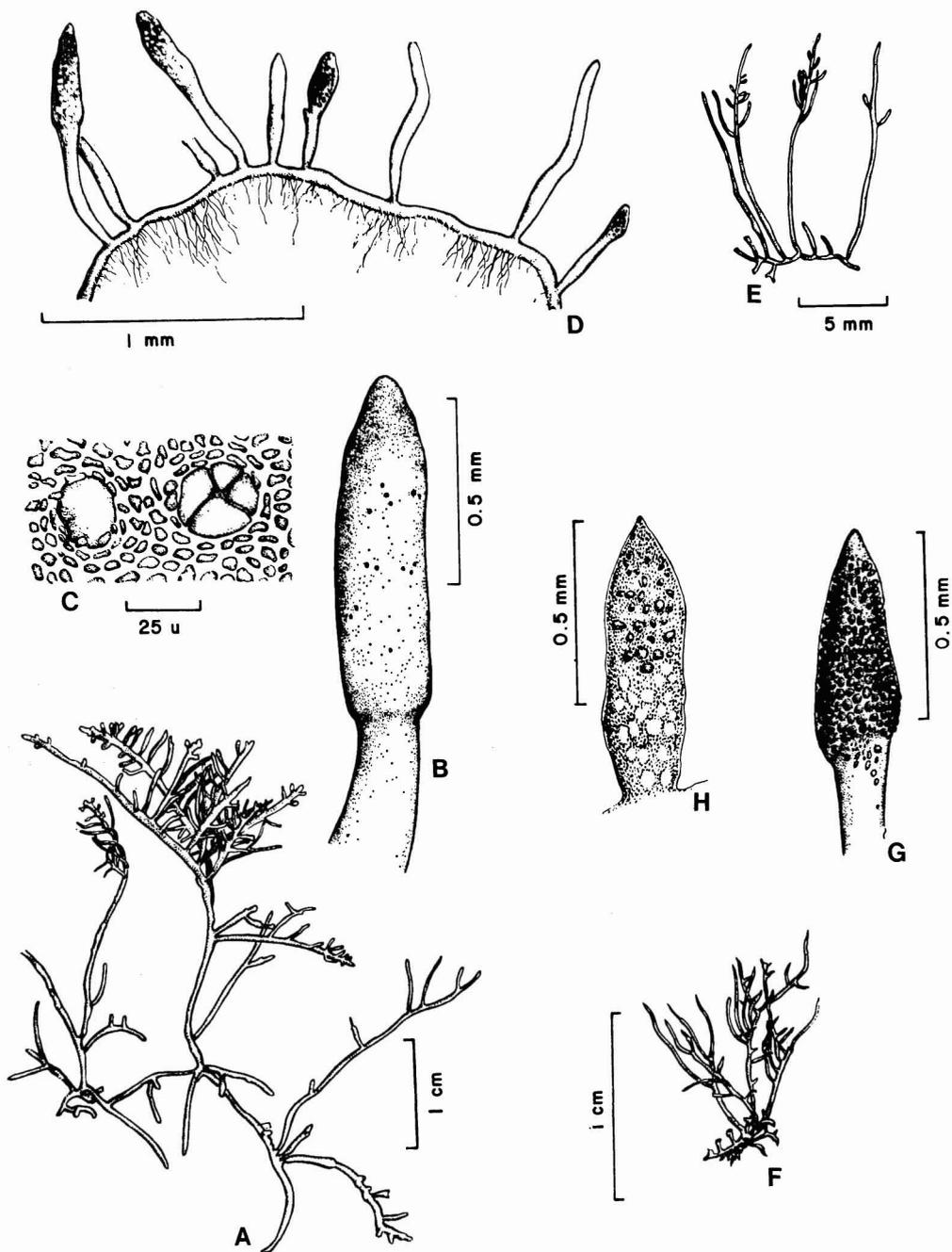


FIGURE 1. Species of *Gelidiella* from Hawaii. *A*, general habit of *G. acerosa*; *B*, fertile branch of *G. acerosa*; *C*, tetraspores and undivided monospores in *G. acerosa*; *D*, general habit of *G. adnata*; *E*, external habit of *G. macbrisiana*; *F*, external habit of *G. myrioclada*; *G*, details of old fertile branch in *G. myrioclada*; *H*, details of young fertile branch in *G. myrioclada*.

Thallus differentiated into a prostrate, terete, branched rhizome and several erect, cylindrical to slightly lanceolate axes. Basal rhizome up to 85  $\mu\text{m}$  diameter, attached from most of its undersurface by unicellular rhizoids, issuing singly in great profusion from ventral cortical cells, forming a more or less continuous attaching surface of up to 90  $\mu\text{m}$  in height. Erect axes usually simple or laterally branched once, up to 75  $\mu\text{m}$  in diameter and close to 900  $\mu\text{m}$  in length, ending in conical apices. Tetrasporangia oblong, cruciately divided, 30 by 20  $\mu\text{m}$ , without obvious arrangement in transverse rows in the apical portions of modified swollen branches of conical shape. Fertile portion of branches up to 160  $\mu\text{m}$  diameter, and 360  $\mu\text{m}$  in length, on pedicels as short as 60  $\mu\text{m}$  but more frequently on taller axes, similar to the vegetative branches.

#### Discussion

*Gelidiella adnata* was described by Dawson (1954a) from specimens collected on intertidal surfaces along the rocky shore of Nha Trang, Viet Nam, on 13 February 1953. Since then, it has been found at Isla San Benedicto, Revilagigedo Archipelago (Dawson 1954b) and at Arno Atoll in the Marshall Islands (Dawson 1956). The Hawaiian specimens that were collected by Doty (8685) were living on top of high rocks near the Elks Club, Waikiki, Oahu Island, and constitute a new record for the islands. Nevertheless, the Hawaiian population shows several morphological differences from the original description. The diameter of the fertile portions of branches and that of the creeping axes are 10–15  $\mu\text{m}$  wider than given by Dawson; the unicellular rhizoids attaching the thallus to the substratum are sparser and longer; the terminal fertile parts of branches are commonly at the apex of long axes rather than on short pedicels; and the tetrasporangia are only infrequently arranged in regular transverse tiers.

The identification of these specimens is further complicated by the fact that the description of each of four other species of *Gelidiella* could partially fit the Hawaiian material. One of these species is *Gelidiella bornetii* (Weber van Bosse) Feldmann et Hamel. Originally described from the Kei Islands (Weber van

Bosse 1926) and later found in India (Børgesen 1938) and at Enewetak Atoll (Dawson 1957a), this is the only small species of *Gelidiella* with sporangia not arranged in a transverse series as the Hawaiian specimens more often show. However, *Gelidiella bornetii* is much taller (up to 5 mm) than the Hawaiian specimens and its axes are at least 35  $\mu\text{m}$  wider. In addition, the erect axes in *G. bornetii* are unbranched, the creeping axes are attached by localized peglike holdfasts, and the cortical cells are seriatly arranged in surface view—all of these characters differing from the Hawaiian thalli.

Two other species, *Gelidiella antipai* Celan and *G. stichidiospora* Dawson, are close to the Hawaiian populations. Both species are very similar, and Boudouresque (1972) considers them the same entity in spite of their different geographic origins in Caliacra, Roumania (Celan 1938), and in Baja California, Mexico (Dawson 1952). They differ by as much as 25  $\mu\text{m}$  from DORY 8685, and by the narrower creeping and erect axes, lack of branching, presence of narrower, longer, and rectangular fertile branches, the regular arrangement of the tetrasporangia and cortical cells, and the presence of cortical hairs.

*Gelidiella pannosa* (Feldmann) Feldmann et Hamel is the fourth species morphologically similar to the Hawaiian plants. Originally described from Biarritz, France (Feldmann 1931c), it passed under the name of *G. tenuissima* Feldmann et Hamel (1936) until Fan (1961) clarified its nomenclature. The species has been reported from several warm seas (Dawson 1954a, 1956, 1957a, b, 1961, Blomquist and Almodovar 1961, Joly et al. 1963, Boudouresque 1969, Egerod 1971), appearing as the most widespread species of minute *Gelidiella*. By comparison, the Hawaiian specimens are much shorter, with narrower axes and fertile branches, larger tetrasporangia arranged in transverse rows in some young fertile branches, and smaller cortical cells. It should be mentioned, however, that at least two reports (Dawson 1954a, 1957a) have mentioned variations in several morphological characters of this species, including axis size and sporangial arrangement. Some authors (Dawson, 1956, Egerod 1971) have remarked upon difficulties encountered in distinguishing among these and the other four species

mentioned above, especially when only sterile material is at hand, and a recent study (Boudouresque 1969) has reported much intra-specific difference between Atlantic and Mediterranean populations of *G. pannosa*. Boudouresque's interpretation that the Atlantic and Mediterranean populations belong to the same species has expanded considerably the known range of morphological variability of *G. pannosa*, placing it very close to *G. bornetii* and *G. adnata*. Future field studies are likely to reduce the number of these species, accommodating more thoroughly such variants as the Hawaiian specimens. Until then, the Hawaiian populations, in spite of the morphological differences, seem better referred to *G. adnata* Dawson than to any of the other small species of *Gelidiella*.

*Gelidiella machrisiana* Dawson

Reference

Dawson 1957*b*, pp. 15–16, fig. 48.

