Micronesica 33(1/2):45-98. 2000

A Review of *Ceramium* (Rhodophyceae, Ceramiales) from Fiji and Samoa, South Pacific

G. ROBIN SOUTH[1]

&

POSA A. SKELTON

Marine Studies Programme, The University of the South Pacific
PO Box 1168, Suva, Republic of the Fiji Islands

Abstract—A revision of *Ceramium* from Fiji and Samoa is provided, following an evaluation of previously published records, study of type specimens and voucher collections, and on the basis of field and laboratory investigations. Eight extant species are recognized [*Ceramium affine* Setchell and Gardner, *C. codii* (Richards) Mazoyer, *C. punctiforme* Setchell, *C. flaccidum* (Harvey ex Kützing) Ardissone, *C. macilentum* J. Agardh, *Ceramium* sp. aff. *Ceramium marshallense* Dawson, *C. subdichotomum* Weber-van Bosse and *C. vagans* P. Silva], and 3 that are new [*Ceramium krameri*, *C. rintelsianum* and *C. upolense*]. The occurrence or status of four previously reported species [*Ceramium camouii* Dawson, *C. clarionensis* Setchell & Gardner, *C. subverticillatum* (Grunow) Weber-van Bosse and *C. zacae* Setchell & Gardner] could not be confirmed, while a number of other previously reported species are placed in synonymy. The most abundant species is *Ceramium flaccidum*. Keys and illustrations for all species are included, and the taxonomy and nomenclature of the Fijian and Samoan species are discussed. All of the species are microscopic, mostly less than 5.0 mm tall, and most occur as epiphytes on corals or larger algae. One species (*C. punctiforme*) is restricted to the surfaces of the crustose coralline *Hydrolithon* on the exposed reef crest.

Introduction

Species of *Ceramium* (Rhodophyta: Ceramiales, Ceramiaceae) are widespread throughout the Pacific Islands, and more than twenty species have been recorded in the literature, of which 13 are reported from Fiji (N'Yeurt et al. 1996), and 3 from the Samoan Archipelago (Skelton & South 1999). Plants are common microscopic epiphytes in many tropical habitats, where the species are universally small, morphologically variable and are often ill-defined, making it difficult to

---

[1] Author for correspondence: email South_R@usp.ac.fj

identify specimens. This has meant that they are frequently overlooked in floristic surveys. A number of the species overlap morphologically.

Illustrations and descriptions of the Pacific Island species are often inadequate and are widely scattered in the literature; there is no single reference source to assist with their identification. The genus has been extensively reviewed for other parts of the world, such as the eastern Mediterranean (Feldmann-Mazoyer 1941), Pacific coast of North America (Dawson 1950), Mauritius (Feldmann-Mazoyer 1952), northern Japan (Nakamura 1965), South Africa (Simons 1966), southern Japan (Itono 1972, 1977), and southern Australia (Womersley 1978, 1998). Dixon (1960) provided a detailed analysis of thallus structure and reproduction. *Ceramium* species are well represented in many modern algal floras, and the exhaustive catalogues of the Philippine and Indian Ocean floras (Silva et al. 1987, 1996) provide up-to-date information on nomenclature and taxonomy of many of the species occurring in the Pacific Islands. The recent floras of Millar (1990), Price & Scott (1992) and Abbott (1999) provide important and regionally relevant modern overviews of tropical Pacific species.

Species of *Ceramium* have a triphasic diplohaplontic life history (Edwards 1973, Garbary 1988) and appear to be strictly dioecious. Garbary et al. (1980) reported that in *Ceramium rubrum* (Huds.) C.Ag., there are size differences between the phases, with the male plants being the smallest, followed by the female gametophytes, with the tetrasporophytes the largest. It is not known whether this rule applies to other species.

At the species level a great deal of emphasis has been placed on the details of cortical cell development as a specific character. Maggs & Hommersand (1993) have pointed out that this is of little practical value in delimiting British Isles *Ceramium*. Garbary et al. (1978, 1980) have demonstrated experimentally that in *Ceramium rubrum* (Huds.) C.Ag., branching patterns and the degree of nodal cortication are markedly influenced by environmental conditions (e.g., temperature, daylength and irradiance) and that these characters are of little taxonomic value. Meneses (1992) studied variations in thallus form in three species of *Ceramium* (including *C. clarionensis*) under field and culture conditions. For the Pacific Island species the nodal structure has been considered useful for species delimitation, although the details of nodal development are often poorly described. In the absence of experimental studies of local species, this feature continues to be the most useful.

Molecular studies may well throw light on the taxonomic confusion with *Ceramium*. Evans et al. (1999) report on taxonomic re-evaluation of some species of *Ceramium* using both molecular (rbcL sequence) and morphological data. From this preliminary study it is evident that several species of *Ceramium* fall outside clear groupings of species; they transferred *Ceramium deslongchampii* Chauv. ex Duby to *Gongroceras* Kützing (1842: 730), long considered synonymous with *Ceramium* (Silva et al. 1996: 410).

For the genus as a whole, species may be divided into two morphological groups: those with and those without cortical spines. Those lacking spines can be further subdivided into those with continuous, and those with discontinuous cortical bands. There are no spiny species known from Fiji, Samoa or the wider western Pacific region. As pointed out by Maggs & Hommersand (1993) the taxonomy and nomenclature of the non-spiny species are in a state of chaos not only in the British Isles, but elsewhere. This state of affairs certainly applies to the Pacific Island species. An important character which has been largely neglected (see Meneses 1995), is the branching pattern, in particular the intervals between branches, and the degree of incurvature of the apices. Womersley (1978) has noted that the gametangial reproductive structures are of little value in species delimitation; on the other hand, the arrangement of the tetrasporangia appears to be a valuable character at the species level.

This paper reviews the current nomenclatural and taxonomic information on the *Ceramium* species occurring in Fiji and Samoa, and discusses them in the wider context of the Pacific Islands flora. Diagnostic keys are provided, followed by descriptions and illustrations. Wherever possible, new collections have been examined. It is hoped that the review will provide a useful starting point to a more detailed monographic treatment of the species in the wider Pacific Islands region.

Geographical Scope

The geographical scope of this review covers the Fiji and Samoa Archipelagos, South Pacific. The Fiji Islands straddle the 180th meridian from 177º E to 178º W, and lie between 16º S to 20º S. A land area of 18, 276 km^2 is scattered over 332 islands, occupying 260,000 km^2 of ocean. There are four main islands in the group, Viti Levu, Vanua Levu, Taveuni and Kadavu, and three smaller island groups, the Yasawas, the Lomaiviti Group and the Lau Group. The small island of Rotuma is isolated from the rest of the Fiji Group, some 465 km north of Viti Levu. The Samoan archipelago lies between latitudes 13-15º South and longitudes 168-173º West. A total land area of 3,131 km^2 is scattered over two politically distinct (Western Samoa now ‘Samoa’ and American Samoa) yet ethnically identical island groups. The two island groups are of volcanic origin, but include a few coral islets and atolls. The climate is tropical with a temperature range of 20-32º Celsius and relatively high humidity (mean 83%) (Wells & Jenkins 1988).

The distribution of *Ceramium* species is also noted from the selected Pacific Islands from which records of the genus have been published (Solomon Islands, Tuvalu, New Caledonia, Nauru, Palau, Kiribati, Federated States of Micronesia, Marshall Islands, Fiji, Johnston Atoll and French Polynesia).

Materials and Methods

The primary sources of material were published reports and recent *Ceramium* collections from Fiji and Samoa, and the collections housed in the

Phycological Herbarium, South Pacific Regional Herbarium [designated as SUVA (USP) to avoid confusion with the Vascular Plant collections]. Collections were made by snorkeling or by use of SCUBA, and preserved in 5% formaldehyde in seawater. Specimens were mounted on slides in a 1% solution of acidified Aniline Blue in 60-80% Karo™ sugar solution. Specimens are housed in the Phycological Herbarium, South Pacific Regional Herbarium. Specimens preserved as slides are given numbers in the slide series (as USP S). Drawings were made using a Zeiss Standard WL microscope fitted with an Abbé drawing tube, while photomicrographs were taken with an Olympus BX50 compound microscope using Kodak Pan X black-and-white film. Counts of the number of cortical cell rows were possible by focusing at the axial cell level and recording the results photographically.

