

New Taxa of Ceramieae (Rhodophyta) from Hawai'i¹

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ABSTRACT: A new genus and five new species belonging in the Ceramieae have been found in recent analyses of the Hawaiian Ceramiaceae. *Ardreanema*, the new genus, is a microscopic plant having a simple moniliform structure with light cortication where cells meet (nodes) in the filament. Several gonimolobes composed of uniseriate rows of carposporangia are formed on female plants, and tetrasporangia, one per segment, are borne in a series near distal ends of branches. A single species, *A. farifructa*, n. sp., is assigned to the genus. The other new species are *Ceramium dumosertum*, *Ceramium womersleyi*, *Ceramium hanaense*, and *Ceramium ptilocladioides*.

THERE ARE MANY SPECIES in *Ceramium* in tropical and subtropical regions of the world, and separating them from one another is a difficult and often frustrating exercise. An analysis of the species occurring in the Hawaiian Islands revealed that several undescribed taxa are present in this flora, including five new species, one of which is assigned to a new genus.

Ceramium is restricted to species that have upright to decumbent branches that are pseudodichotomously branched. All branches are indeterminate. Cortication in *Ceramium* is composed of a ring of pericentral cells attached to distal ends of axial cells, each pericentral cell forming two acropetal and, usually, two basipetal corticating filaments. The acropetal filaments are longer than the basipetal ones in most species of *Ceramium*, but some have reduced development of acropetal filaments, most corticating cells being formed by basipetal filaments that are often arranged in a regular and aligned series of cells.

MATERIALS AND METHODS

Field collections were preserved and stored in 3% formaldehyde-seawater. Sorting of specimens occurred in the laboratory, usually under magnification of a dissecting microscope. Separated species were mounted on microscope slides, where they were stained with 1% aniline blue followed by 1% HCl. After washing in deionized water, the specimens were mounted under a cover glass in corn syrup. Some specimens were mounted directly in a corn syrup mounting medium containing ca. 1% acidulated aniline blue.

Specimens are all on microscope slides that are in the collection of the Bishop Museum, Honolulu, Hawai'i (BISH), or in the personal collection of I. A. Abbott (IAA).

DESCRIPTIONS OF TAXA

Genus *Ardreanema* Norris & Abbott, n. genus
Figures 1–4

LATIN DIAGNOSIS: *Thalli filamentosi et microscopici; cellulae axiales cellulis 3 pericentralibus corticantibusque aliquando efferentibus cellulas 1–2 acropetas. Filamenta monopodialia pseudodicotome ramosa. Tetrasporangia*

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tetradice divisa, unum tetrasporangium per segmentum in serie in partibus distalibus ramorum. Gonimoblasti gonimolobis 1–3, carposporangia uniseriata; unum filamentum subtentum et determinatum et involucre.

DESCRIPTION: Thalli microscopic (Figure 1); axes with moniliform cells, each segment between cells having three pericentral cells. Axes with monopodial growth and pseudodichotomously branched (Figures 1,2). Branches decumbent, attached by rhizoids on the ventral side (Figure 1). Tetrasporangia tetrahedrally divided, borne in a series of nodes near branch distal apices (Figure 4). Gonimoblasts borne laterally near the middle of the upright thallus; one to several gonimolobes, each composed of a uniseriate long row of carposporangia (Figures 1,3). A single adventitiously developed determinate involucreal filament formed on axial cell proximal to bearing cell of gonimolobes (Figures 1,3).

ETYMOLOGY: This filamentous (= *nema*) alga is named in honor of Dr. Françoise Ardré of the Muséum National d'Histoire Naturelle, Paris, in recognition of her studies on the Ceramieae.

TYPE SPECIES: *A. farifructa* Norris & Abbott, n. sp.

Ardreanema farifructa Norris & Abbott, n. sp.
Figures 1–4

LATIN DIAGNOSIS: *Thalli 1 mm alti, 40 µm lati; apices ramorum recti. Rhizoidea unicellularia, in rami parte decumbenti proximalique portata; ramus adventitius in latere adverso eiusdem segmenti plerumque formatus. Cellulae 3 pericentrales per nodum; omnis cellula pericentralis 1–2 uni- aut bicellularia filamenta corticantia formans. Tetrasporangia usque ad 45 µm diametro, unum per segmentum et filamentum 3-cellulari involucreali. Carposporangia in serie lineari portata, unumquidque formans gonimolobum. Unum filamentum determinatum involucrealeque in cellula subsidiaria ad cellulam ferentem gonimoblasti.*

DESCRIPTION: Thalli (Figure 1) up to ca. 1 mm tall, 40 µm wide; monopodially developed, with pseudodichotomous branching (Figure 2); branch tips straight. Unicellular rhizoids on ventral side of decumbent branches