Description

Thallus forming small tufts of up to 2.0 cm tall, differentiated (Figure 1E) into erect filaments rising from a subcylindrical creeping axis. Erect axis compressed and slightly flattened, unbranched in its most basal half, then scarcely branched alternately or subdistichously above. Creeping filaments up to 300  $\mu\text{m}$  diameter with erect parts to 250  $\mu\text{m}$  broad by 160  $\mu\text{m}$  thick. Branches up to 2 mm long, contracted at their bases and slightly clavate. External cortical cells rectangular in surface view, with rounded edges, 6 by 9  $\mu\text{m}$  and without obvious regular arrangement; anticlinally elongated in transection, 4 by 6  $\mu\text{m}$  with granular contents and gradual increase in size inwardly. The most internal medullary cells spherical, up to 9  $\mu\text{m}$  diameter, with thick cell walls. Reproduction not seen.

Discussion

So far the species appears to have been found only twice before. The type locality is Bahia Ballena, Golfo de Nicaya, Puerto Rico (Dawson 1957*b*), collected on 7 June 1957 where sterile specimens occurred on a shell fragment in a rock crevice about 1.5 m above mean low water level.

The second collection was made intertidally at Wreck Bay, Galápagos Islands (Dawson 1963), and these specimens were larger and tetrasporangial. The Hawaiian material (DORY 13405) was found by M. S. Doty and A. J. Bernatowicz on 12 November 1956, living on a consolidated, well-worn, intertidal basalt bench and in pools on that bench, at Hookena, south Kona, island of Hawaii. The occurrence of this species adds a new record for Hawaii and extends the known geographic distribution of the species.

The Hawaiian populations differ from the original description in the diameter of the erect filaments and in the size of the thalli. However, this last character is known to vary because the specimens from the Galápagos were up to 25 mm in height. On the other hand, as Dawson (1957*b*) noticed, the fairly regular, alternate branching pattern of the upper half of the erect axes of this species is so distinct that the Hawaiian specimens cannot be assigned more accurately to any other of the nearly 20 specimens of *Gelidiella* so far described.

*Gelidiella myrioclada* (Børgesen)  
Feldmann et Hamel

Synonyms

Feldmann and Hamel 1934, p. 533. *Echinocaulon myriocladum* Børgesen 1934, p. 5, figs. 4, 5 (obligate synonym).

Description

Thalli 1 to 2 cm high (Figure 1F) forming small, dense tufts, composed of cylindrical to somewhat compressed erect axes rising from a basal, frequently anastomosed, creeping axis, attached to the substratum by sparse groups of short rhizoids. Erect axes up to 180  $\mu\text{m}$  diameter, irregularly branched through most of their lengths. Branches rising distichously, alternately, oppositely or unilaterally, and of variable length, sometimes with secondary branches, all ending in a conical, attenuated apex. External cortical cells somewhat ovoid or rounded in surface view, up to 6  $\mu\text{m}$  diameter, and without regular arrangement; slightly anticlinally elongated in transection, 4–5  $\mu\text{m}$  diameter by 6  $\mu\text{m}$  in height, inwardly followed by two internal layers of cortical cells grading

into rounded medullary cells, of about 7.5  $\mu\text{m}$  diameter, with little granular content and thick cell walls. Tetrasporangia on fertile, swollen portions (Figure 1G, H) at the end of axes and lateral branches. Tetrasporangia tetrahedrally divided, oblong in shape, 30 by 45  $\mu\text{m}$ , and not arranged in obvious transverse series except close to the youngest, more apical portions of fertile branches where there are up to six tetrasporangia in each transverse row.

### Discussion

This species was described by Børgesen (1934) from thalli collected at Malabar Hill, Bombay, on rocks in exposed places near the high water mark. Since then, it has been found again in Bombay, in the sea at Tuticorin, and in the vicinity of Nha Trang, Viet Nam, living on rocks (Dawson 1954a). The Hawaiian specimens were collected in April 1974 at Pupukea, island of Oahu, at the seaward edge of the reef, close to the low water mark. They were found living together with several species of *Gelidiopsis*, *Gelidium pluma*, and *Gelidium pusillum* strongly attached to melobesoid algae and exposed to the incoming waves. The occurrence constitutes a new record for the Islands.

The Hawaiian specimens, all secured in a single gathering, are morphologically alike but show some variation from the type description. Their main axes and fertile branches are 20 and 40  $\mu\text{m}$  wider, respectively, and the tetrasporangia do not form evident transverse rows of three and six, as Børgesen described them. The inflated fertile branches are more crowded with spores and have fewer sterile cells, although several older fertile branches (Figure 1H) resemble those illustrated by Børgesen. In all other characters the Hawaiian thalli are closer to *G. myrioclada* than to the description of any other species of *Gelidiella*, with the exception of *G. setacea* (Feldmann) Feldmann et Hamel. This latter species was originally described from the West Indies (Feldmann 1931a) and is vegetatively similar to *G. myrioclada*. Børgesen (1934) based the distinctions between the two species on the absence of fertile thalli in *G. setacea* and on their different geographic distribution. Apparently no fertile thallus of *G. setacea* has

been reported (Taylor 1960) and its known geographic distribution does not go beyond the tropical Atlantic; therefore, the differences mentioned by Børgesen are still valid. However the morphological differences between the two species are restricted to a couple of centimeters in height and to less than 40  $\mu\text{m}$  of diameter of the erect axes, with clear overlapping of their size ranges. The Hawaiian specimens are shorter than is typical for *G. setacea* but wider than typical *G. myrioclada*, narrowing still further the slight differences between the two species. Fertile thalli of *G. setacea* should be examined before any action is taken on the status of these two species. Until then the present material is assigned to *G. myrioclada* because the Hawaiian specimens fit the more complete description of this taxon.

### GELIDIUM

#### *Gelidium crinale* (Turner) Lamouroux

#### Synonyms

Lamouroux in Bory 1825, p. 191. *Fucus crinalis* Turner 1819, pl. 198 (obligate synonym). Facultative synonyms: *Acrocarpus crinalis* (Turner) Kützing 1868, pl. 33, figs. a-c; *Acrocarpus spinescens* Kützing 1868, pl. 33, figs. d-e; *Acrocarpus corymbosus* Kützing 1868, pl. 36, figs. a-c.

#### Description

Forming tufts of up to 7 cm high (Figure 2A), composed of thin, erect axes often twisted together, sparsely and irregularly branched, arising from cylindrical creeping axes attached to the substratum by stoloniferous rhizoids at irregular intervals. Erect axes cylindrical at the base, up to 180  $\mu\text{m}$  diameter, and cylindrical or flattened apically. When flat, the apical portions up to 50  $\mu\text{m}$  thick and 350  $\mu\text{m}$  broad at the apices and up to 500  $\mu\text{m}$  broad at the origin of branches; apices narrowing distally finishing in a distinct apical cell. Branching sparse, irregular, often restricted to the apical half of the erect axes (Figure 2B) appearing as dichotomies rather than as pinnules. External cortical cells slightly ovoid in surface view, 4–6  $\mu\text{m}$  by 6–8  $\mu\text{m}$  and completely rounded in transection; up to 6  $\mu\text{m}$  diameter. Inner cortical cells increasing in size

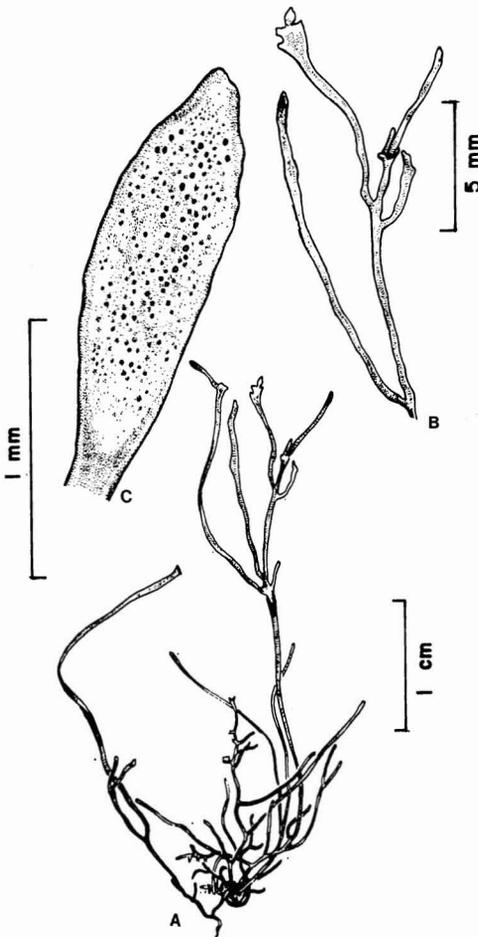


FIGURE 2. *Gelidium crinale* from Hawaii. A, external morphology of a group of large plants; B, typical branching pattern; C, tetrasporangial sori on terminal portions of a flattened branch.

inwardly, up to  $10\ \mu\text{m}$  diameter, grading into a medulla of elongated cells, ovoid in transection, of  $6\text{--}15\ \mu\text{m}$  diameter surrounded by few inconspicuous rhizoids. Tetrasporangia on irregularly shaped sori (Figure 2C) at the upper and more or less compressed end of branches and axes, spherical in surface view, cruciately divided, and up to  $30\ \mu\text{m}$  diameter. Cystocarps not seen.