Species of Ceramium from Fiji and Samoa

ARRANGEMENT OF THE LIST

The nomenclature, taxonomy and format of the entry for each species generally follow Silva et al. (1987, 1996). Keys to the species are provided, with an emphasis on vegetative characters specific to Fijian and Samoan taxa where applicable. The basionym is provided, together with the type locality and a list of the principal regional checklists in which the species is included. A supplementary list of references important to the description and illustration of the species is provided. The Pacific Island and world distributions of all species are given. Descriptions are provided for each taxon, drawing on up to date accounts and our own collections.

TAXONOMIC CRITERIA

Dixon (1960), Itono (1972), Womersley (1978, 1998) and Maggs & Hommersand (1993) have provided detailed information on the value of the various morphological characters employed in delimiting *Ceramium* at the species level. Morphological variation is high within and between taxa. Taking previous work into account, the most consistently useful characters for the identification of Pacific Island species are:

1. The branching pattern
2. The number of periaxial cells and the presence or absence of pseudoperiaxial cells
3. The curvature of the apices
4. The arrangement of tetrasporangia, and the presence or absence of tetrasporangial involucres
5. The structure and development of the cortical band.

1. The branching pattern

The largely microscopic thalli of tropical Pacific species of *Ceramium* are uniaxial and composed of creeping filaments of unlimited growth giving rise to laterals (or “uprights” in the frequently prostrate species), which may in turn be sparsely to profusely branched. The branches of limited growth are confined to nodal bands which form a partial (in all Pacific Islands species) investment of the axes. Adventitious branches of unlimited growth are not uncommon. Axes are affixed to the substratum by rhizoids developed from the periaxial or cortical cells of the nodes. The rhizoids may be unicellular, or multicellular, and may terminate in a discoid pad.

Branching in *Ceramium* is essentially distichous, and pseudodichotomous or alternate; true dichotomy does not exist. The apical cell may be conspicuous, or very inconspicuous. The distance (i.e. number of nodes) between pseudo-dichotomies may occur with some regularity, but distinction should be made between genuine pseudo-dichotomies and adventitious branches, a distinction that may be difficult to make in older specimens (Dixon 1960).

2. The number of periaxial cells and the presence or absence of pseudoperiaxial cells

Species of *Ceramium* produce from (3) 4–10 periaxial cells. One “complex” of Pacific Island species possesses 4 periaxial cells (e.g., *Ceramium codii* group), while others may possess up to 8 (e.g., *C. marshallense*). Norris & Abbott (1992) erected the genus *Ardreanema* to accommodate Hawaiian ceramiacious algae possessing three periaxial cells and a uniseriate arrangement of the carposporangia forming linear gonimolobes, in contrast to the branched spheroidal gonimolobes characteristic of the genus *Ceramium*. Norris (1994: 154) later transferred *Ceramium seriosporum* Dawson (1963: 13, pl. 4 fig. 1–6) from the Galapagos Islands to *Ardreanema seriosporum* (Dawson) R.E. Norris. N’Yeurt (1997: 275, figs 242–248; 275) reported this species from Fiji. His specimen lacks female structures but was included on the basis of having three periaxial cells and a terminal tetrasporangial stichidium. The nodal bands of *Ardreanema* are very different from those of the *Ceramium* species with 4 periaxial cells. The possession of less than 4 periaxial cells with simple cortical band structure is not inconsistent for *Ceramium sensu lato*, whereas the seriate gonimolobe of *Ardreanema* is unlike any *Ceramium* species.

Dixon (1960) has provided a detailed description of the sequence of formation of the periaxial cells. He pointed out that the only sure way of determining the number of axial cells is by sectioning the thallus and even then a decision may be difficult when the section does not pass through the upper part of the axial cell where the primary pit connections are to be found. They are cut off from the apical region of the axial cell. The frequent method of estimating the number of periaxial cells from an examination of whole specimens is open to question, especially since in some species pseudoperiaxial cells are formed, which may become embedded in the cortical node beside the periaxial cells. However, the extremely small size of all southwestern Pacific Island species of *Ceramium* makes it nearly impossible to produce acceptable sections of the axis, so it is usually necessary to resort to the whole-mount counting method.

3. The curvature of the apices

Dixon (1960) described how the curvature of the apices in *Ceramium* develops. The degree of curvature, to produce forcipate and circinate tips, is determined by the relative rates of development of the lateral branches of limited growth in each segment. The first periaxial cell is formed in the secund position, i.e. on the outer face of the axis relative to the previous pseudo-dichotomy. In species where the apices are strongly incurved, the apical cells of the lateral branches of limited growth are produced by the first-formed periaxial cell immediately after its formation. In this way, the cortical band is well established on the outer face of the axis by the time the first periaxial cell is cut off on the inner side. Thus, when each cortical band is formed, it is wedge-shaped in longitudinal section, with the apices of the wedges pointing inwards. When the axes are formed by the aggregation of these wedge-shaped cortical bands, they are therefore strongly incurved (Dixon 1960), e.g., *Ceramium marshallense*. For those species where the apices are straight or nearly so (e.g., *C. subdichotomum, C. flaccidum, C. vagans, C. upolense* sp. nov.), the periaxial cells are cut off in rapid succession, and the further development of the filaments of limited growth does not take place until after the complete ring of cells has been formed.

4. The arrangement of the tetrasporangia and the presence or absence of tetrasporangial involucres

Tetrasporangia are produced in the cortical bands and develop laterally from cells of the corticating branches of limited growth. In all South African species examined by Simons (1966) the tetrasporangia were produced from the periaxial cells. There is considerable variation in the number of tetrasporangia produced per cortical band. According to Dixon (1960: 351) when the tetrasporangia are solitary, they are always formed in the secund position, i.e. on the outer (abaxial) face of the axis relative to the previous dichotomy (e.g., *Ceramium codii*). In the majority of species, tetrasporangia are produced in whorls (e.g., *C. marshallense, C. vagans*), and they may be emergent (*C. marshallense*) or submerged in the cortical layer. In one species (*Ceramium rintelsianum* sp. nov.) the tetrasporangia are produced in discrete stichidium-like structures, which may occur in series interspersed with non-reproductive axis. The presence or absence of partial or complete tetrasporangial involucral branches is an important and apparently consistent character at the species level. The majority of Ceramium species have tetrahedrally divided tetrasporangia, although some (e.g., *C. upolense* sp. nov., *C. vagans*) are normally cruciately divided; since variation in division can occur in the same species or on the same plant, the mode of division of the tetrasporangia should be considered along with other diagnostic characters for species determination.

Dixon (1960) noted that *in situ* germination of tetrasporangia is not uncommon on British species of *Ceramium,* although this has not as yet been observed for species from the southwestern Pacific Islands. Polysporangia have been reported on a number of *Ceramium* species elsewhere, but not from specimens from Fiji or Samoa.

5. Structure and development of the cortical band

The structure and development of the cortical band has been widely used as a discriminating character at the species level. Experimental work by Garbary (1975) on *Ceramium rubrum* has shown, however, that the morphology of the cortical bands is easily modified by environmental conditions. Similarly Dixon (1960) stated that cortical band structure cannot always be relied upon since it may be influenced by a number of factors as yet poorly understood. By contrast, Womersley (1978) states that the most important diagnostic feature in *Ceramium* is the pattern of cortical cell development from the periaxial cells. Not all of the original descriptions of *Ceramium* species recorded from Fiji and Samoa adequately describe the cortical pattern.