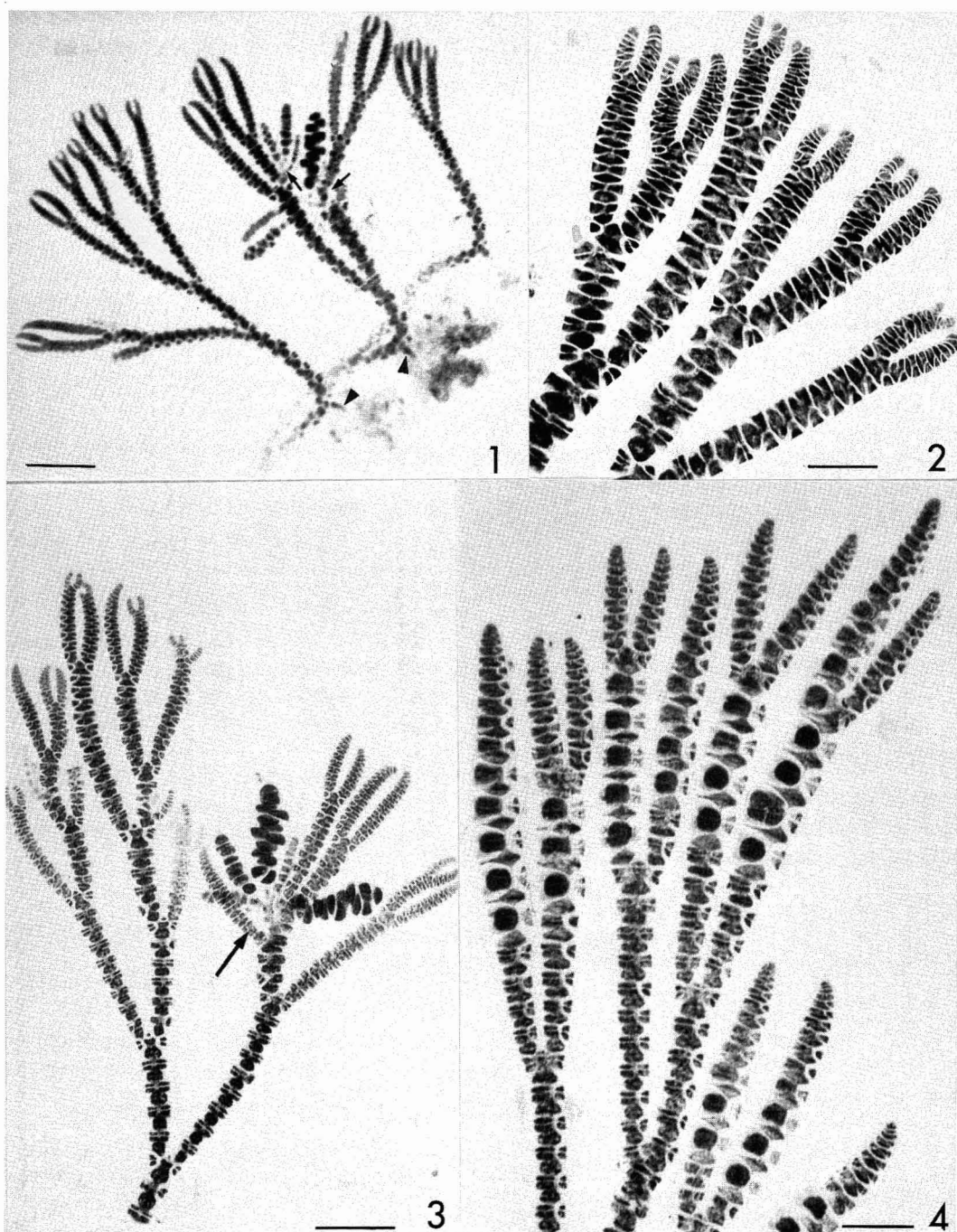
(Figure 1); an adventitious upright branch often develops opposite rhizoids. Gland cells not present. Internodal length is approximately equal to nodal length except in some decumbent areas, where internodes may be 1.5 times nodal length; axial cells may be up to twice as long as broad. Three pericentral cells attached at distal end of axial cell at each node; each pericentral forms one or two uni- or bicellular acropetal corticating filaments; basipetal filaments not present. Tetrasporangia borne in a series of nodes near branch tip, one per node, and enclosed by a single three-celled involucreal filament; tetrahedrally divided and up to 45 µm in diam. (Figure 4). Procarys near branch tips where cortex is mature, one per node. Carposporangia in linear unbranched gonimolobes of up to 16 carposporangia (Figures 1,3), several gonimolobes usually produced in a series. A single indeterminate involucreal filament on cell proximal to bearing cell of gonimoblast (Figures 1,3). Male plants were not found.

HOLOTYPE: BISH 612650 (Figure 3); subtidal, –2 ft, on encrusting coralline red algae on lava rock, south of Kealakekua Bay, Kona District, Hawai'i Island, May 1990, *legit* W. H. Magruder.

OTHER MATERIAL EXAMINED: Hawai'i Island: Mauna Lani, IAA 20617, *legit* Audrey Asahina; Waikoloa, IAA 20687, 20688, *legit* Wayne Iwaoka; Maui Island, Mā'alaea, IAA 14386, *legit* I. Abbott.

ETYMOLOGY: The species name denotes the row of cells (*fariam*) in the gonimoblast (*fructa*).

COMMENTS: The decumbent upright branches and pseudodichotomous branching pattern of *Ardreanema* are characters similar to those of *Ceramium*. Cortication in *Ceramium*, however, is basically not less than four pericentral cells; the three pericentral cells of *Ardreanema* are characteristic of the genus. The most unusual character of *Ardreanema*, however, is the uniseriate, mostly unbranched arrangement of carposporangia that form linear gonimolobes. Species of *Ceramium*, *Ceramothamnion*, and *Corallophila* are different in having highly branched carposporangial filaments forming spheroidal gonimolobes.



FIGURES 1–4. *Ardreanema farifructa*. (1) Female plant showing decumbent thallus attached in proximal regions by rhizoids (arrowheads). Two gonimoblasts are present on the central branch (arrows); the older one on the right has two gonimolobes broken free and lying next to the left-hand branch. Scale = 100 μm . (2) Distal parts of branches showing apical cells and stages in formation of cortication. Note the triangular cell often cut off between the pseudodichotomies. Scale = 50 μm . (3) The holotype specimen (BISH 612650), a female plant with a well-developed gonimoblast and several young gonimoblasts. Arrow identifies an involucral branch subtending the gonimoblast. Scale = 100 μm . (4) Distal parts of branches of a tetrasporangiate plant showing tetrasporangia in series of segments. Scale = 50 μm .

Genus *Ceramium* Roth

Ceramium dumosertum Norris & Abbott, n. sp.