#### Discussion

This species was originally described by Turner (1819) from thalli collected at Kilmouth,

England. Later authors have reported the species (Weber van Bosse 1921, Børgesen 1925, Gardner 1927, Newton 1931, Okamura 1934, Feldmann and Hamel 1936, Dawson 1952, 1954a, 1957a, Dawson, Aleem, and Halstead 1955, Taylor 1960) from several places in the Atlantic—both Europe and North America, the Red Sea, the Indian Ocean, the Mediterranean, and the Pacific. The species is rather scarce in the Hawaiian archipelago where it has been found only six times from the islands of Kauai and Oahu. The two gatherings in Kauai (DORY 9906 and 10076) have tetrasporangial thalli. They were found in February 1952, living on rocks close to the point north of the entrance of Aliomanu stream to Papaa Bay and in front of the stream mouth in Moloaa Bay, respectively. Three of the other collections (UC 1452046, 145239, and BFBM 106490) were apparently made by Reed in 1908, at Makua, Haleiwa Hotel, and Waikiki, respectively. The specimens collected last (DORY 14075) are the ones with more explicit ecological information, with the species being reported as growing in relatively thick mats in sand at the low tide level along the shore beneath the Diamond Head Light House in Honolulu. The three specimens collected in 1908 apparently were identified by Setchell. Nevertheless, the species has never been formally reported for the islands and these are the first records for Hawaii.

The Hawaiian specimens show much ecological variation when compared collectively. Thalli such as DORY 10076 or DORY 9906 are about 1 cm high, cylindrical, and almost unbranched, whereas those of DORY 14075 or UC 1452046 are up to 3 cm tall, sparsely branched, and slightly flattened. The largest thalli are those in UC 1453039. They are more robust, branched in the apical half, and flattened. They agree fairly well with both the description of *Gelidium heteroplastos* Børgesen from Bombay, India, and with the account of *Gelidium crinale* var. *platycladum* Taylor, from Texas, U.S.A. *Gelidium heteroplastos* was distinguished from typical *G. crinale* by its broader, flattened thallus and by the presence of tetrasporangial sori covering the surface of the upper branches and branchlets (Børgesen 1934). The material from Texas had both characteristics, in addition to a clearer clustering of branches at the upper parts

of the frond (Taylor 1943). Taylor (1943) recognized them as being clearly different from *G. crinale* from northern waters but some of these tropical and subtropical specimens were found to be similar to those of typical *G. crinale* from the north, and Taylor interpreted the differences as being varietal. In the Hawaiian specimens, the large forms such as UC 1452039, which agree with the description of *Gelidium heteroplastos*, were gathered together and found to grade into terete, shorter thalli which in turn graded into the smaller, somewhat more typical *G. crinale* such as UC 1452046, thus supporting Taylor's interpretation.

#### *Gelidium pluma* Loomis

##### Reference

Loomis 1960, p. 2, pl. 1, figs. 1–4; pl. 2, figs. 1–2.

##### Description

Thalli crispate and cartilaginous, up to 20 cm tall, consisting of one to several erect axes distichously and plumosely branched at their upper end (Figure 3A), arising from cylindrical creeping axes with numerous short haptera that form a massive disc-like holdfast. Erect fronds cylindrical at the base, subcylindrical above, and compressed at their upper parts, up to 1.1 mm in diameter near the base, up to 1.5 mm broad and 0.8 mm thick at the flattened portions, finishing in a rounded, somewhat spatulate apex of 0.7 to 1.2 mm broad and up to 0.4 mm thick. Margins of axes subentire at the basal third, irregularly sinous-dentate or erose dentate above, and distichously branched along the edges of the upper half of the erect axes (Figure 3B). Primary branches lanceolate or spatulate when young, irregularly lanceolate and pinnately branched when mature, increasing in size basipetally, up to 3.5 mm long by 0.5 mm broad (Figure 3C). Secondary pinnae up to 0.7 mm long, also increasing in length basally, irregularly ligulate or spatulate and frequently branched. Primary branches deciduous, especially in fertile thalli, leaving scars at both margins of the lower parts of the erect axes. External cortical cells ovoid in surface view, up to 6  $\mu\text{m}$  in length, and arranged without order, anticlinally elongated in transection,

up to 10  $\mu\text{m}$  in height by 3  $\mu\text{m}$  diameter, followed by two–three layers of deeply pigmented cells, the inner ones mixing with medullary cells rounded or ovoid in transection and up to 20  $\mu\text{m}$  diameter. Rhizoidal filaments abundant in the innermost cortical layer and sparse in the inner layers of the medulla. Tetrasporangia cruciately divided, 30  $\mu\text{m}$  diameter, and arranged without order in sori (Figure 3D, E) on pinnately compound, somewhat twisted, and densely congested branches with undulate margins. They appear only on the terminal portions of primary branches but on the whole surface of secondary branches (Figure 3E, F). Proximal parts of the primary branches usually sterile, appearing as a supporting axis for terminal and lateral tetrasporangial blades. Cystocarps on pinnately compound branches, normally ovoid, 0.5 by 0.7 mm in surface view and up to 0.5 mm thick, with one or, more rarely, several openings toward both surfaces of the frond (Figure 3G, H). Occasionally two cystocarpic cavities coalesce laterally, forming enlarged cystocarps of up to 0.8 mm long.

##### Discussion

The species was first described by Loomis (1960) from tetrasporic thalli (Reed 495 = AHF 79134) collected at Nawiliwili, Kauai, on 25 September 1905. Since then it has been collected 45 times from Kauai, Oahu, Molokai, Maui, and Hawaii, producing tetraspores from December to September and cystocarps in February in Kauai and from April to July in Oahu. In spite of the numerous collections of the species, its habitat has been infrequently characterized. On Oahu it has been found at Pupukea, living on vertical faces at the seaward edge of abruptly cut reefs in places with very intense water movement. In such places, the thalli form clumps, 10–20 cm high, extending from zero tide level to 1.5 m below, and bleaching or becoming yellowish at the upper limits of their vertical distribution. A similar habitat was recorded by DORR (10745), collecting the species at the edge of a bench at Laie Point, Oahu.

*Gelidium pluma* is known so far only from the Hawaiian Islands where it is one of the most distinctive and less variable species of Geli-

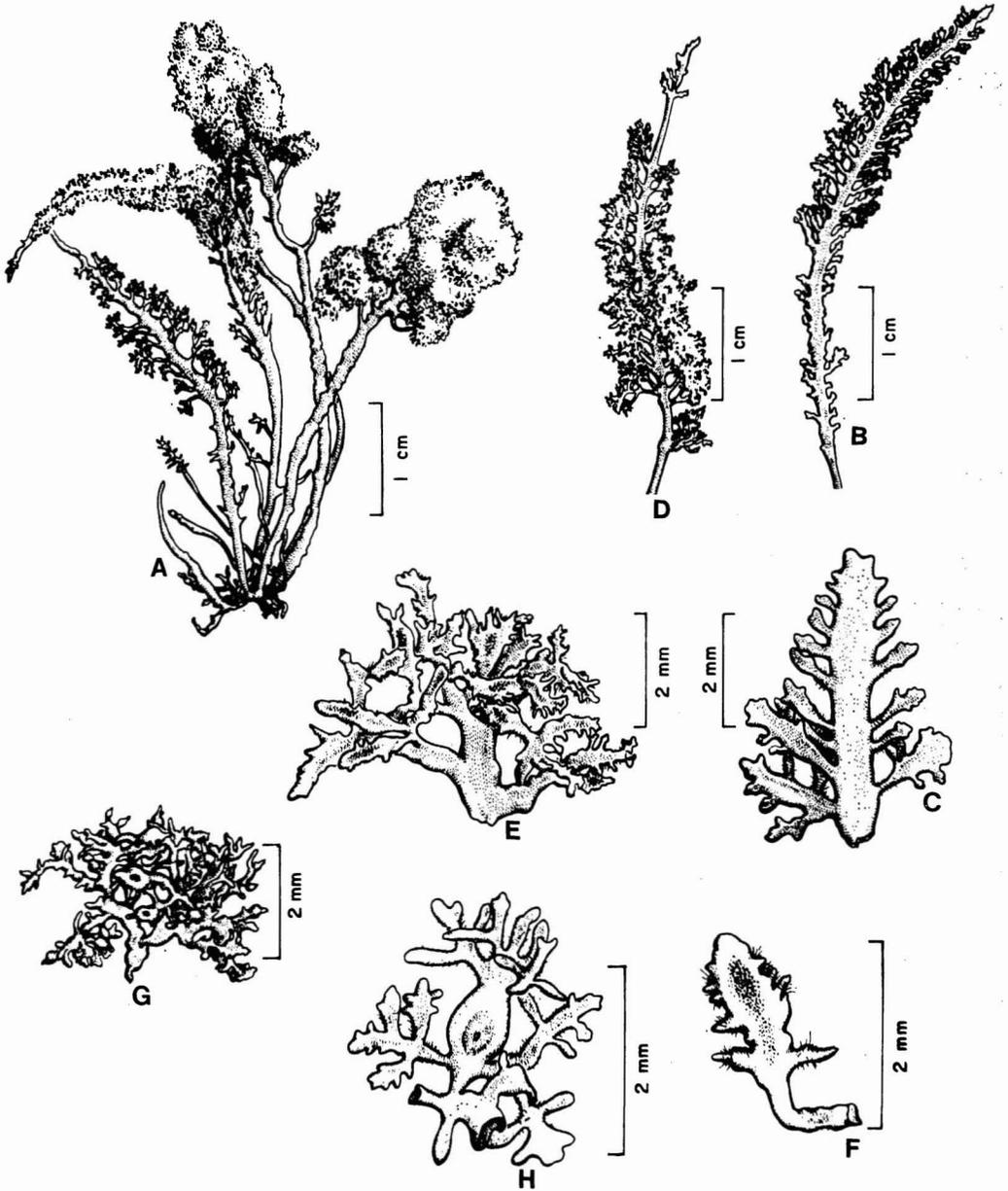


FIGURE 3. *Gelidium pluma*. A, external habit of a cystocarpic plant with dense branching and sinous-dentate scars along the margins; B, details of the apical portion of a sterile axis with simple distichous branching; C, sterile secondary branch; D, details of the apical portion of a tetrasporangial branch with dense secondary branching; E, pinnately compound tetrasporangial branch; F, secondary tetrasporangial branch; G, pinnately compound cystocarpic branch; H, surface view of a cystocarp.