Cortical band development occurs through successive acropetal and basipetal divisions of the periaxial (and when present the pseudoperiaxial) cells. For many species the nodal structure is constant, while for others it may continue development, although the number of periaxial and pseudo-periaxial cells appears to be constant. The nodal structure is always disrupted during the formation of reproductive structures. Distinctions can be made between those species where there is uneven development of the acropetal and basipetal sections of the node, or when only one (the acropetal) develops (e.g., *Ceramium macilentum; C. codii*). The division may be regular (e.g., *C. flaccidum, C. upolense* sp. nov.) or disorderly. For several species (*C. codii, C. flaccidum, C. punctiforme*) the presence of horizontally elongated cells in the lowermost region of the cortical band is a consistent and reliable character. The distance between cortical bands and the ratio between corticated and uncorticated regions of the axis (the "index of cortication" of Dixon 1960) is variable within and between species, and is affected by the relative enlargement of the axial cells: in some species (e.g., *C. affine, C. codii* and *C. macilentum*) the internodal distance may be several times the height of the nodal bands, while in others the internodal space may be extremely narrow (e.g., *C. vagans*).

Simons (1966) is one of the few authors to show longitudinal sections of the cortical bands; it would be valuable to examine these for Fijian and Samoan species, although their small size would make this a challenging exercise.

Key to the species of *Ceramium* from Fiji and Samoa

1. Cortication more or less continuous, with no clear internodes ***C. krameri* sp. nov.**
1. Cortication restricted to the nodes, with clear internodal spaces 2
    2. Periaxial cells 4 (C. codii group) 3
    2. Periaxial cells more than 4 6
3. Node development acropetal, mostly in two rows 4

3. Node development acro- and basipetal, mostly more than 2 cell rows . . 5
    4. Uprights unbranched; tetrasporangia involucrate, arranged in pairs in stichidia . . . . ***C. rintelsianum* sp. nov.**
    4. Uprights branched with forcipate tips; tetrasporangia with well developed involucre . . . . *C. codii*
5. Nodes with up to four cell rows; plants epiphytic; tetrasporangia solitary, with a distinct hyaline sheath and lacking an involucre . . . . *C. affine*
5. Nodes with four or more rows, the cells of the lowermost row frequently horizontally elongated; plants restricted to the surface of Porolithon on the reef crest; tetrasporangia whorled . . . . *C. punctiforme*
    6. Nodal development largely or exclusively acropetal . . *C. macilentum*
    6 Nodal development both acro- and basipetal 7
7. Branching sympodial . . . . *C. subdichotomum*
7. Branching irregular, alternate or subdichotomous, not sympodial 8
    8. Branch tips forcipate and/or circinate 9
    8. Branch tips straight, or more or less so. 10
9. Branch tips forcipate, not circinate; basipetal cells in a distinctly elongate transverse series . . . . *C. flaccidum*
9. Branch tips strongly forcipate and circinate; basipetal nodal cells not in a distinctly elongate transverse series . . . . *Ceramium* sp. aff. *C. marshallense*
    10. Uprights unbranched, or sparsely subdichotomously branched; periaxial cells 5-7; nodal bands of 5 or more rings of cells; slender hairs frequently formed from acropetal corticating cells; tetrasporangia tetrahedrally divided . . . . ***C. upolense* sp. nov.**
    10. Uprights irregularly and sparsely branched; tetrasporangia whorled, cruciately divided, verticillately arranged. . . . . *C. vagans*

The *Ceramium codii* group: Species with four periaxial cells and with limited nodal development

This group includes *Ceramium* species with four periaxial cells and with limited nodal development from the periaxials. For our region we recognize four taxa in this group: *Ceramium codii, C. affine, C. punctiforme;* and *C. rintelsianum* sp. nov. *Ceramium serpens* Setchell & Gardner (1924: 775, pl. 27: fig. 58) has been recorded from the Pacific Islands, but is placed in synonymy with *C. codii* here. Other species that have been linked to this group are *Ceramothamnion adriaticum* (Schiller 1911), *C. camouii* and *C. cimbricum* H. Petersen in Rosenvinge (1924: 378). *Ceramium camouii* is discussed later in this report, while *C. cimbricum* H. Petersen has 4-6 periaxial cells and much more developed nodes than members of the *C. codii* group reported here (Maggs & Hommersand 1993: 49-52, Fig. 14). A comparison of the characters of the five species of the complex reported from the Pacific Islands is presented in Table 1.

From Table 1 it could be concluded that the species are clearly separable on the basis of the presence or absence of a partial tetrasporangial involucre, on the

Table 1 Comparison of South Pacific Island representatives of the *Ceramium codii* group (for sources, see text).

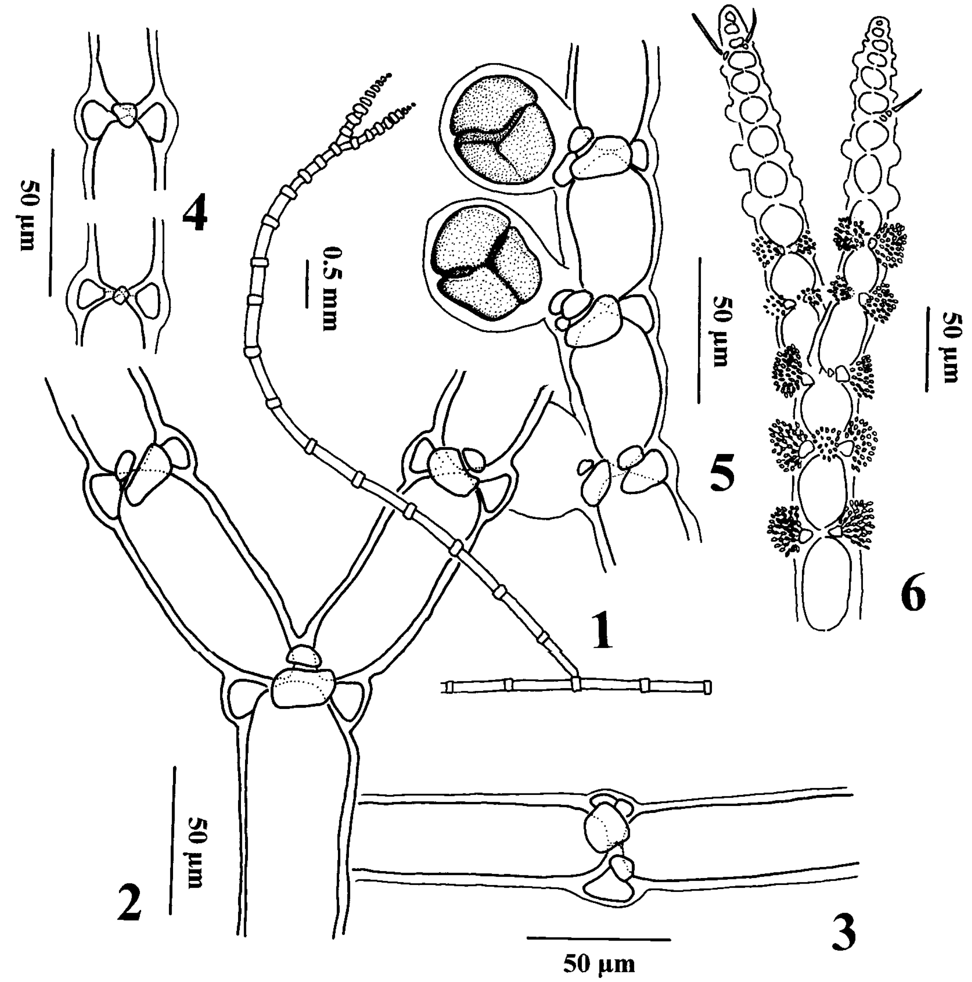
Species	Periaxials	Node	Tetrasporangia	Branching
C. codii	4	2 rows Acropetal	Tetrahedral ± involucre, protruding.	Pseudodichot.
C. affine	4	2 rows Acropetal	Tetrahedral, naked, protruding.	Pseudodichot.
C. serpens	?4	Up to 4 rows Acropetal & Basipetal	Tetrahedral + involucre, partially embedded.	Pseudodichot.
C. punctiforme	4	(3)4-6(9) Cell rows	Cruciate in swollen terminal structures; tetrasporangia in whorls of 4.	Mostly unbranched
C. rintelsianum sp. nov.	4	2(-3)	Tetrahedral in seriate pairs; involucrate.	Unbranched