Figures 5–9

LATIN DIAGNOSIS: *Thalli erecti decumbentes, incrementum monopodiale ramificatione pseudodichotoma, omnis ramus indeterminatus. Apices ramorum involuti, saepe se transeuntes. Cellulae 6–8 pericentrales in omni nodo; filamenta corticantia, acropeta 2 et basipeta 2; unum filamentum acropetum in spinam valde acutam 2–5-cellularemque terminans; spina abaxialis saepe longior quam aliae. Filamenta basipeta spinas parum minores saepe faciunt. Cellulae axiales usque ad 2-plo longiores quam diameter. Tetrasporangia cruciatim divisa, in serie nodorum abaxialiter portata, 1–5 per nodum, involucrata spinis in cellulis involucribus. Gonimolobi spherici, aliquot sequenter formati et per filamenta 5–6 involucria determinataque subteni.*

DESCRIPTION: Thalli erect, often decumbent, monopodial, but pseudodichotomously branched (Figure 5); the tips often involute and crossing one another (Figures 7,8); four to eight nodal intervals may be present between pseudodichotomies. Branches up to ca. 200 μm in diam. Six to eight pericentral cells per node, each with two acropetal and two basipetal corticating filaments. One of the primary cells of an acropetal filament usually with two- to five-celled acutely pointed spine (Figure 8), the number of spines often corresponding to the number of pericentral cells, but the spine on the first (abaxial) pericentral cell often longer than the others; tips of spines straight, not recurved; smaller spines of one to three cells on some of the primary cells of basipetal filaments, but usually fewer than the acropetal spines. Distal and proximal edges of corticating bands straight (Figure 7); distal edge bordered mostly by tertiary cells, proximal edge by primary and secondary cells; gland cells not present. Axial cells up to twice as long as wide. Rhizoids originate from pericentral cells and primary cells of corticating filaments; three to four often at each node; rhizoids have multicellular shafts and disks.

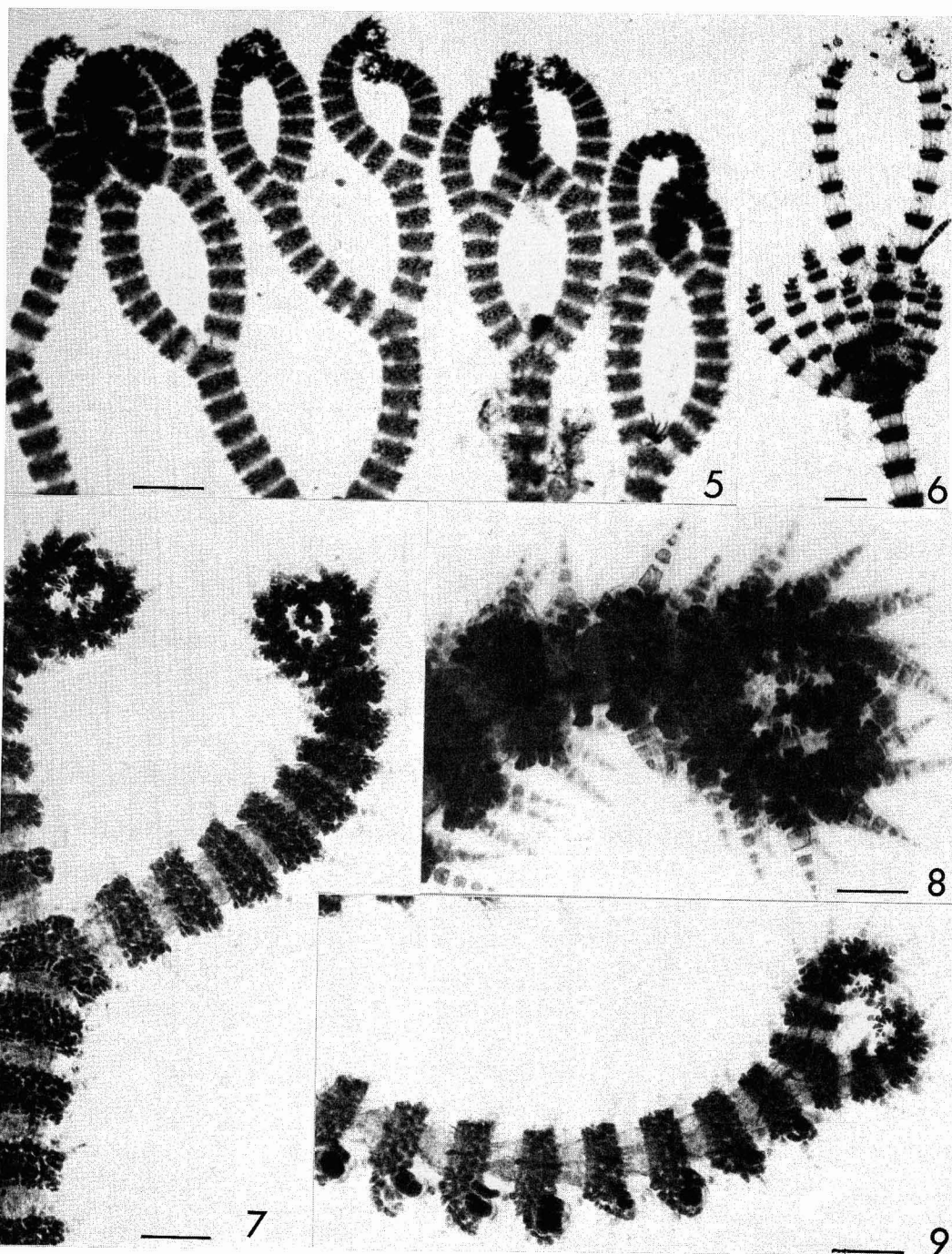
Tetrasporangia abaxial (Figure 9), enclosed by a broad and open involucre with filaments

often ending in spines; one to five tetrasporangia at each node and in long series of segments on branches. Mature involucre may be as broad as the supporting filament; some involucre may have several small spines in addition to the larger primary spines. Tetrasporangia cruciately divided and measure $33 \times 40 \mu\text{m}$. Occasional tetrasporangia occurring on opposite sides of branches tend to appear whorled if multiple sporangia are produced in each involucre.