diales. Only two characters, size of erect fronds and density of branching, varies in the specimens studied. However, the variation is slight and the plumose habit of the species is very distinct even

in thalli as short as 3 cm. Previously *G. pluma* was consistently misidentified as *G. filicinum* by Reed (species in herbarium) and also apparently by Setchell (species in herbarium). The con-

fusion lasted until 1906 when Setchell sent some specimens to Bornet for proper identification. Bornet answered (Setchell letters deposited at the University of California at Berkeley) on 8 October 1906, indicating that the Hawaiian species was different from *G. filicinum* and that he had already seen the alga from Farlow's Herbarium where it remained without a name. In addition to discussing the most striking differences between both species, Bornet added, referring to the Hawaiian entity: "Le nom de *Gelidium pluma* lui convendrait tres bien." For this reason several specimens at the Herbarium of the University of California (e.g. UC 622908, 622980, 622985, 622986, 622989, UC M 110608 and UC M 110607) have been labelled as *Gelidium pluma* Bornet ex Loomis. Nevertheless, Bornet never provided a formal description of the species and Loomis (1960), even though she recognized that Bornet thought that this was a distinct species, did not ascribe the species to him. Therefore, the use of the words "Bornet ex" in the specific epithet is superfluous (Article 46, Recommendation 46C; Stafleu 1972).

*Gelidium pusillum* (Stackhouse) Le Jolis

*Synonyms*

Le Jolis 1863, p. 139. *Fucus pusillus* Stackhouse 1801, pl. 6 (obligate synonym). Facultative synonyms: *Fucus caespitosus* Stackhouse 1801 pl. 12; *Acrocarpus pusillus* (Stackhouse) Kützing 1849, p. 762.

*Discussion*

The species was originally described by Stackhouse (1801) from material collected at Sidmouth and Brighton, England. Later, numerous authors extended its distribution to a number of localities in northern Europe, the Mediterranean and Adriatic seas, Australia and New Zealand, Japan, the Red Sea, the Pacific, and the Atlantic—Central America, North America, and the Caribbean, thereby confirming an almost cosmopolitan distribution in temperate and warmer waters. Throughout this wide range, several different varieties have been assigned to the species, some of which were originally described as separate entities. Several

varieties seem to be the result largely of variable ecological conditions, but critical ecological studies on the specific limits of these small forms are scanty and they do not always show a continuum from one form to another. Until transplant or other types of experimental study throw light upon the taxonomic status of these varieties, it seems pertinent to mention the several forms and their habitats separately as they occur in the Hawaiian Islands.

The smallest thalli of this species are represented by DORY 13173 by individuals forming dense, short tufts of simple erect fronds, up to 3 mm tall, rising from cylindrical creeping axes of 120  $\mu\text{m}$  diameter with short stolons. The erect fronds rise opposite the stolons, are cylindrical at the base, expand upwardly, and are up to 400  $\mu\text{m}$  broad. Tetrasporangia ovoid, 35 by 25  $\mu\text{m}$ , irregularly placed in sori on spatulate leaflets or at the broadly rounded apex of erect axes. This form was first described by Weber van Bosse (1921) as the variety *minusculum* from specimens collected at Daram Island, the Nias reef, and the west coast of New Guinea. Later authors have reported the species from places, among others, as distant as Algeria (Feldmann 1931b), China (Fan 1951), the Pacific coast of Mexico (Dawson 1952), and the coast of Brazil (Joly 1965). In Hawaii it was found at La Perouse Bay, Maui, in December 1955.

Equally diminutive are some of the thalli in BPBM 106501 identified by Abbott (1947) as *G. pusillum* var. *conchicola* Piccone and Grunow. This variety was first described (Piccone 1884) from Massawa in the Red Sea. The Hawaiian thalli can be as short as 1.55 mm but generally they reach up to 1.5 cm high. Several narrow, flattened, simple or sparsely branched, erect axes rise from a cylindrical, somewhat arcuate, basal filament of up to 150  $\mu\text{m}$  in diameter. Most erect axes have one or two alternate branches appearing as dichotomies, all ending in flat, arcuate apices. As Abbott (1947) observed, the thalli resemble closely Taylor's (1928) specimens from Florida; they also resemble those illustrated by Joly (1965) from São Paulo, Brazil. The Hawaiian specimens, collected by C. J. Engard, were first included and determined in I. Abbott collection (no. 1764) and later were deposited at the Bernice P. Bishop Museum of Honolulu. They were gathered at

Molii Pond, island of Oahu, on 26 June 1945. This is an artificial fishpond with shallow, turbid, and muddy waters and with the algae growing preferentially on the pond walls (Abbott 1947).

The forms collected by the Tanager Expedition at Laysan Island (BPBM 106503) and by Tsuda at Lisianski Island (BPBM 160500) are of similar size with the previous form but with fronds expanded and flat. With the exception of BPBM 106499, which was collected on a shore reef of Laysan, no indication of locality was given for any of these specimens. They are close to those illustrated by Dawson (1944, pl. 42, fig. 5) as one of the many forms of *G. pusillum* in Costa Rica or to the form which Dawson (1961) recognized later as *Gelidium pusillum* var. *pusillum*.

A fourth form occurring in Hawaii corresponds to that described (Kützing 1849, Bornet 1892, Feldmann and Hamel 1936) as *Gelidium pusillum* var. *pulvinatum* (Ag.) Feldmann or as *Gelidium pulvinatum* (Kützing) Thuret (Figure 4A). These algae appear as dark red, almost blackish cushions of entangled filaments. The thallus is cylindrical, up to 200  $\mu\text{m}$  in diameter, slender and creeping through most of its extension, producing short, erect axes and holdfasts at short intervals. The erect axes are cylindrical, lanceolate, or broadly ovoid, up to 100  $\mu\text{m}$  broad, with small proliferations from the margins. Cortical cells rounded, about 6  $\mu\text{m}$  diameter at transection, followed by one–two layers of internal cortical cells, gradually increasing in diameter up to 8  $\mu\text{m}$ . Medullary cells isodiametric at transection, up to 10  $\mu\text{m}$ , surrounded by rhizoidal filaments. Tetrasporangia rounded, up to 20  $\mu\text{m}$  diameter, on flat, broadly ovoid proliferations (Figure 4B).

Characteristically this form was restricted in Oahu to the vertical faces of black igneous rocks, 10–40 cm above mean low tide level and frequently associated with freshwater runoffs where salinities were as low as 10‰ and nitrate content as high as 12 ppm during low tides. It was often observed at Kahala, Honolulu, Oahu, withstanding 2–4 hours of emersion under sunlight intensities above 10,000 ft-c and temperatures close to 32°–34° C. The variety has been found eight times from the islands of Oahu, Maui, and Hawaii.

On intertidal rocks, corals, or other types of hard substratum with high water movement, there is a fifth form of *G. pusillum* (Figure 4C) that could fit Taylor's (1945) description of *G. pusillum* var. *cylindricum* or Dawson's illustrations (1944, pl. 42, fig. 1) of some varieties from Costa Rica. This form is dark red, reaches up to 2.5 cm high, and is composed of erect fronds rising from cylindrical, slender, creeping axes, 150  $\mu\text{m}$  diameter, attached by small holdfasts. The erect axes are compressed and flat, linear oblong or linear clavate, up to 0.5 mm wide and up to 60  $\mu\text{m}$  thick, finishing in a truncate apex with two to four proliferations. Tetrasporangia rounded or somewhat ovoid, up to 28  $\mu\text{m}$  in diameter, irregularly disposed in ovoid sori (Figure 4D) occurring at the lanceolate end of axes and branches. Cystocarps on small branches (Figure 4E), round or ovoid, up to 600  $\mu\text{m}$  diameter, and occasionally with more than one opening on each surface.

*Gelidium pusillum* var. *cylindricum* was first described by Taylor (1945) from material collected in Ecuador. The Hawaiian specimens, gathered at eight localities on the island of Hawaii and at one on Oahu, are at variance with the original description and illustration. They have tetrasporangial sori and cystocarps on broad, flat blades of lanceolate shape rather than at the end of terete filaments as Taylor described them. In addition, the dimensions of the Hawaiian algae are larger, being similar perhaps to those which Taylor (1945) reported as *G. pusillum* from Revillagigedo, which was intermediate between the species and the larger form *G. pusillum* var. *pacificum*.