number of cell rows in the nodal band, or on the presence or absence of forcipate tips. A review of the species reported from the Great Barrier Reef (Cribb 1983, Price & Scott 1992), from the Marshall Islands (Dawson 1956), and from Pacific Mexico (Dawson 1962), as well as an examination of the type material of *C. affine*, *C. serpens*, and *C. punctiforme* has revealed, however, that the distinguishing features given in Table 1 are variable within and between at least two of the taxa (*C. codii* and *C. serpens*). Price & Scott (1992: 88) note that the usual cortical band structure in Great Barrier Reef material of *C. codii* is similar to that originally illustrated for *Ceramium serpens*. Millar (1990: 394) includes *C. serpens sensu* Dawson (1962: 64, pl. 25: fig. 6) in synonymy with *C. codii. Ceramium affine* differs from *C. codii* by the lack of an involucre around the tetrasporangia, and by its possession of forcipate branch tips. This is in agreement with the statement in Itono (1977) that *C. codii* is distinguished from *C. affine* by its production of tetrasporangia in whorls, involucrated by cortical cells [as in the original description by Richards (1901: 264-265); as *Ceramothamnion codii*].

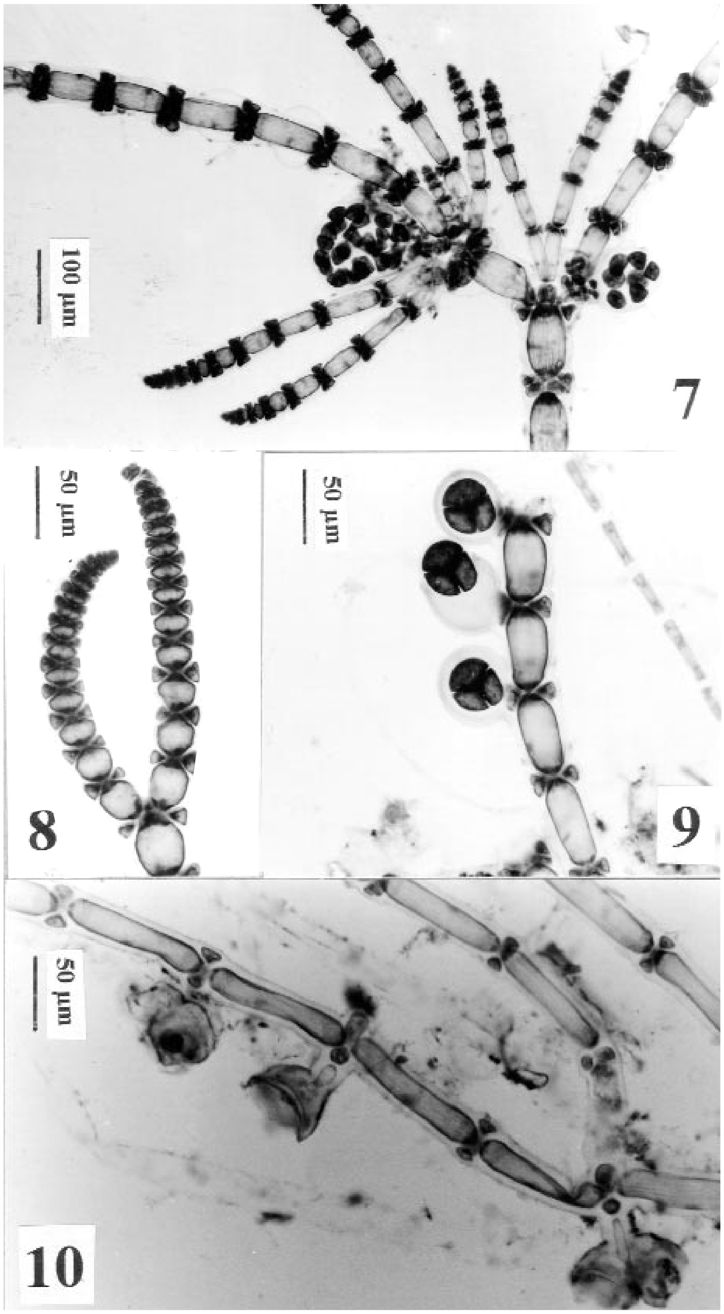
We propose to place *C. serpens* in synonymy with *C. codii*, which has nomenclatural priority. The emended description of *C. codii sensu lato*, means that this species is not restricted in habitat as an epiphyte on *Codium* species. *Ceramium affine, Ceramium punctiforme* and *Ceramium rintelsianum* sp. nov., are distinct species in Fiji and Samoa. *Ceramium punctiforme* is distinguished from the other species on the grounds of the greater development of its cortical bands, including the more or less regular formation of basipetal cortical filaments, and on the tetrasporangial arrangement and their cruciate division. This species is also unique in that it only occurs on the surface of encrusting coralline algae on the reef crest (Price & Scott 1992: 107). *Ceramium rintelsianum* sp. nov. is easily separated on the basis of its stichidia-like tetrasporangial sori.

1. *CERAMIUM AFFINE* SETCHELL & GARDNER
(Figs 1-10)

Ceramium affine Setchell & Gardner 1930: 171 (type locality: Guadalupe Island, Mexico)—Buggeln & Tsuda 1966: 19; Trono 1969; Abbott & Hollenberg



Figures 1-6. Camera lucida drawings of *Ceramium affine*. Palolo Deep, Samoa. September 18, 1998. Fig.1. Habit; Fig. 2. Detail of branch and nodal structure; Fig. 3. Detail of node in basal system; Fig. 4. Detail of nodes in upright branch; Fig. 5. Tetrasporangia showing lack of involucre and hyaline sheath; Fig. 6. Male branch showing spermatangial clusters.



Figures 7-10. *Ceramium affine*. Palolo Deep, Samoa. September 18, 1998. Fig. 7. Upright with branches, and mature cystocarps; Fig. 8. Tip with pseudodichotomous branching and forcipate branch tip; Fig. 9. Solitary tetrasporangia tetrahedrally divided and with thick hyaline sheath, lacking involucre; Fig. 10. Basal system with short rhizoids with expanded bases.

1976: 592, fig. 531; Tsuda & Wray 1977: 104; Payri 1987; Silva et al. 1996: 390; Payri & N'Yeurt 1997: 894.

ADDITIONAL REFERENCES: Dawson 1944: 371, pl. 51, fig. 4; 1950: 132; 1962: 50, pl. 17: fig.6; Taylor 1945: 272; Itono 1972: 78, fig. 5; Silva et al. 1987: 54; Wynne 1995: 290, fig. 32.

TYPE: H.L. Mason 36, CAS 173642 in UC (on *Codium*).

MISAPPLIED NAME: *Ceramium codii* (Richards) Mazoyer in Price & Scott (1992: 86-88, fig. 26)

DESCRIPTION: *Thallus* 1-12 mm tall, epiphytic, 30-40 (60) µm diam. at the base and tapering to the apex; attached by unbranched rhizoids in the lower portions; branching sub-dichotomous, adventitious branches lacking; apices straight to slightly incurved; axial cells cylindrical to 30-40 µm diam below, 24-28 µm diam. above, 4-6 times as long as broad; periaxial cells 4, corticating bands very narrow, development primarily acropetal of two, sometimes three cell rows of rounded cells, the larger ones (periaxial cells) below; *tetrasporangia* prominent, solitary, tetrahedrally divided, naked and secund at the nodes, or occasionally whorled, 30-40 µm diam. including a thick hyaline envelope; spermatangia surrounding nodal cortical cells; *gonimoblasts* 100-120 µm diam., with a few large carpospores (after Dawson 1962: 50; Abbott & Hollenberg 1976: 592)

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton*, September 17, 1998: USP S18: 1; *Skelton & Afiti*, September 16, 1998; USP S18: 3; *Skelton, Afiti & Faletoese*, September 18, 1998: USP S18: 4).