Procarys borne on abaxial side of most distal curve of branch tips; at least four to five procarys in a series, one per node, on the first-formed pericentral cell. The supporting cell of the procary also the bearing cell of the spine, the largest of spines in the node; the spine is the sterile filament in the procary. Several spheroidal gonimolobes formed at different stages of development and five to six determinate involucrial filaments on the subsidiary cell (Figure 6); bearing filaments indeterminate and a second indeterminate filament may develop on the second proximal cell to the bearing cell of the gonimoblast. Spermatangia adaxial in young corticating nodes but develop on abaxial sides in older ones; spermatangia often not formed in the vicinity of the long abaxial spine so that they are mostly proximal and on adaxial sides of corticating bands.

HOLOTYPE: BISH 612652; intertidal on basalt, Ka'inalimu Bay, Hāna, Maui Island, Hawai'i, legit I. A. Abbott (20307), 21 July 1990. (Isotypes: I. A. Abbott 20133, 20147, 20191, 20339, 20147a, b, 20174.)

OTHER MATERIAL EXAMINED: Hawai'i Island: Kaloko, legit S. & D. Carper, July 1988 (IAA 20119). Maui Island: drift, Launiupoko, legit D. P. & I. A. Abbott, 31 August 1976 (IAA 12544); intertidal, Ka'inalimu Bay, Hāna, legit K. McDermid, 29 March 1984 (IAA 17173); intertidal, Hāna Bay, 26 August 1976 (IAA 14821). O'ahu Island: by diving to 20–40 ft, Mākaha Caverns, legit L. M. Hodgson, 5 August 1988 (IAA 18856, 18869, 18885, 18913); by diving to 35–40 ft, Mākaha Caverns, legit L. M. Hodgson, 21 July 1990 (IAA 20440, 20492, 20497, 20542); intertidal, Kaloko, legit I. A. Abbott (IAA 17213);



FIGURES 5–9. *Ceramium dumosertum*. (5) Distal ends of branches of a single plant, showing regular pseudodichotomous branching and overlapping of branch tips. Scale = 210 μm . (6) Distal end of female plant with a single gonimoblast. Seven determinate involucre branches are present and the indeterminate bearing branch has one pseudodichotomy distal to the gonimoblast. Scale = 200 μm . (7) Branch tips showing overlapping branch tips and surface view of corticating cells. Scale = 50 μm . (8) Branch tip showing detail of spines on corticating bands. Scale = 100 μm . (9) Distal end of tetrasporangiate branch. Note abaxial sporangia and involucre filaments. Scale = 100 μm .

dredged on dead coral, 50–90 ft, off Honolulu Harbor, *legit* K. Hunt, 4 November 1981 (IAA 16002).

COMMENTS: As interpreted by Norris (1992), *Ceramium hamatispinum* Dawson, 1950, a species that also has spinose nodal cortication, has six to seven pericentral cells and six to seven pseudopericentral cells. Pericentral cells in that species bear one acropetal and two basipetal corticating filaments and pseudopericentral cells bear two acropetal and one basipetal filaments. *Ceramium dumosertum* has no pseudopericentral cells, in contrast to *C. hamatispinum*, and forms two acropetal and two basipetal corticating filaments from each pericentral cell. There may be up to five to six spines, up to three cells long and often recurved apically, on each corticating band in *C. hamatispinum*. The presence of more spines on corticating bands, including some secondary smaller spines, and longer straight primary spines in *C. dumosertum* also distinguish it from *C. hamatispinum*.