*Gelidium pusillum* var. *pacificum* Taylor also occurs in Hawaii. In Oahu it is found at the same habitat as the previous form, a few centimeters below in intertidal height. It appears as a short filamentous cover attached to the rocks by cylindrical creeping axes, up to 400  $\mu\text{m}$  diameter, with holdfasts at regular intervals. Erect axes are cylindrical below (Figure 4F), up to 500  $\mu\text{m}$  diameter and flat, lanceolate, or somewhat spatulate distally, appearing as blades with short stalks. Blades entire with lanceolate or spatulate branches from the margins or with proliferations from the truncate upper end, to 4 cm high, 1.5 mm broad, and 100  $\mu\text{m}$  thick. External cortical cells rounded on surface view,

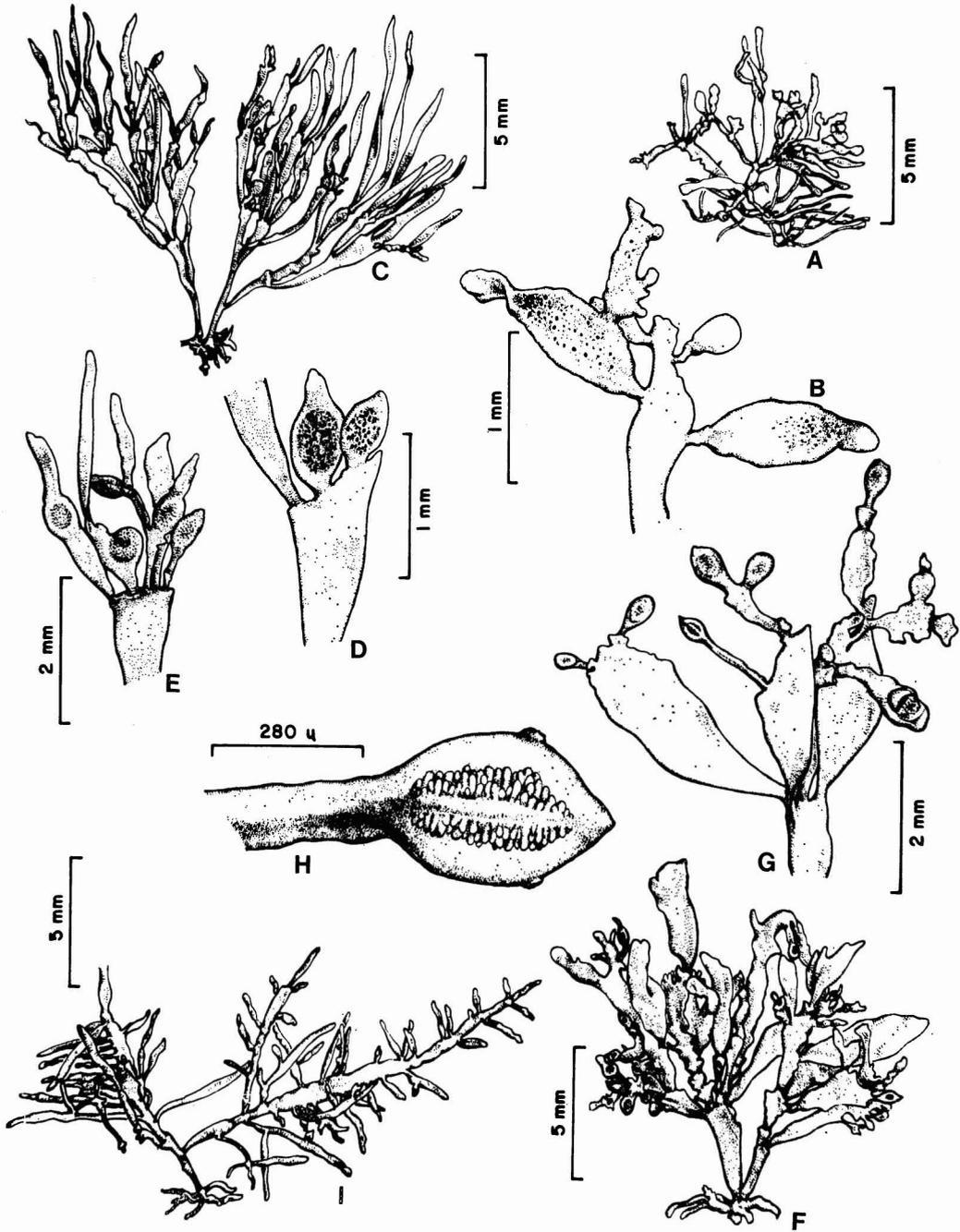


FIGURE 4. *A*, external habit of *Gelidium pusillum* var. *pulvinatum*; *B*, tetrasporangial branch of *G. pusillum* var. *pulvinatum*; *C*, external habit of *G. pusillum* proximum to var. *cylindricum*; *D*, tetrasporangial branch of *G. pusillum* proximum to var. *cylindricum*; *E*, cystocarpic branch of *G. pusillum* proximum to var. *cylindricum*; *F*, external habit of *G. pusillum* var. *pacificum*; *G*, cystocarpic branch of *G. pusillum* var. *pacificum*; *H*, cystocarpic branch of *G. pusillum* var. *pacificum* in side view; *I*, unnamed variety of *G. pusillum* as it occurs on shaded places of the reef flat.

5–7  $\mu\text{m}$  diameter and disposed without order, slightly periclinally elongated in transection, up to 6  $\mu\text{m}$  diameter and followed by two to three layers of larger—up to 10  $\mu\text{m}$ —cortical cells that grade into large, isodiametric, medullary cells. Rhizoids surround the medullary cells in the younger parts but are concentrated in the cortex in the mature fronds. Cystocarps are rounded and simple, of about 300  $\mu\text{m}$  diameter, and formed close to the distal margins of small fertile blades (Figure 4G, H). Tetrasporangia irregularly disposed in rounded sori near the end of blades, ovoid or rounded, cruciately divided, and up to 300  $\mu\text{m}$  diameter. This variety was first described by Taylor (1945) from Ecuador and later was reported by Loomis (1960) from the Hawaiian Islands where it has been found nearly 20 times on Kauai and Oahu.

On the reef flat, living below other algae, there exists a seventh form of what seems to be *Gelidium pusillum*. The erect axes rise from cylindrical creeping axes (Figure 4I) of up to 400  $\mu\text{m}$  diameter, and are linear or linear lanceolate, up to 18 mm high, 400  $\mu\text{m}$  broad and 200  $\mu\text{m}$  thick. Branching is sparse, alternate or opposite, always along both margins of the frond and finishing in narrow, arcuate, and sometimes incurved apices. Frequently, several erect axes or branches incurve downward, becoming creeping axes. A few specimens have erect, distichously and somewhat pinnately branched erect axes, resembling the *Gelidium pusillum* described by Smith (1944) from the coast of California. Other, unbranched erect blades resemble *G. pusillum* var. *pacificum*. The cortex is formed by three to four layers of pigmented cells, the outermost anticlinally elongated, 3 by 9  $\mu\text{m}$ , inwardly followed by larger (up to 12  $\mu\text{m}$ ), rounded, pigmented cells. The medullary tissue is notably thicker than in any other of the forms of *G. pusillum* (up to 100  $\mu\text{m}$  thick), and is formed by cylindrical cells of up to 15  $\mu\text{m}$  diameter, surrounded by abundant rhizoidal filaments.

This form occurs on eroded coral reefs, living beneath other algae close to the seaward edge of the Sand Island reef on Oahu. At times it appears to be some modified form of *Pterocladia capillacea*, especially for the similarity in its thick medullary tissue. However, it could also represent a variety of *Gelidium pusillum* adapted to

shaded, creeping habitats, where almost each axis can become prostrate.

*Gelidium reediae* Loomis

#### Reference

Loomis 1960, p. 3; pl. 2, fig. 3; pl. 3, figs. 1–3.

#### Description

Thalli to 5.5 cm high (Figure 5A), with one or many distichously-branched erect axes arising from holdfast of entangled stolons. Erect axes straight, subcylindrical near the base, and strongly flattened throughout most of their lengths, up to 0.25 mm thick and 0.8 mm broad in the subcylindrical portions and up to 1.8 mm broad at the upper, flattened parts. All axes ending in spatulate apices and having up to five orders of alternate or opposite branches. Branching can be loose, with wide intervals, or be dense and congested (Figure 5B, C). The most basal branches are slightly larger than the apical one, and each order decreases in size, forming pinnately branched, broadly pyramidal fronds. Primary branches similar to the main axes but smaller, up to 1.5 mm broad and 0.3 mm thick. Cortex with three to five layers. The outermost layer with deeply pigmented, anticlinally elongated, regularly arranged cells of 4 by 6  $\mu\text{m}$ ; the second cortical layer with periclinally elongated cells grading internally into larger (9 by 12  $\mu\text{m}$ ), cylindrical, and irregularly arranged, pigmented, internal cortical cells. Medullary cells rounded, up to 20  $\mu\text{m}$  in diameter, and thick walled. Rhizoidal elements numerous and conspicuous in the inner cortex and in the most external medullary layers, with few isolated filaments in the most internal medullary tissue. Tetrasporangial sori (Figure 5D) elongated or extensive on the enlarged ultimate portions of the branches, or limited to short, somewhat laterally swollen branchlets. Tetrasporangia cruciately divided, 30–40  $\mu\text{m}$  diameter, found during May, October, November, and December. Cystocarps medial on the branches (Figure 5E) ovoid or almost spherical, of 350 to 500  $\mu\text{m}$  diameter.