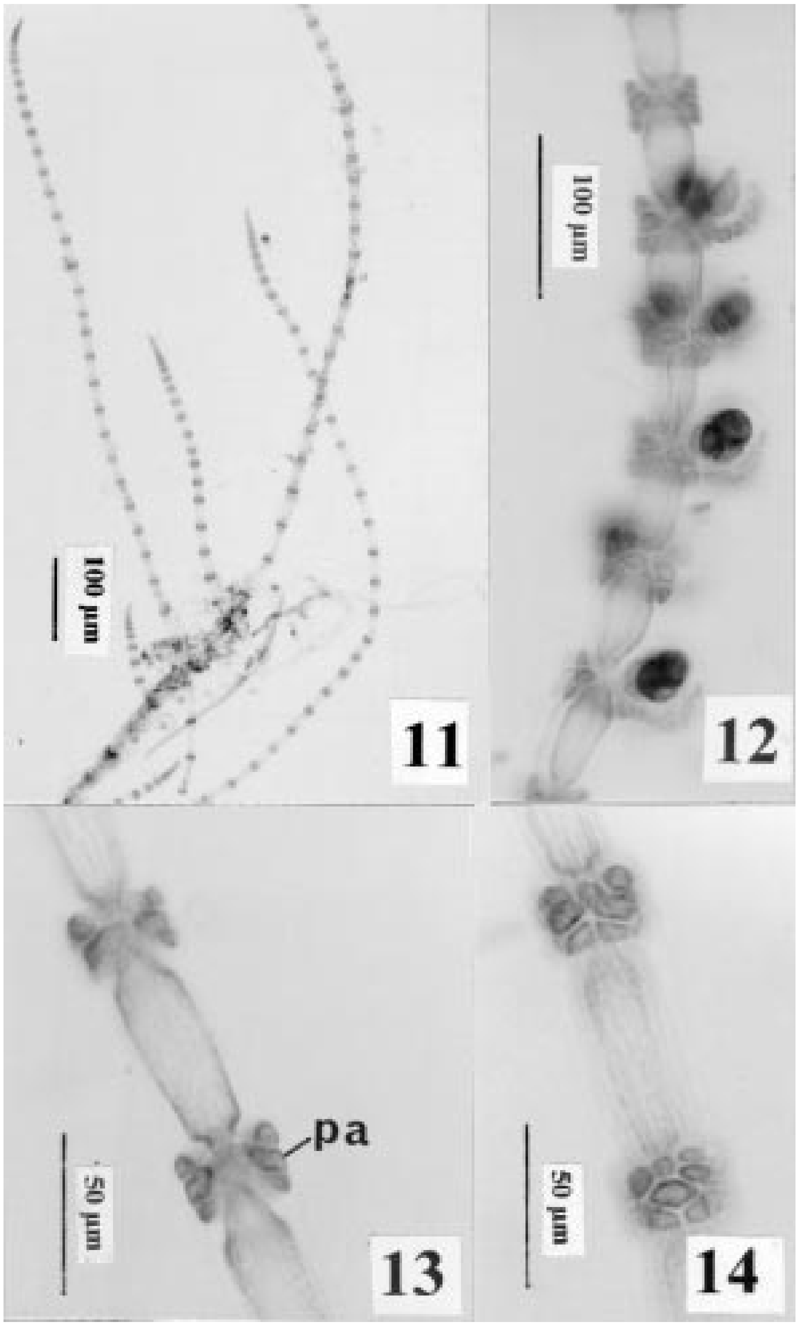
HABITAT & REMARKS: Epiphytic on various larger algae. We have examined the type, and find that local material matches it and the original description. Sterile plants closely resemble *C. codii*. The naked tetrasporangia and hyaline sheath around the solitary tetraspores easily distinguish *C. affine* from *C. codii*. Confusion between *C. affine* and *C. codii* is common, and the illustrations in Price & Scott (1992: fig. 26) attributed to *C. codii* are of *C. affine*. Buggeln & Tsuda (1966: 19) commented that *C. affine* is commonly encountered as a small fragment in many collections from Johnston Atoll. Its thin diameter, long internodes and two rows of cortical cells are distinctive. Dawson (1950: 132) described a large variant of *C. affine* as var. *peninsularis*, it being twice the size in all vegetative dimensions of the type of the species, although Abbott & Hollenberg (1976: 292) did not recognize this variety. There is no comparable variety occurring in Fiji, Samoa or the Pacific Islands.

PACIFIC ISLANDS DISTRIBUTION: FIJI, SAMOA, Johnston Atoll, Federated States of Micronesia, French Polynesia.

WORLD DISTRIBUTION: California, Mexico; Philippines, Southern Japan; Seychelles; Galapagos Islands; Ecuador.

2. *CERAMIUM CODII* (RICHARDS) MAZOYER
(Figs 11-14)

Ceramothamnion codii Richards 1901: 264-265, pls 21, 22 (type locality: Bermuda).–Collins & Hervey 1917: 134, pl. 3: fig. 22, pl. 4: fig. 23; Howe



Figures 11-14. *Ceramium codii*. Palolo Deep, Samoa. September 18, 1998. Fig. 11. Habit; Fig. 12. Solitary tetrasporangia with well developed involucres; Fig. 13. Detail of periaxial cell (pa) showing one acropetal and one basipetal cell row; Fig. 14. Surface view of node with three cell rows.

1918: 532; Weber-van Bosse 1923: 355; Setchell 1926: 105, pl. 22: fig. 2; Kylin 1956: 377, fig. 300; Kajimura 1972: 136, pls 1-4

Ceramothamnion adriaticum Schiller 1911: 90 (*vide* Price & Scott 1992: 86).

Ceramium codii (Richards) Mazoyer, 1938: 324-325.—N'Yeurt 1993a: 176, figs 189, 200; 1993b: 9; 1996: 422: figs 155a, b; 166; South et al. 1993: 191; N'Yeurt et al. 1996: 82; Payri & N'Yeurt 1997: 895.

ADDITIONAL REFERENCES: Feldmann-Mazoyer 1941: 285, figs 40, 59a-b, 105; Feldmann 1942: 46, figs 48-49; Funk 1955: 116, pl. 15: fig. 7; Dixon 1958: 14, fig. 1; Nakamura 1965: 124, fig. 1, pl. 1: fig. 1; Itono 1972: 80, fig. 9; 1977: 30, 97, 195, 230, 261, figs A1-5, 37A, 50C, 59A-B; Jaasund 1976: 107, fig. 216; Cribb 1983: 80, pl. 27: figs 1-4; Millar 1990: 393, fig. 41D-F; Silva et al. 1996: 393.

NOTE: The report of *C. codii* from the British Isles in Dixon (1958) has been included under *Ceramium cimbricum* H. Petersen in Rosenvinge by Maggs & Hommersand (1993: 52). Dawson (1950) ruled out Taylor's (1945) Ecuadorian record as belonging to this species.

TAXONOMIC SYNONYM: *Ceramium serpens* Setchell & Gardner 1924: 775, pl. 27: fig. 58 (type locality: La Paz, Baja California Sur, Mexico).—Dawson 1956: 54, fig. 53; 1957: 122; 1962: 64, pl. 25: fig. 6; Abbott & Hollenberg 1976: 598: fig. 540; Tsuda & Wray 1977: 104; Silva et al. 1987: 55; 1996: 403; Garbary et al. 1991: 254; South & Kasahara 1992: 63; Wynne 1995: 294, fig. 43; N'Yeurt et al. 1996: 82.