Ceramium womersleyi Norris & Abbott, n. sp.
Figures 10–14

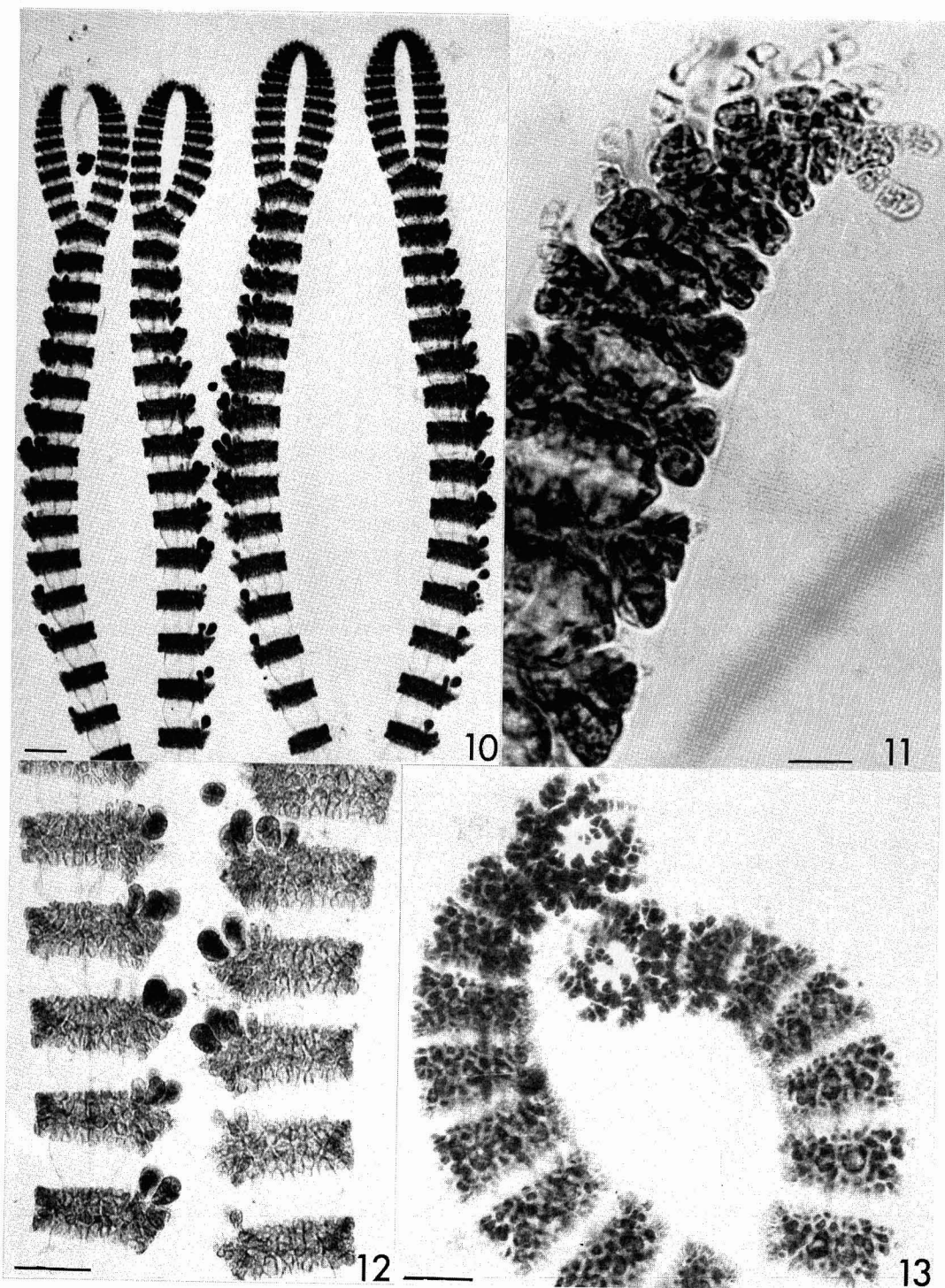
LATIN DIAGNOSIS: *Thalli recti, pseudodichotome ramosi apicibus imbricatis; ramificatio omni intervallo nodali decimo aut plus. Cellulae pericentrales 8 partim exposae remanentes ubi corticatio matura est. Aliquot filamenta acropeta in pilis deciduos longosque terminantia et cicatrices in margine distali fasciae corticalis relinquentia. Curvamen distalis ramorum plerumque spinis abaxialibus, multicellularibus, deciduis in serie unica. Glandicellulae parvae plerumque adsunt, aliquot per nodum. Segmenta tetrasporangiorum corticatione expansa in latere abaxiali; corticatio sporangia exserta non tegens. Aliquot segmenta fecunda in regionibus maturis sporangia verticillata habent, usque ad 2 per nodum. Filamenta 2–3 indeterminata involucria gonimoblastos subtendent; filamentum ferens indeterminatum.*

DESCRIPTION: Plants upright or partly decumbent, up to ca. 2 cm tall, the primary axes up to 300 μ m wide; pseudodichotomous branching with overlapping, involute, abruptly tapering branch tips (Figures 10, 13); branches usually with 10 or more nodal intervals between branches. Usually eight pericentral

cells, sometimes nine, each with two acropetal and two basipetal corticating branchlets; mature cortical band with straight edges and mostly with partly exposed pericentrals (Figures 10–13); proximal edge of corticating band bordered mostly by secondary cells in basipetal filaments; distal edge bordered mostly by secondary to tertiary cells of acropetal filaments. Some thalli have acropetal filaments terminating in long, slender deciduous hairs leaving scars on most distal cells. Branch tips often with a row of abaxial one- to three-celled spines on distal curve (Figure 11); spines usually deciduous when branch becomes straight. Gland cells small, derived from outer cortical cells; several in each cortical band in both acropetal and basipetal filaments; large gland cells may be present in older parts of thalli. Internodes up to four times the length of nodes, and axial cells approximately twice as long as broad when mature. Cortical bands in old parts of thalli often lack or with little secondary cortical growth. Rhizoids formed by pericentral cells; shaft and disk multicellular; older rhizoids may become bulbous.

Tetrasporangia exserted (Figures 10, 12), developing first on abaxial side but later becoming whorled and up to 12 tetrasporangia per node; tetrahedrally divided and up to 65 μ m in diam. Node expands on abaxial side in early stages of tetrasporangial development, forming a group of sporangia (Figure 12).

Procargs formed in branch tips on abaxial side by first pericentral cell. Some thalli also bear a one- to three-celled deciduous spine on the same cell. Procargs also seen on some involucrial filament tips. Gonimoblasts developing near branch apices on an indeterminate bearing filament (Figure 14); gonimolobes globular, two or three forming at different times; two to three involucrial filaments formed by subsidiary cell, each indeterminate and often with a dichotomy (Figure 14). Male fertile areas (Figure 13) at first adaxial and proximal on cortical bands but become equally distributed in older stages, often in two acropetal and basipetal bands, separated by the exposed pericentral cells. Some male plants form few to many unbranched adventi-



FIGURES 10–13. *Ceramium womersleyi*. (10) Distal ends of a tetrasporophyte plant. Scale = 150 μm . (11) Branch tip showing deciduous cellular spines on abaxial side of branch. Scale = 20 μm . (12) Tetrasporophyte branches showing exserted sporangia occurring in abaxial clusters. Scale = 100 μm . (13) Distal end of male branches, spermatangial sori occurring mostly on adaxial sides of branches. Scale = 100 μm .