The species was first described by Loomis (1960) from Hawaiian specimens and was typified by the cystocarpic specimen no. *Reed 999a*, gathered at Haleiwa Hotel, Oahu, on 24 December 1908. This specimen has been lost

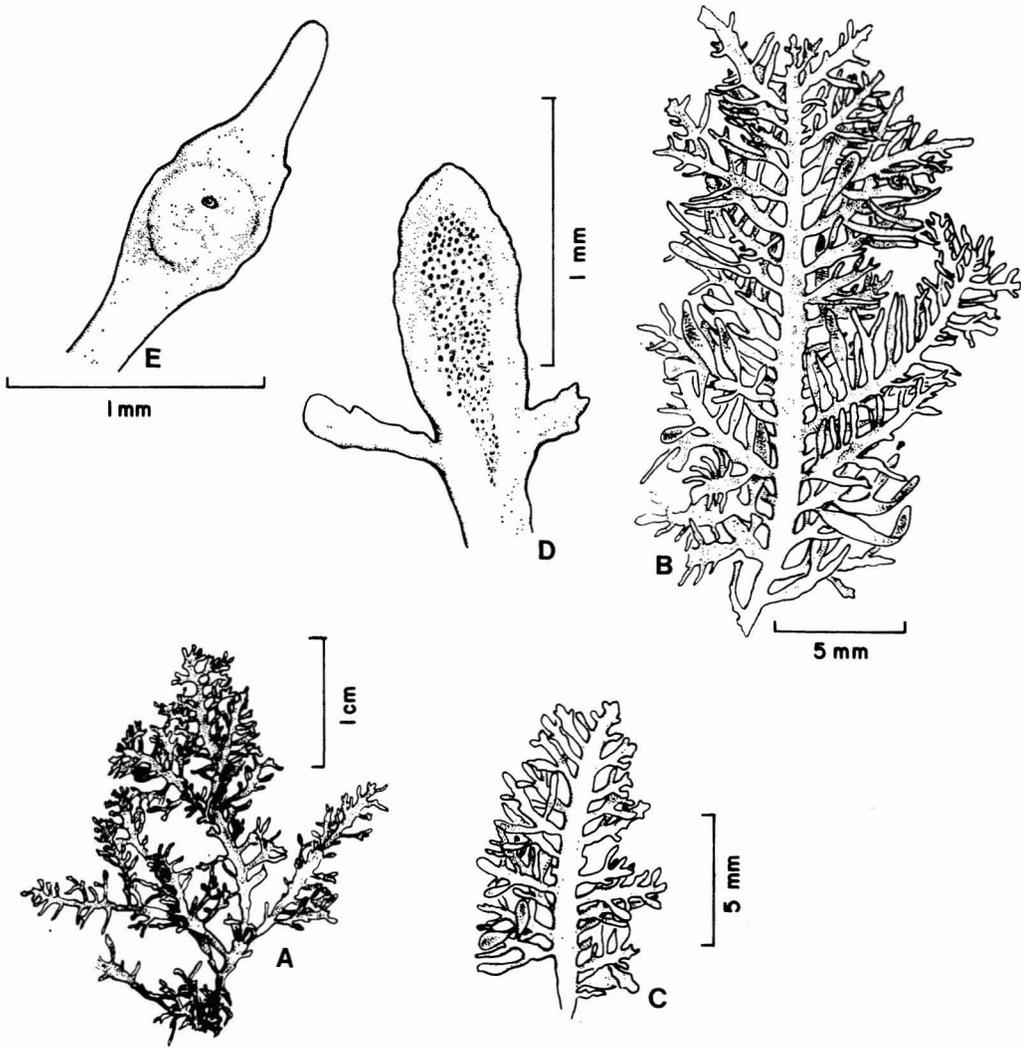


FIGURE 5. *Gelidium reediae*. A, external habit of a poorly branched specimen; B, details of pinnate branching in primary branch; C, details of pinnate branching in secondary branch; D, tetrasporangial branch; E, cystocarpic branch.

and Silva designated as lectotype some tetrasporic specimens (*Reed 999b* = AHF 79133) included in the original account of the species and collected at the same place and on the same date as the holotype. Two other herbarium sheets (UC 622993 and UC 1452136), both numbered *Reed 999* and collected on the same date and at the same locality as the type, have been selected isotypes. However, these specimens were sent to Setchell by Reed previous to Loomis' study and apparently only one of them

was studied by Loomis. None of them were included in the original publication and, as such, they are not part of the protologue. Their selection as isotypes does not follow the recommendations in the guide for the determination of types in the *International Code of Botanical Nomenclature* (Stafleu 1972).

In total there are 11 specimens of *Gelidium reediae* in the collections studied, all of them having been obtained between 1905 and 1908 on Oahu and Maui. Apparently, the species was

never found thereafter and the complete absence of ecological characterization of the specimens collected has prevented more intensive searching. Several of the specimens studied were identified previously by Setchell and Reed as *Gelidium micropterum*, *Pterocladia capillacea*, or *Gelidium latifolium*. The branching pattern and the general appearance of the frond of *G. reediae* sometimes resembles *P. capillacea* but the former species is less pyramidal. The primary branches of *G. reediae* commonly rise from comparatively lower portions of the main axes, whereas in the Hawaiian populations of *P. capillacea* branching is commonly restricted to apical portions of main axes. In addition, the branching intervals of *G. reediae* are shorter, its internal axial structure has numerous rhizoids mainly restricted to the cortex, and its cystocarps are bicameral, with openings to both sides of the frond.

It is more difficult to separate *Gelidium reediae* from the descriptions of *G. latifolium*, a species also known to be very variable and widely distributed (Turner 1819, Bornet and Thuret 1876, Feldmann and Hamel 1936), occurring, among other places in the southeastern Pacific (Cotton 1915, Fan 1951). A comparative study of some specimens of *G. latifolium*, now at the Herbarium of the University of California (uc 476281), previously identified by J. Feldmann and collected at Guethary (Basses Pyrenées), showed only minor differences in hyphae distribution in relation to *G. reediae*, being externally very similar. In addition, comparisons with specimens from Formosa, identified as ?*Gelidium latifolium* by Fan (uc 949764), showed complete agreement in internal morphology, despite some differences in branching pattern. Because little is known on the variation pattern of *G. reediae* in Hawaii and since the type of *G. latifolium* was not included in this study, *Gelidium reediae* is recognized here as a separate entity but of questionable validity.

#### PTEROCLADIA

##### *Pterocladia bulbosa* Loomis

#### Reference

Loomis 1960, pp. 7-8; pl. 9, figs. 2-3; pl. 10, fig. 3; pl. 11, figs. 1, 4.

#### Description

Thalli up to 4 cm high (Figure 6A) with pectinate erect fronds rising from cylindrical creeping axes with small holdfasts at short intervals. Several holdfasts can coalesce, forming a massive attachment surface. Erect axes cylindrical at the base, up to 0.3 mm in diameter, flattened above, up to 0.7 mm broad and 150  $\mu\text{m}$  thick, ending in acute or rounded tips. Branching distichous, pectinate or opposite, covering both edges of the flattened axes, starting 1-2 cm above the creeping filaments and rising at short intervals at a broad, almost 90° angle from the margins of the main axes. Most branches short, 2-4 mm, cylindrical, of about 150  $\mu\text{m}$  diameter, slightly clavate, especially if tetrasporangial, and frequently ending in a rounded apex. Intermixed without any evident order are larger (up to 3 cm long), flat, and broader branches, similar to the main axes bearing small, pectinate branches. Cortex with three layers of cells, the outermost anticlinally elongated, 6 by 12  $\mu\text{m}$ , which grade into sparser, more rounded, internal, cortical cells. Medullary elements isodiametric, thick walled, and up to 30  $\mu\text{m}$  diameter. Rhizoidal filaments moderately abundant, surrounding the medullary cells. Tetrasporangia in sori at the terminal swollen parts of pectinate branches, some so strongly clavate (Figure 6B) as to seem composed of a bulbous protrusion on a supporting branch. Tetrasporangia ovoid, up to 21 by 30  $\mu\text{m}$ , cruciately divided.

#### Discussion

The species was first described by Loomis (1960) from Hawaiian material. The type was designated to be a cystocarpic specimen (Reed 338a), collected at Waialau, Molokai, on 19 July 1905. This specimen has been lost and a lectotype (Reed 338 = uc 623018) was selected by Silva (unpublished memorandum). These are tetrasporangial thalli, morphologically approaching very closely the original description, and collected at the same place and on the same date as the holotype. Regrettably, this herbarium sheet was sent to Setchell by Reed previous to Loomis' study and apparently was neither studied by Loomis nor included in her original account of the species. Its selection as lectotype