DESCRIPTION: *Thallus* of branched prostrate axes, to 5 mm long, bearing occasional to frequent, simple or sparingly branched erect branches, to 3 mm high; occasional adventitious branches also formed in mature parts of the thallus. Erect branches arising more or less at right angles to prostrate axes; branch tips usually simple, straight or slightly curved, pseudodichotomous. Mature segments 30-50 (-80) mm diam. 100-150 mm long, with L/D (1.5) 2-5. Axial cells cylindrical, 20-50 mm diam. Periaxial cells 4, transversely elongate, rectangular to rhombic in surface view; a single pseudoperiaxial cell rarely also present. Periaxials 10-(16)-25 µm diam., sometimes remaining undivided, but often cutting off (1-)2 acropetal cortical initials arranged in an irregular ring; initials occasionally dividing further to form a second acropetal ring. Periaxials rarely cutting off a regular ring of basipetal initials, which undergo no further development. Cortical cells triangular to polygonal in surface view. Attachment by frequent rhizoids along prostrate axes. Rhizoids 12.5-(18)-25 µm diam., to 430 mm long, unicellular or uniseriate, with tips unbranched, or with multicellular attachment pads. *Tetrasporangia* spherical, 38-(44)-53 mm diam. (including thick hyaline envelope), tetrahedrally divided, borne in pairs on nodal bands, strongly protruding, with a well developed involucre. *Sexual reproductive stages* not observed.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton & Faletoese*, September 18, 1998 USP S18: 6; USP S18: 7; *Skelton*, September 18, 1998: USP S18: 5); Naukacuru Is., Fiji (*S. Villeneuve*, February 25, 1982: UBC A46048); Beachcomber Is., Fiji (*S. Villeneuve*, February 21, 1982: UBC

A14853); Nam Vaimada, Fiji (*D. J. Garbary*, August 4, 1981: UBC A50214); Yasawa-i-rara, Fiji (*S. Villeneuve*, February 24th, 1982: UBC A54819).

HABITAT & REMARKS: Common, epiphytic on macro- as well as some microalgae; from the intertidal to 5 m depth. Millar (1990) placed *C. serpens sensu* Dawson (1962: 64, pl. 25: fig. 6) under *C. codii*, with which we concur. We have examined the type of *C. serpens* (CAS in UC 1462247). The material is severely dehydrated and difficult to examine, but we observed sufficient axes, which together with the excellent original illustrations confirmed their placement under *C. codii*. The arrangement of the cells in the type material shows the occasional development of a basipetal cell row with the cells transversely elongate (as in *C. punctiforme* and *C. flaccidum*).

PACIFIC ISLAND DISTRIBUTION: FIJI, SAMOA, Federated States of Micronesia, Marshall Islands, French Polynesia

WORLD DISTRIBUTION: Australia (W.A., N.S.W., Qld.), Southern Japan, Mauritius, Tanzania, South Africa, Philippines, Mediterranean, tropical Atlantic Ocean, California, Pacific Mexico, Seychelles.

3. *CERAMIUM PUNCTIFORME* SETCHELL

(Figs 15-19)

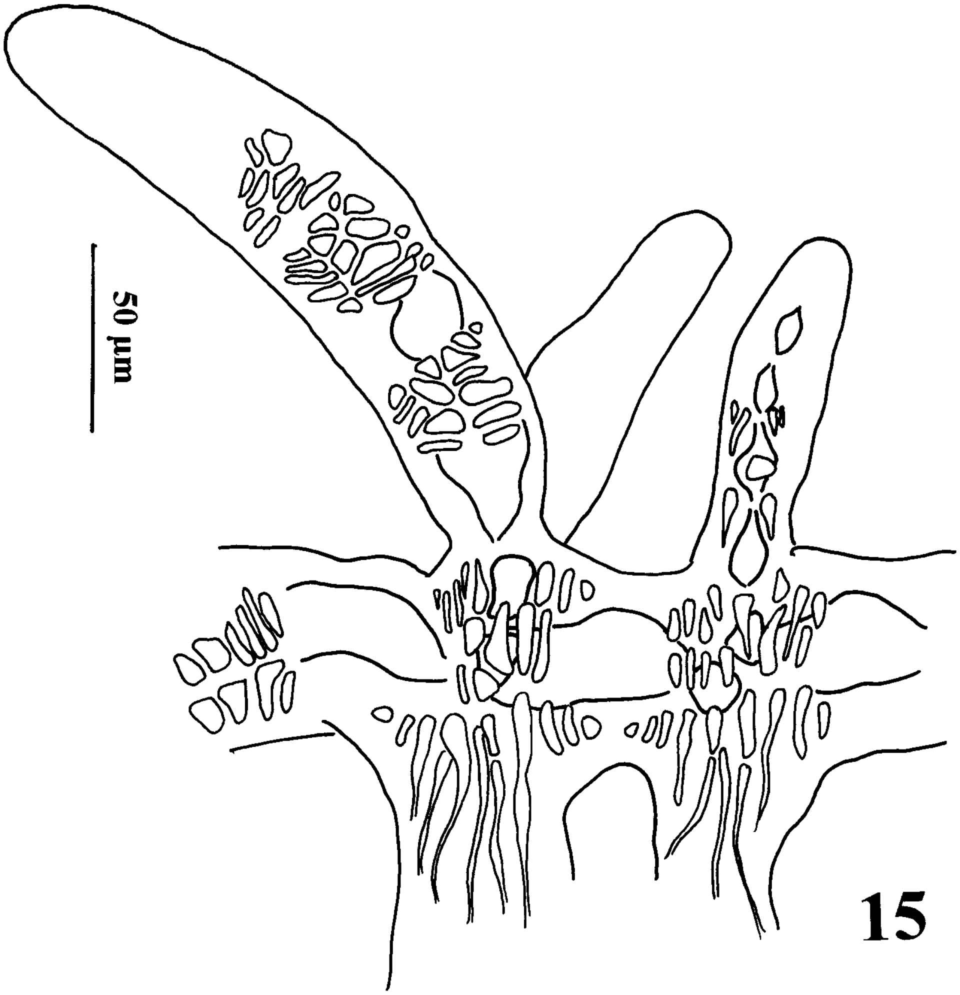
Ceramium punctiforme Setchell, 1924: 158, fig. 29 (type locality Faga'alu, American Samoa).—Skelton & South 1999: 12.

ADDITIONAL REFERENCES: Cribb 1983: 86-87, pl. 61: figs 3-4; Price & Scott 1992: 105, fig. 33A-D.

TYPE: UC221221, *leg*. W.A. Setchell, July 15, 1920. On *Porolithon onkodes*, Faga'alu Reef, American Samoa.

MISAPPLIED NAME: *Ceramium punctiforme* Setchell in N'Yeurt et al. 1996: 82; N'Yeurt 1997: 424 [= *Ceramium flaccidum* (Harvey ex Kützing) Ardissone].