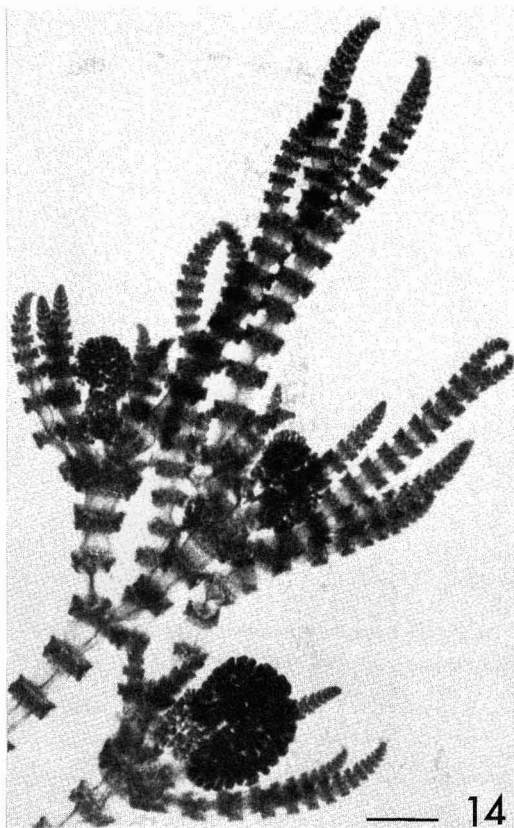


FIGURE 14. *Ceramium womersleyi*. Branch tips of a female plant showing three gonimoblasts, indeterminate bearing filaments, and the associated determinate involucral filaments. Scale = 200 μ m.

tious branchlets with straight tips that become fertile.

HOLOTYPE: BISH 612653; drift, near Līpoa St., Kīhei, Maui Island, Hawai'i, *legit* I. A. Abbott (IAA 12545), 31 August 1976.

OTHER MATERIAL EXAMINED: Maui Island: reef flat, 1–4 ft deep, between Keālia Pond and Mā'alaea, *legit* S. Hau, April 1989 (IAA 19065a–d, 19066, 19069); drift, near Līpoa St., Kīhei, *legit* I. A. Abbott, 31 August 1976 (IAA 12545); drift, near Līpoa St., Kīhei, *legit* I. A. Abbott, 30 June 1990 (IAA 19996).

COMMENTS: *Ceramium womersleyi* differs from *C. ornatum* Setchell & Gardner, 1930, in having fewer small cortical cells that are angular only in early stages of development, and by the presence of gland cells, which

are usually not present in *C. ornatum*. This species was compared with the holotype of *C. ornatum*, a specimen that is in poor condition, however, and difficult to interpret. The exerted tetrasporangia in *C. womersleyi* and *C. ornatum* are a major difference from *C. clarionense* Setchell & Gardner, 1930, which always has an involucral covering.

Ceramium womersleyi has fewer small cortical cells and more exposure of the pericentral cells than in *C. aduncum* Nakamura, 1950, a species also occurring in Hawai'i with which it may be confused. The multicellular hairs that are often present on abaxial sides of branch tips in *C. womersleyi* are absent in *C. aduncum*, but unicellular hairs may be present in the latter species. Also, fertile tetrasporangial segments of *C. womersleyi* have enlarged cortical bands on the abaxial side of the thallus where multiple sporangia are formed, a condition not found in *C. aduncum*, which usually has fewer sporangia per fertile segment, and they occur exerted on the adaxial side.

Ceramium womersleyi also has characters similar to *C. isogonum* Harvey, 1855, but the Hawaiian plants are smaller and have less cortication than in nodes of *C. isogonum*. Womersley (1978), in his description of *C. isogonum*, did not mention the abaxial deciduous spines nor the deciduous hairs or hair scars that border the distal margins of many nodes in the Hawaiian species, characters that seem to be distinctive. The fringe of hairs on the distal margin of the cortical band is also characteristic of *C. cupulatum* Womersley, 1978, but other cortication characters as well as the branching pattern are very different from those of the Hawaiian plants. The branching pattern of *C. cupulatum* strongly suggests that it is a species of *Ceramothamnion*.

ETYMOLOGY: It is a pleasure to name this species for Professor H. B. S. Womersley, of Adelaide, South Australia, in recognition of his outstanding work on the *Ceramium* species in southern Australia.

Ceramium hanaense Norris & Abbott, n. sp.

Figures 15–19

LATIN DIAGNOSIS: *Thalli axibus monopodialibus prostratisque laterales rectos plerumque*

non ramosos efferentibus; usque ad 150 μ m diametro. Cellulae 5–7 pericentrales in omni segmento; primariae cellulae acropetae magnae, aequantes usque ad 1/2 diametri cellulae pericentralis. Fasciae corticantes superantes diametrum cellulae axialis et proxime angustiores. Tetrastromata in fasciculis abaxialibus, aliquando verticillata, involuata; apertura distalis lata. Cystocarpia parva, filamentis 3–4 involucribus determinatisque; filamentum ferens indeterminatum.

DESCRIPTION: Axes monopodial and prostrate (Figures 15–17), adventitiously producing mostly unbranched upright laterals that occasionally have a pseudodichotomy. Branch tips abruptly tapering; straight or curved when immature (Figure 16). Filaments up to 150 μ m in diam. Five to seven pericentral cells per segment, each with two acropetal and two basipetal corticating filaments. Distal margin bordered by tertiary to quaternary cells of cortical filaments; proximal margin bordered by primary and secondary cells. The two primary cells of acropetal filaments on each pericentral cell large and approximately 1/2 the diameter of pericentral cells; they lie on its upper surface, radiating from the center as does the pericentral cell. Gland cells not present. Internodes up to twice the length of nodal bands but nodal bands exceeding the diameter of axial cells; nodal bands often broader distally than proximally. Axial cells isodiametric in upright filaments but two to three times their width in proximal part of uprights and in prostrate filaments. Rhizoids formed by any larger cell in the cortication including pericentral cells; shaft unicellular but with multicellular disks.

Tetrastromata in abaxial clusters (Figures 18, 19) or becoming whorled in some plants, in a short series of segments near distal ends of upright laterals; involucribus with broad distal openings; cruciately divided and up to ca. 30 μ m in diam. Procarps in a series of segments near upright branch tips. Gonimoblast small and with few lobes; three to four involucribus filaments, determinate, short and narrower than vegetative filaments; bearing filament indeterminate. Spermatangia on small cells of cortex, in a series of mature segments near branch tips of upright filaments; some-

times only on basipetal cells in early stages of development.