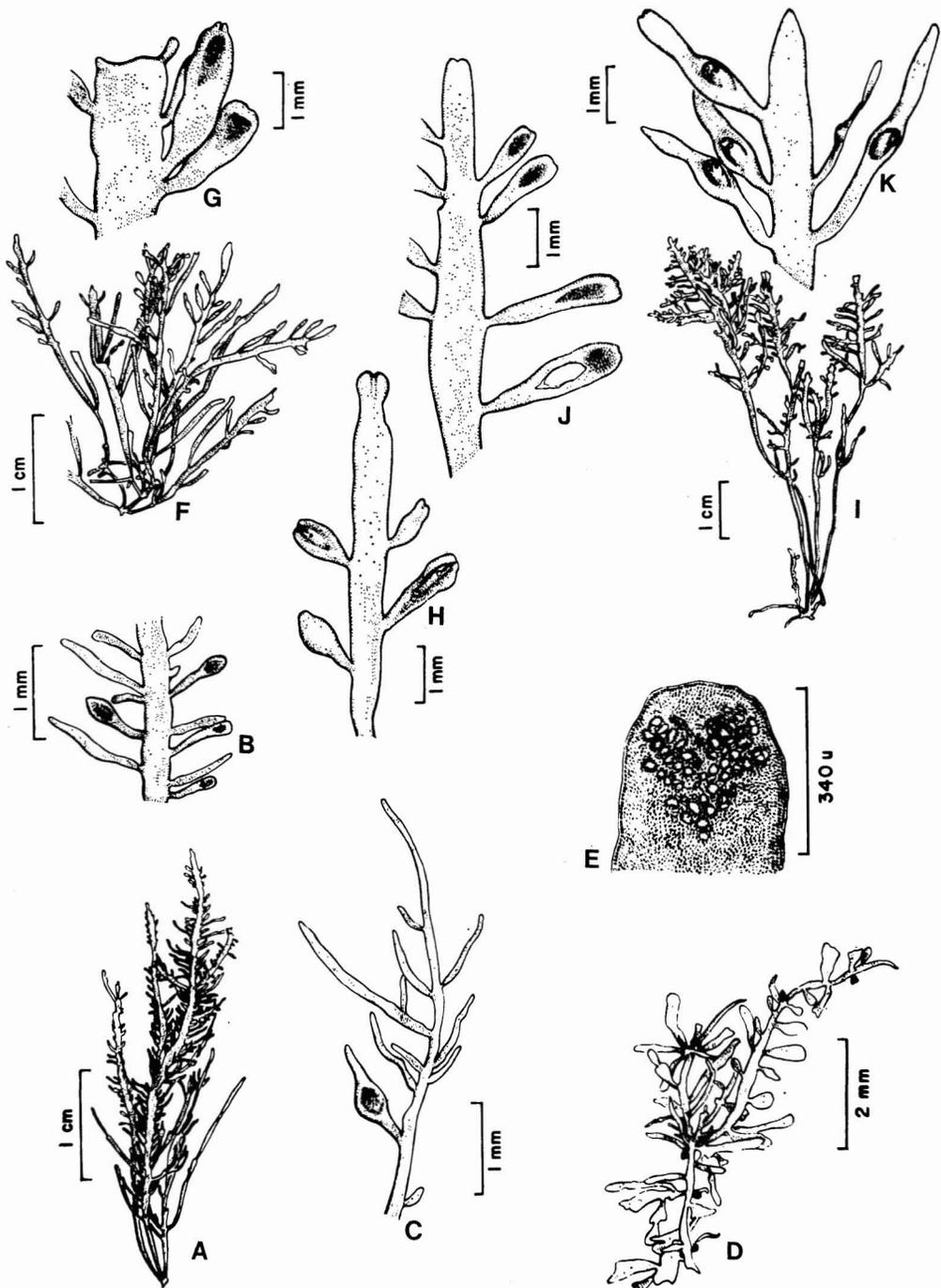


FIGURE 6. Species of *Pterocladia* from Hawaii. *A*, external habit of *P. bulbosa*; *B*, tetrasporangial branch of *P. bulbosa* with clavate apex; *C*, cystocarpic branch of *P. bulbosa*; *D*, external habit of a portion of *P. caloglossoides*; *E*, tetrasporangial branch of *P. caloglossoides* with tetraspores borne in V-shaped rows; *F*, external habit of a simply branched specimen of *P. caerulescens*; *G*, tetrasporangial branch of *P. caerulescens*; *H*, cystocarpic branch in *P. caerulescens* with sterile margins around the elongated cystocarp; *I*, external habit of *P. capillacea*; *J*, tetrasporangial branchlets of *P. capillacea* with some sori partially eroded after spore release; *K*, cystocarpic branch of *P. capillacea* with protruding peristome.

violates Article 8 and the "Recommendations for Determination of Types" of the *International Code of Botanical Nomenclature* (Stafleu 1972).

A second herbarium sheet with tetrasporic specimens of *Pterocladia bulbosa* exists at the Herbarium of the University of California. Originally numbered *Reed 151b* (= uc 1452147), it was included by Loomis in her publication and was collected at Paia, Maui, on 30 March 1905. This is the only original material still existing and it should be designated as lectotype in compliance with the articles and recommendations mentioned above.

The species has been infrequently found thereafter. Only two more specimens in all collections (DORY 28252 and uc 623020) agree fairly well with the original descriptions and illustrations. Four other collections from Oahu (DORY 14181, 19499, BPBM 106517 and DAWSON 11910) seem to correspond to variations of this species and are identified here with doubts. The main axes of such specimens are shorter, narrower, and more cylindrical than the original material; the pectinate branches are sparser, alternate rather than opposite, and rising at a smaller angle from the main axes as they are incurved upwardly from the base. All of them are assigned to this species because they have unilocular cystocarps, pectinate branching, and tetrasporangial sori, typically on bulbous branches (Figure 6C). Most of these specimens are bleached in about two-thirds of their lengths, probably because of suboptimal ecological conditions, which, as has been shown in other species of *Gelidium* and *Pterocladia* (Dixon 1966, Stewart 1968), can modify the external morphology of these algae.

*Pterocladia caloglossoides* (Howe) Dawson

#### *Synonyms*

Dawson 1952, pp. 76–77; pl. 6, fig. 1. *Gelidium caloglossoides* Howe 1914, p. 96, pl. 34, fig. 7; pl. 35, figs. 1–12 (obligate synonym).

#### *Description*

Thallus small, creeping, repent (Figure 6D), in part erect, up to 1.2 cm high, consisting of linear, cylindrical, or somewhat flattened creeping axes, about 150–200  $\mu\text{m}$  wide,

attached to the substratum by small peglike holdfasts. Branches divaricate, arising sometimes radially in numbers of two to five from the creeping axes opposite to the holdfasts. Branches either repent, with attachment discs and erect branches, or erect, usually simple, up to 75  $\mu\text{m}$  wide, with attenuate, acute, or, in a few cases, broadly rounded apices. Younger branches generally lanceolate, acuminate, or acute, with the younger surface cells in oblique rows. Cortex with three to four layers of rounded, pigmented cells, up to 12  $\mu\text{m}$  diameter. Medulla with a simple row of larger (up to 15  $\mu\text{m}$ ) thick-walled cells surrounded by rhizoidal filaments. Tetrasporangia usually borne in regular V-shaped rows (Figure 6E) in sori on somewhat expanded or broadly rounded tips of erect branches. Cystocarps not seen.

#### *Discussion*

The species was first described by Howe (1914) from specimens living in shells dredged in 2.5 fathoms near Isla San Lorenzo, Perú. It was later found (Weber van Bosse 1921) in the reef of Nias, to the south of Sumatra in the Indian Ocean, and along the coast of Oregon (Doty 1947), Monterey, and southern California (Hollenberg 1942, Smith 1944, Dawson, Neushul, and Wildman 1960), and in Baja California. Most of the gatherings are from vertical faces and crevices in shaded intertidal rocks. The transfer of the species to *Pterocladia* was made by Dawson (1952) on a study of sexual thalli collected at Isla Guadalupe and Jalisco, Mexico, and was based on the similarities between the Peruvian and the Mexican tetrasporangial thalli.

The species had never been reported for Hawaii before and had been found only once (DORY 20140), collected by Hollenberg in 1965, forming bright red patches on living crustose corallines near mean low tide level at Black Point, Kahala, Honolulu. The Hawaiian populations have a number of morphological differences when compared with the descriptions of the other populations. They differ from Howe's account in having more cylindrical and narrower creeping axes, and in the lack of dwarf ventral branchlets near the attaching discs. This last character was also missing in the

populations from California, and neither Smith, nor Dawson, nor Doty mentioned them. The tetrasporangia in the Hawaiian specimens occur in diagonal rows in most young blades, as described for the species, but the arrangement is less obvious in older, partially shaded sori. Most young, vegetative blades in the Hawaiian plants are acuminate or lanceolate, with cells diagonally arranged at the tips, but the pattern is lost in older blades, most of which seem to have been grazed over previously. From Dawson's description, the Hawaiian populations differ only in the fact that the cortical cells do not become successively smaller internally but remain the same size, as Howe illustrated them. With such morphological modifications and in the absence of sexual thalli, the present specimens are difficult to segregate from *Gelidium pusillum* var. *minusculum*. The present determination of the Hawaiian plants is based on the presence of radially produced, divaricate branches, the occurrence of only one row of medullary cells, the large size of the cortical cells, and the V-shaped arrangement of young sporangia.

*Pterocladia caerulescens* (Kützinger) Santelices

*Synonyms*

Santelices, 1976. *Gelidium caerulescens* Kützinger 1868, p. 19, pl. 56 *c, d* (obligate synonym). Facultative synonyms: *Pterocladia tropica* Dawson 1959, pp. 40–42, figs. 21 *A–D*, fig. 22; *Gelidium irregulare* Loomis 1960, pp. 6–7; pl. 9, fig. 1; pl. 10, figs. 1, 2; pl. 11, figs. 2–3; *Pterocladia rigida* Loomis 1960, pp. 8–9; pl. 12, figs. 2–4.

*Description*

Thallus light green, dark green, or almost blackish, up to 7 cm high (Figure 6F), formed by erect, branched, ligulate axes arising at variable intervals from subcylindrical creeping axes up to 250  $\mu\text{m}$  diameter attached to the substratum by peglike holdfasts. Erect axes subcylindrical at the base, up to 450  $\mu\text{m}$  diameter, flattened or ligulate above, up to 1.3 mm broad by 100  $\mu\text{m}$  thick. Branching extremely variable, ranging from quadripinnate in large specimens to almost

none or simple alternate in smaller thalli. Branches similar in appearance to main axes but of smaller dimensions. External cortical cells anticlinally elongated in transection, 4–6  $\mu\text{m}$  high by 3–4  $\mu\text{m}$  broad and arranged in a palisade-like tissue, internally followed by two cortical layers of sparser and somewhat periclinally elongated cells of up to 15  $\mu\text{m}$  diameter. Rhizoidal elements surround the medullary elements. Tetrasporangia irregularly disposed in sori at the apex (Figure 6G) of axes and branches, sometimes with sterile margins. Tetrasporangia spherical, cruciately divided, and up to 50  $\mu\text{m}$  in diameter. Cystocarps unilateral (Figure 6H) near the apex of fertile branches, appearing as elongated swellings at the medial part of the branch, sometimes with more than one ostiole on only one surface of the thallus. Without prominent peristome but with evident sterile margins around the cystocarps.