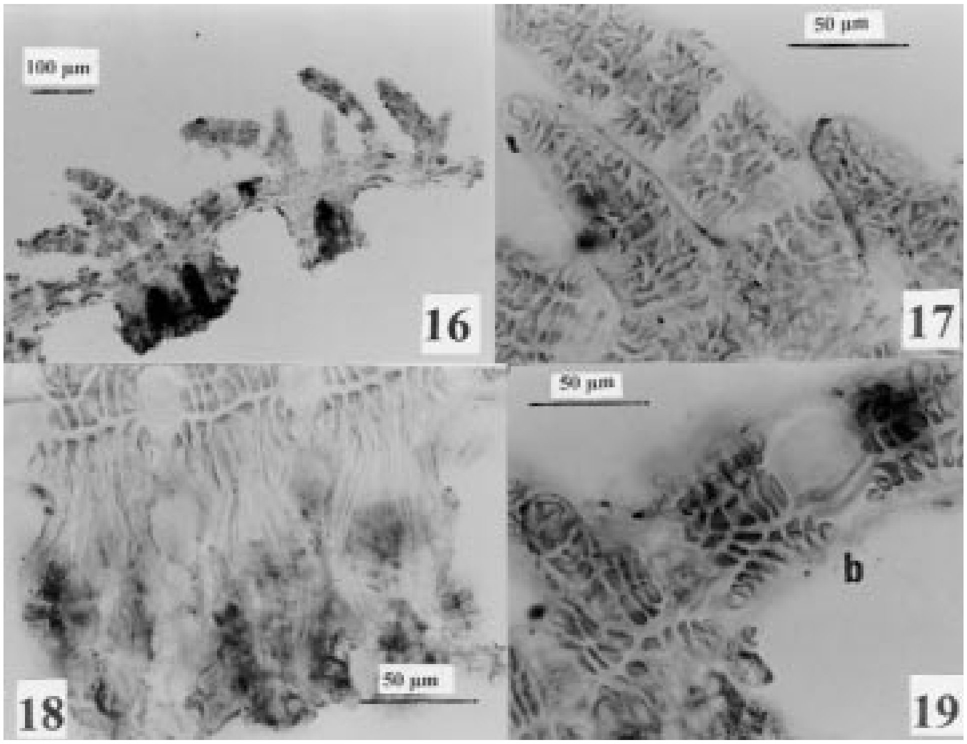
DESCRIPTION: We have not collected this very distinctive species from Samoa. Plants agree with the original description, and with the description of this species newly reported from Hawaii (Abbott 1999: 281).We have examined the type specimens, which are beautifully preserved and exactly as illustrated by Setchell (1924, fig. 29). The illustrations in Price & Scott (1992) and Cribb (1983) are also in agreement with the type. *Thallus* minute, composed of sparingly branched prostrate axes, to 3 mm long, bearing occasional to frequent erect branches, to 1(-2) mm high. Erect branches arising at right angles to prostrate axes, mostly unbranched, rarely with sparse lateral branching; branches occasionally borne in pairs, with one of the two branches sometimes developing into a prostrate axis. Branch tips straight or slightly curved; apical cell conspicuous. Mature segments 35-50(-60) µm diam., (50-)70-125 µm long, with L/D (1.1-) 1.3-2.8 (-3.2). Cortical bands (3-)4-6(-9) cells and (15-)20-35(-50) µm long, the longer bands mostly occurring in prostrate axes. Axial cells cylindrical to narrowly obovate, (30-)35-55 µm diam.; each cortical band with a central ring of 4 larger periaxial cells, the cells mostly triangular to elliptical in surface view, 10-12(-15) µm broad, (10-)15-20 µm long. Proximal cortical cells usually markedly elongate



15

Figure 15. Camera lucida drawings of the holotype of *Ceramium punctiforme*. The origins of the uprights and multiseriate rhizoids from the nodal band are clearly shown.

transversely, (2-)4-6 mm broad, (13-)15-22 μm long, arranged in a regular longitudinal and transverse series; a narrow, more or less transparent, transverse zone often prominent between proximal cortical cells and remainder of cortical band. Cells of distal cortical tissue often angular in form, isodiametric to moderately elongate, but varied in shape and size, and more or less irregularly arranged. Attachment by dense tufts of rhizoids along prostrate axes, arising from most or all cortical bands. *Tetrasporangia* borne on erect branches, in swollen, stichidium-like distal parts; sporangia subspherical, 20-25(-35) μm diam., cruciate, usually in whorls of 4, in 3-6 successive cortical bands, protruding; involucral filaments produced, but outer surfaces of sporangia remaining largely



Figures 16-19. *Ceramium punctiforme* holotype. Fig. 16. Habit; Fig. 17. Uprights indicating the presence of horizontally elongate basipetal cell rows in the node; Fig. 18. Detail of multiseriate rhizoids; Fig. 19. Detail of nodal band of the prostrate system; b denotes the basipetal cell row of node.

uncovered. *Spermatangia* spherical, 2-3 µm diam., formed in dense patches on cortical bands in distal parts of erect branches, produced mostly by acropetal cortical cells. *Carposporophytes* globular, to 100 µm diam., appearing terminal on erect branches, subtended by 2(-3) involucral branches (after Price & Scott 1992: 105-106; Cribb 1983: 86-87).

HABITAT & REMARKS: In his original description of this species Setchell (1924) noted that this minute species occurs as small spots on the *Porolithon* [*Hydrolithon*] pavement of the reef-rim. He also stated that his species might be the same as *Ceramium kuetzingianum* var. *subverticillatum* Grunow [= *Ceramium subverticillatum* (Grunow) Weber-van Bosse], but that the description of that variety (under *Gongroceras subtile* Kütz.) seemed to preclude the possibility of their being identical. Cribb (1983: 87) pointed out that Setchell's original description lacked important details such as the diameter of the filaments and the number of periaxial cells; by measurements deduced from Setchell's illustrations, however, Cribb was convinced that his Queensland material was of this species. Cribb (1983: 87) also noted that *C. punctiforme* has much in common with *Ceramium procumbens* Setchell & Gardner (1924), although he was unable to

make a detailed comparison. Abbott (1999:281) states that this species occurs on other crustose coralline algae, and on *Dictyota* in Hawaii.
PACIFIC ISLAND DISTRIBUTION: SAMOA
WORLD DISTRIBUTION: Australia (Qld.)

4. *CERAMIUM RINTELSIANUM* SP. NOV

(Figs 20-31)

Ceramium rintelsianum sp. nov. (type locality: Palolo Deep, Upolu Island, Samoa).

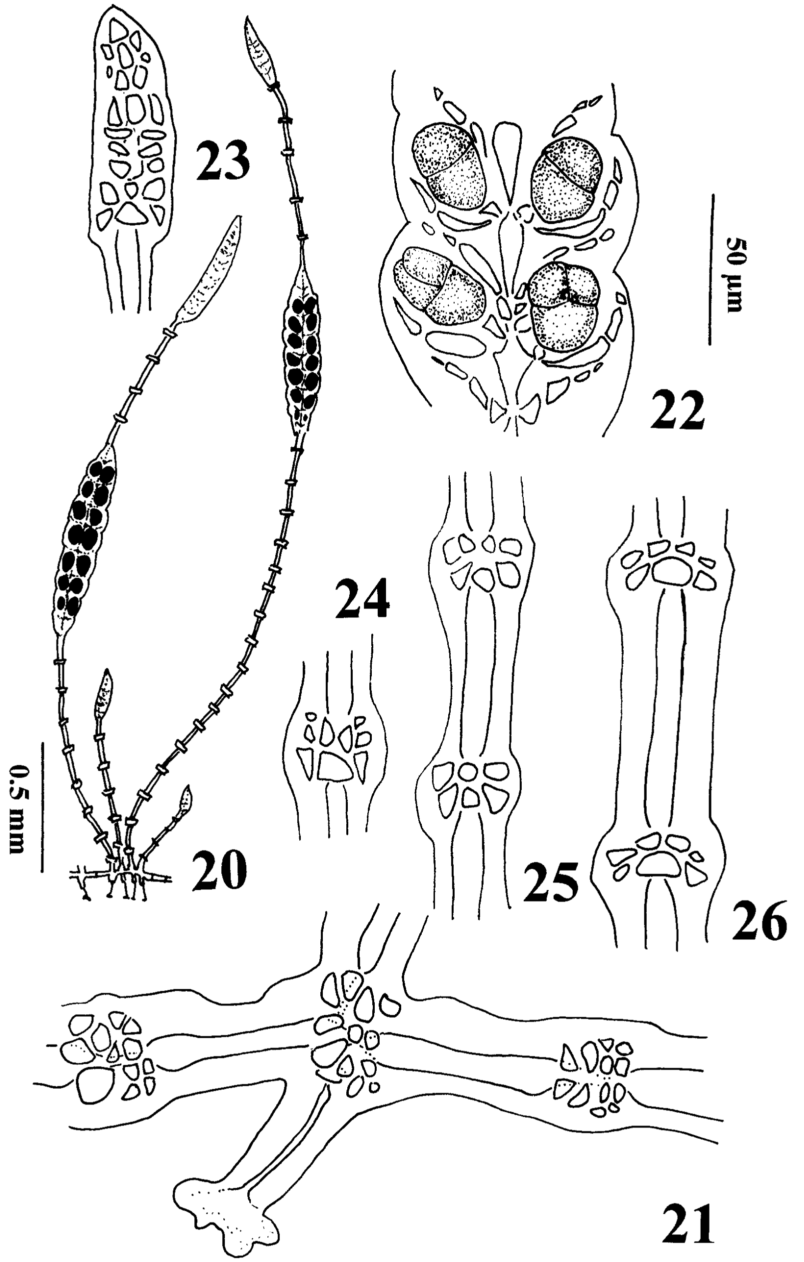
TYPE: Palolo Deep Marine Reserve, Samoa [*Skelton & Faletoese*, July 2, 1998: SUVA (USP) 5026].