HOLOTYPE: BISH 612651; intertidal, Ka'inalimu Bay, Hāna, Maui Island, Hawai'i, legit L. M. Hodgson (IAA 20311). (Isotypes: I. A. Abbott 20300, 20310, 20329, 20334, 20335, 20337, 20346C, 20355, 20359, 20360.)

OTHER MATERIAL EXAMINED: Hawai'i Island: Kaneleau lava flow, Puna, legit M. S. Doty, 21 December 1955 (IAA 12914); black sand beach, Punalu'u, legit C. M. Smith, 23 May 1990 (IAA 19706a); Whittington State Beach Park, Honu'apo, legit C. M. Smith, 23 May 1990 (IAA 19690). Maui Island: 'Āhihi Bay, legit L. M. Hodgson, 1 July 1990 (IAA 19907); Keonioio, legit I. A. Abbott, 18 July 1990 (IAA 20236). O'ahu Island: by diving to 90 ft, Wai'anae, legit L. M. Hodgson, 11 June 1991 (IAA 20416).

ETYMOLOGY: The species name denotes the type locality, Hāna, on the southeastern coast of the island of Maui.

COMMENTS: Similar to *Ceramium caudatum* (Setchell & Gardner) Norris (1992), but with slightly larger thalli and usually with somewhat more proximal cortication. The main differences between these two species, however, are the more variable number of pericentral cells in *C. hanaense*, five to seven, whereas seven are present in *C. caudatum*, and the involucribus filaments surrounding tetrastromata in *C. hanaense*, an involucribus being absent in *C. caudatum*.

Ceramium ptilocladioides Norris & Abbott, n. sp.

Figures 20–24

LATIN DIAGNOSIS: *Thalli axibus prostratis ramos determinatos rectosque et non ramosos formantibus. Omnes rami omnino corticati; cellulae (7–)9 pericentrales in omni nodo filamenta breviter acropetaque plerumque usque ad cellulas quaternarias, et filamenta basipeta ex 6° cellulis formantes; filamenta basipeta aliquando ramificantia prope extremitates distales (proximalia in thallo). Filamenta basipeta cellulas elongatas primarias ad tertiarias habentia tectas a cellulis parvis quas abscindunt, omnis cellula magna series 2 cellularum parvarum in latere exteriori formans. Corticatio cellularum axialium incohaerens, plerumque*



FIGURES 15–19. *Ceramium hanaense*. (15) Habit of plant showing prostrate (large arrow) and upright branches (small arrows). Scale = 250 μm . (16) Enlargement of distal end of prostrate branch in Figure 15. Arrows indicate upright branches; arrowheads indicate some rhizoid groups. Scale = 100 μm . (17) A more robust specimen with prostrate branch (large arrow) having large discoid rhizoids (arrowheads) and with two upright branches (small arrows). Scale = 160 μm . (18, 19) Distal ends of tetrasporangiate branches; involucrate tetrasporangia in two segments near distal ends. Scale = 100 μm .

spatium magnum inter pariem cellulae axialis et cellulas corticales exteriores. Tetrasporangia in stichidiis terminalibus aut aliquando intercalariis in ramis rectis, usque ad 9 per segmentum, a cellulis corticalibus tecta. Spermatangia etiam in apicibus ramorum rectorum, ab omnibus cellulis exterioribus corticalibus facta.

DESCRIPTION: Plants mostly prostrate, monopodial, with erect adventitiously formed branches (Figure 20). Thallus up to ca. 1 cm long and 300 μm wide, axial cells less than 150 μm in diam., slightly longer than wide, leaving a broad space between the outer cortical layer and the axis. Upright branches mostly unbranched but some becoming decumbent and prostrate, assuming indeterminate growth and then forming adventitious branches. An occasional pseudodichotomy develops in upright branches, and older upright branches often have one or two proximal adventitious branches. At early stages in the formation of these branches, which are formed by pericentral cells, they consist of a moniliform series of up to a dozen very short cells terminated by a dome-shaped apical cell, a condition strongly resembling the formation of branches in the Crouanieae, including *Ptilocladia* in which they are also borne on pericentral cells. Cortication of axial cells complete (Figures 21, 22), mostly composed of at least two layers of cells: inner large cells, up to ca. $10 \times 20 \mu\text{m}$, loosely arranged in filaments, and an outer layer of small cells, up to 7–8 μm in diam. Nine pericentral cells, up to ca. 18 μm in diam. and mostly isodiametric, each with two acropetal and two basipetal filaments. The acropetal filaments are shorter than the basipetal filaments (Figure 22), composed of up to four to five cells, at least two to three of which are submerged. The basipetal filaments are up to 10 cells long, four to five of them submerged and having a form similar to the internal acropetal cells. Internal cortical cells, except the pericentral cells, form a small-celled cortex on the thallus surface (Figure 22).

Male and tetrasporangiate specimens have been collected. Spermatangia (Figure 23) terminate short filaments of elongate cells produced in fascicles by outer cortical cells. Only a single male branch has been found and it is producing spermatangia in a short series of

intercalary segments at an expanded part of the branch. Erect branches bearing tetrasporangia (Figure 24) are slightly wider than sterile upright branches and often remain indeterminate for a relatively long period, producing long fertile branches. Tetrasporangia are up to ca. 35 μm in diam. and are cut off on the distal sides of pericentral cells, nine often being present in a whorl in each segment. Fertile pericentral cells produce two involucreal filaments, one on each lateral side of the tetrasporangium. Female and cystocarpic plants have not been found.

HOLOTYPE: BISH 612654; epiphytic on *Laurencia brachyclados* on rocks off the old Kona airport, Hawai'i Island, *legit* C. M. Smith, 23 May 1990 (IAA 19609). (Isotypes: I. A. Abbott 19607, 19611, 19612, 19613.)