*Discussion*

This species was first described by Kützinger (1868) from specimens collected at New Caledonia, and it is now known to occur in the Caribbean and in the tropical Pacific. In the Hawaiian archipelago the species has been found close to 50 times, mostly in intertidal habitats in Laysan, Kauai, Oahu, Maui, and Hawaii, producing tetrasporangia from August to May, and cystocarps, both in Hawaii and Oahu, only during June. In Oahu it typically occurs close to the nearshore margin of the reef, being darker, larger, and less branched under shaded conditions. It is one of the most variable species of Hawaiian Gelidiales and, as such, it has received several names previously. Reed (1907) identified it as *Gigartina acicularis*, *Gelidium latifolium*, *G. corneum*, *G. filicinum*, *G. caerulescens*, and *G. crinale*. MacCaughy (1918) named it *Gelidium latifolium* and Loomis called it *Pterocladia rigida* or *Gelidium irregulare*. Apparently this is also the *Gelidium* sp. 1 described by Neal (1930) from Waikiki and referred to on page 43 of her notebook (deposited at the Bernice P. Bishop Museum) where, below the name "*G. latifolium* of MacCaughy," Neal illustrated several aspects of *P. caerulescens* adding "*Gelidium* sp. 1".

*Pterocladia capillacea* (Gmelin)  
Bornet et Thuret

*Synonyms*

Bornet et Thuret 1876, p. 57; pl. 20, figs. 1-7. *Fucus capillaceus* Gmelin 1768, p. 146; pl. 15, fig. 1 (obligate synonym). Facultative synonyms: *Gelidium capillaceum* (Gmelin) Kützinger 1868, p. 18, pl. 50, figs. *d-f*; *Gelidium pyramidale* Gardner 1927, p. 273; pl. 36; pl. 37, fig. *a*; pl. 45; pl. 46, fig. 2; *Pterocladia pyramidale* (Gardner) Dawson 1945, p. 939. *Pterocladia densa* Okamura 1934, p. 63; pl. 30, figs. 1-2; pl. 33, figs. 4-8; *Pterocladia tenuis* Okamura 1934, p. 62, pl. 29; pl. 30, fig. 3; pl. 33, figs. 1-3; *Gelidium okamurai* Setchell et Gardner 1937, p. 75, pl. 6, fig. 16; pl. 17, fig. 38; *Pterocladia okamurai* (Setchell et Gardner) Taylor 1945, p. 161; *Pterocladia okamurai* forma *densa* Taylor 1945, p. 161, pl. 37, fig. 1; *Pterocladia mexicana* Taylor 1945, p. 159, pl. 35; *Pterocladia robusta* Taylor 1945, p. 160, pl. 36; *Pterocladia complanata* Loomis 1949, pp. 4-7, pl. 6, figs. 1-2; pl. 7, figs. 1-4, pl. 9.

*Description*

Fronds sometimes bushy, 3-18 cm high (Figure 6I), consisting of one to several distichously, pinnately branched percurrent axes rising from a holdfast of entangled stolons. Erect axes cylindrical below, flattened above, finishing in a spatuliform or attenuated apex, of up to 0.4 mm in diameter at their bases and up to 1.8 mm broad in the flat portions. Branching of up to five orders, generally restricted to the upper two-thirds of the frond, alternate below and opposite above. External cortical cells anticlinally elongated in transection, 3 by 6  $\mu\text{m}$  followed by two or three layers of pigmented larger and rounded cortical cells, of up to 12  $\mu\text{m}$  diameter, grading into larger medullary cells with thicker walls. Rhizoids varying in number and position according to the portions of the frond sectioned. Tetrasporangia disposed without order (Figure 6J) in sori limited to small branches or covering large areas of the terminal parts of large branches. Tetrasporangia cruciately divided, rounded and up to 30  $\mu\text{m}$  diameter. Cystocarps (Figure 6K) unilateral, up to 550  $\mu\text{m}$  diameter with protruding peristome.

*Discussion*

According to Dixon (1960), this species was first described and illustrated by Gmelin (1768). Originally described from the Mediterranean without exact indication of locality, it is now known to be widespread in temperate and warm seas where it assumes great morphological variation and has received several specific epithets and combinations (see Stewart 1968 for a review). In 1945, Moore pointed to the lack of convincing characters separating *Pterocladia capillacea* from *P. nana*, *P. tenuis*, and *P. densa*; and in 1952 and 1954b, Dawson, noticing that *P. pyramidale* could not be separated consistently from *P. okamurai*, *P. robusta*, *P. mexicana* or *P. capillacea*, insisted on the need for a study of this species. The formal reduction of many of these forms to synonyms was done by Stewart (1968) after comparisons of the corresponding specimens.

Over 100 specimens of *Pterocladia capillacea* were present in the Hawaiian collections studied, collected in several habitats from Kauai, Oahu, Maui, and Hawaii. Most habitats are described as being close to the seaward edge of reef flats where waves dash constantly. This is the type of habitat where *P. capillacea* occurs most frequently on Oahu, reaching sizes of up to 20 cm in shaded conditions. It has been found tetrasporangial in all islands, from August to June, and cystocarpic during April and June in Oahu and during April, August, and November in Maui.

This is one of the species that has been most abundantly collected in the islands. It shows much morphological variation and approaches closely several of the species now reported as synonyms. For example, the specimens on BPBM 106504 are fairly symmetric, with flat branching, and are similar to *Pterocladia pyramidale* Taylor, whereas some of the specimens referred to by Chamberlain (BPBM 106483) are larger and thicker and resemble *Pterocladia robusta* Taylor. The same is true for the algae collected by Doty in Hawaii and Kauai, presently at the Bernice P. Bishop Museum (BPBM 106477, 106480, and 106481) which, although shorter, are also thick and broad with wide branching intervals. Some of the thalli in DORY 12946 are similar to typical *Pterocladia*

*okamurai* from Ecuador as described by Taylor (1945), whereas the individuals in UC 622964 and 622962 have narrower branches irregularly placed at short intervals and densely congested, resembling *Pterocladia okamurai* f. *densa*. The more typical thalli in DORY 8709 and 25754 show small, short-stalked, tetrasporangial leaflets along the axes margins which are characteristic of *Gelidium arbuscula* Børgesen. According to Børgesen (1925), this species was first named by Bory in Bory's herbarium and has never been compared to *P. capillacea*. Upon examination of Bory's original material, Børgesen concluded that some of his own thalli collected at the Canary Islands as well as the plant distributed by Hauck and Richter in the Phycotheca Universalis, no. 557, under the name of *Gelidium latifolium* corresponded to this species. Børgesen also provided the first description and illustration of *G. arbuscula*. In the herbarium sheet numbered DORY 8709, it is written that Doty compared his specimens with those numbered 557 in the Phycotheca Universalis from Orotava and concluded that both sets of plants were very similar. This is consistent with the fact that Børgesen's description could fit perfectly the larger Hawaiian specimens of *Pterocladia capillacea*.

The species was misidentified frequently in Hawaii, accounting for several specific epithets previously reported for the islands. Chamberlain (1860) identified some forms (BPBM 106482) as *Gelidium rigidum*, whereas Reed (1907) named them *G. corneum* var. *capillaceum* or *G. latifolium* and Setchell identified some specimens (UC 623019) as *Gelidium amansii*. In addition, this species seems to have been named by Neal (1930) *Gelidium* sp. 2 together with *Gelidiella acerosa*. The specimens at BPBM 106506 are dwarf *P. capillacea* with thin and acute branches resembling the *G. acerosa* collected by Neal at Rabbit Island.

#### SPECIES INQUIRENDAE

The following species of Gelidiales have been reported for the Hawaiian Islands but neither representative material nor evidence of misapplication of the names was found in the present review.

#### *Gelidium amaresii*

This species was reported by Chamberlain (1860) without exact indication of locality. No one else has found the species in Hawaii or has used the name elsewhere.

#### *Gelidium attenuatum*

This name was used, with a question mark, by Reed (1907) when listing the species of *Gelidium* commonly used in Hawaii. MacCaughy (1918) remarked that the name is absent from the list of species published by De Toni (1897) and that it could constitute a synonym.

#### *Gelidium cartilagineum* (L.) Gaillon

This species was first recorded by Chamberlain (1860) and then included by MacCaughy (1918) in his list of Hawaiian algae. A recent study by Dixon (1967) showed that *Fucus cartilagineus* L. provides the oldest epithet available for a species of *Plocamium* rather than *Gelidium*, so the combination *G. cartilagineum* is presently considered superfluous. The species previously referred to by the name *G. cartilagineum* is now known as *G. versicolor* (Gmelin) Lamouroux. It was first described for South Africa and its presence in Hawaii seems improbable.

A second variety of *Gelidium cartilagineum*, namely *Gelidium cartilagineum* var. *robustum* Gardner (1927) is known for the Pacific coast of the United States from central California to Baja California. This variety was given specific rank by Hollenberg and Abbott (1965) because it had consistent morphological differences with typical *G. cartilagineum*. In California the species reaches 15 to 30 cm high (Smith 1944) and is a conspicuous member of subtidal communities. In Hawaii no one else has found the species after Chamberlain (1860) in spite of its supposedly large size.

#### *Gelidium radicans*

This species was also listed by Chamberlain (1860) and, as in the previous cases, was never found thereafter.

#### *Gelidium sesquipedale*

In common with the above cases, this species was listed by Chamberlain (1860) without exact

indication of locality. This is a common European species unlikely to be found in the Hawaiian waters.

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