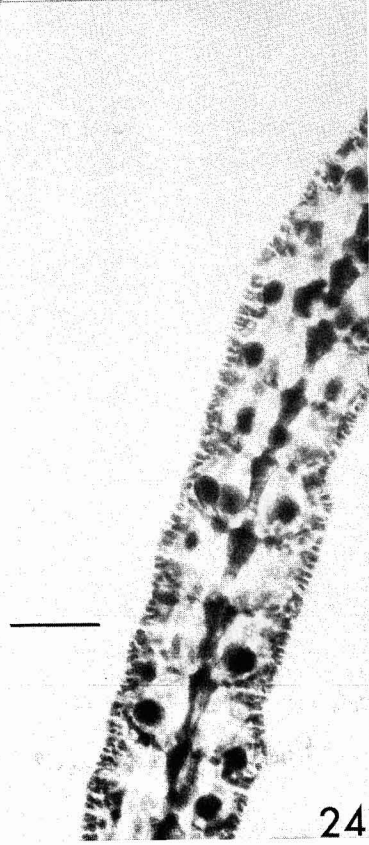
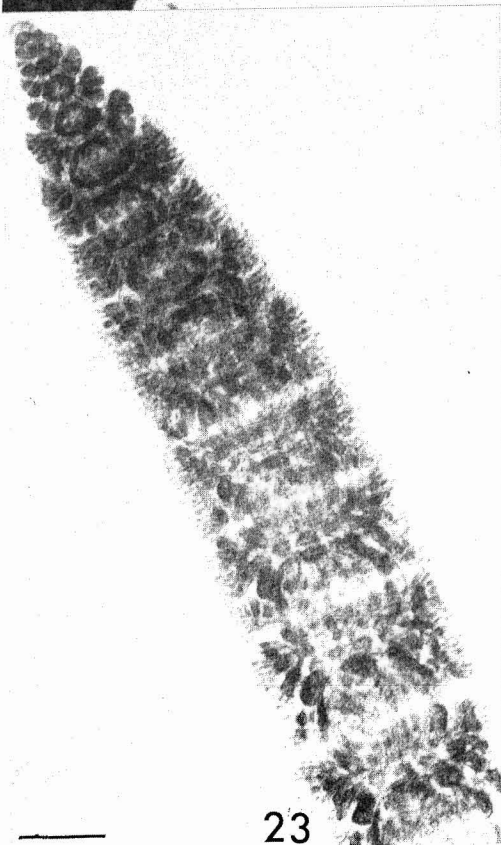
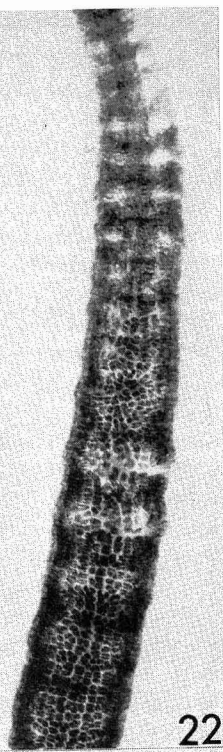
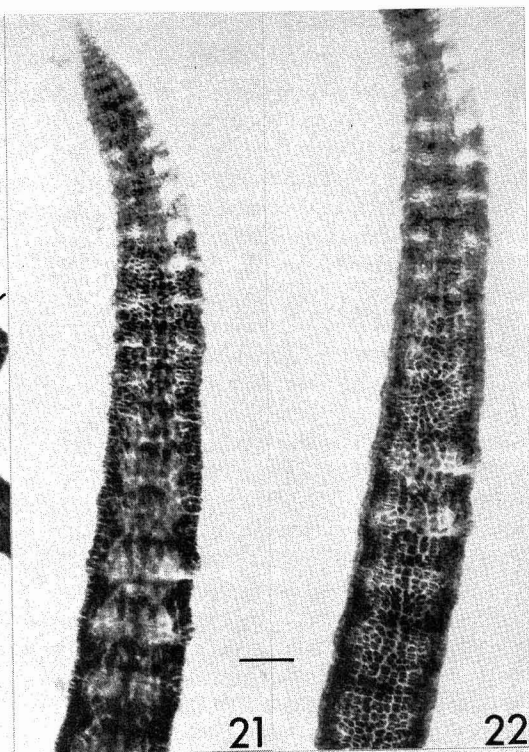
OTHER MATERIAL EXAMINED: Hawai'i Island: known from the type locality, as above, and also epiphytic on *Gelidium* sp., black sand beach, Punalu'u, *legit* C. M. Smith, 23 May 1990 (IAA 19714).

ETYMOLOGY: The combination of corticating characters around the relatively small axial cells, leaving large vacant spaces between cells is similar to the form of some species of *Ptilocladia*, a Ceramiaceae genus in the Crouanieae (see Wollaston 1968), and the species name was selected to emphasize this structural similarity.

COMMENTS: *Ceramium ptilocladioides* has a size comparable to that of *Centroceras apiculata* Yamada (1944), and both species are larger than *Ceramium huysmansii* Weber-van Bosse (1923). The corticating cells in *C. apiculata* are much closer together than in *C. ptilocladioides*, and *C. apiculata*'s corticating cells are larger and more regularly shaped and arranged.

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FIGURES 20–24. *Ceramium ptilocladioides*. (20) A prostrate branch (large arrow) with rhizoids (arrowheads) bearing unbranched upright branches (small arrows). Note the narrow diameter of axial cells. Scale = 200 μm . (21, 22) Different focal levels of same branch showing corticating filaments in profile (21) and in surface view (22). Scale = 100 μm . (23) Distal end of male branch with spermatangia borne on most cortical cells of mature segments. Scale = 50 μm . (24) Two tetrasporangial branches with young tetrasporangia. Scale = 100 μm .