DIAGNOSIS: *Thalli ad 3.5 mm alti, ramis erectis simplicibus 2-4 nodis distantibus ex axe repenti basali exorientibus; cellulae periaxiales 4, 2 cellulas corticales acropete efferentes, auctus basipetus nullus; tetrasporangia valde involucrata, paribus oppositis, tumores stichidiformes subterminales in ramis erectis fascientia; reproductio sexualis ignota.*

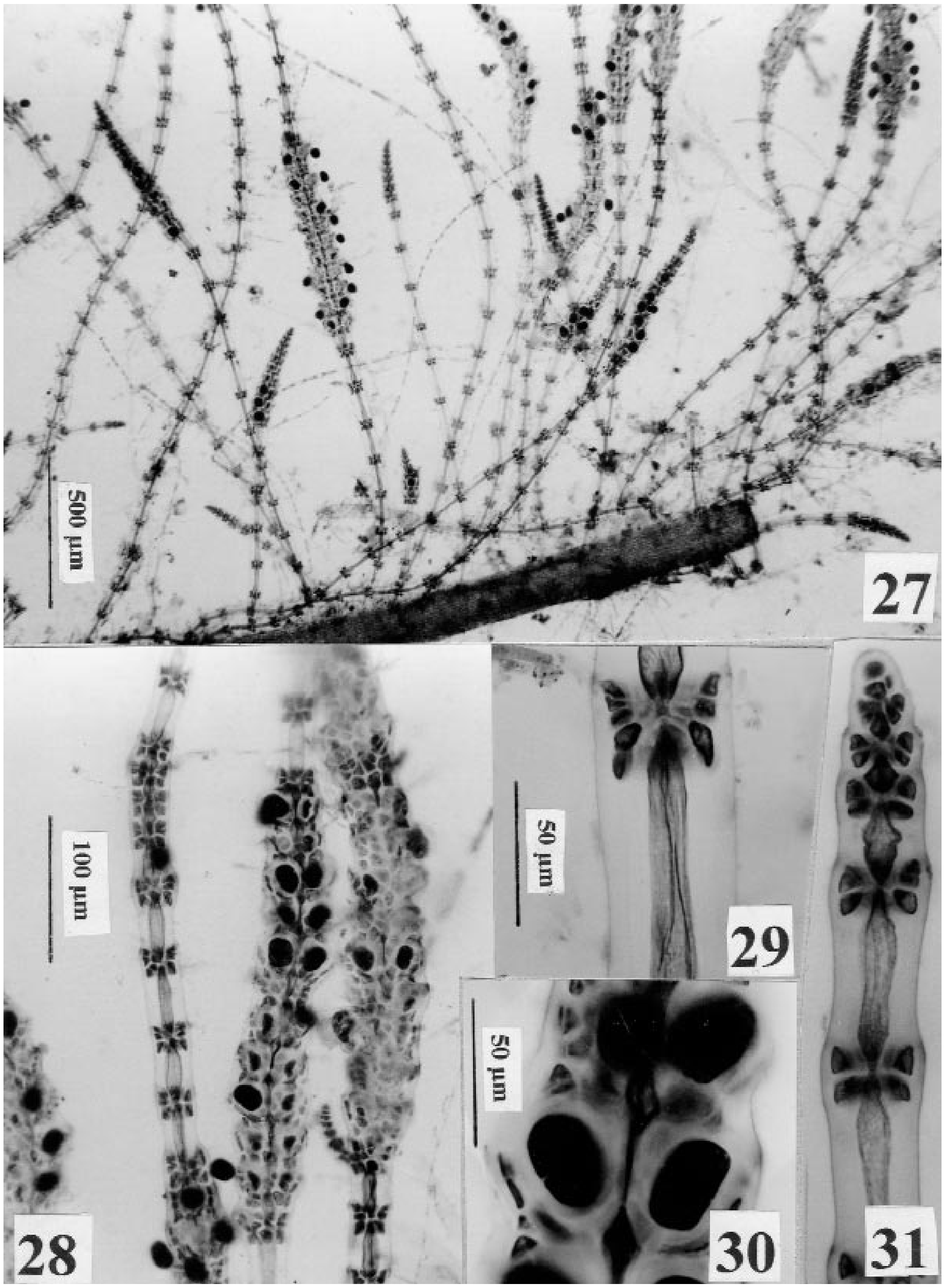
Thalli to 3.5 mm tall, with simple erect branches arising 2-4 nodes apart from the creeping basal axis; periaxial cells 4, producing 2 corticating cells acropetally, basipetal development absent; tetrasporangia strongly involucrate, in opposite pairs forming suberminal stichidia-like swellings in the erect branches; sexual reproduction unknown.

ETYMOLOGY: *Ceramium rintelsianum* is named after Captain Maxwell Rintels, past benefactor of the Skelton family in Samoa and Rintels Va`asili Tuivaiti who assisted in field collections of *Ceramium* at Palolo Deep National Marine Reserve in Samoa.

DESCRIPTION: *Thalli* pinkish-red, minute to 3.5 mm high, epiphytic on coarser algae; simple, very delicate uprights arising every (1-4) nodes from a creeping prostrate system; prostrate filaments 28-(31)-40 µm diam.; rhizoids unicellular, formed at each node from a periaxial cell, truncate at the point of attachment, and forming a discoid holdfast distally; the corticated nodes of the creeping basal filaments 18-(24)-28 µm long to 30-(31)-33 µm diam., and from 35-(51)-60 µm apart; uprights lightly corticated at the nodes, with the four periaxial cells normally giving rise to up to two corticating cells acropetally, with basipetal corticating filaments lacking; nodes 53-(58)-75 µm tall X 25-(28)-30 µm diam., in the lower parts of the uprights, to (15-(16)-23 µm tall X 23-(25)-28 µm diam. in the upper regions; nodes widely separated, 53-(58)-75.0 µm apart in the lower, 87.5-100 µm in the mid and 30-(44)-63 µm in the upper regions; *tetrasporangia* involucrate, in opposite pairs forming subterminal stichidium-like swellings; the stichidium-like swellings up to 70-(95)-125 µm diam., and 525-(600)-630 µm long, tapering both acropetally and basipetally; more than one stichidium-like swelling may be formed on the upright, separated by a sterile vegetative section; secondary corticating filaments developed among the involucres; tetraspores cruciate, 20-(25)-28 µm diam. *Sexual stages* not known.



Figures 20-26. Camera lucida drawings of the holotype of *Ceramium rintelsianum* sp. nov. Fig. 20. Habit; Fig. 21. Prostrate filament and unicellular rhizoid developing from the ventral periaxial cell; Fig. 22. Tetrasporangial stichidium-like swelling (detail) with paired strongly involucrate tetrasporangia; Fig. 23. Branch apex; Figs 24-26. Variations in the arrangement of the nodal band, with cortication strictly acropetal. Fifty-micrometer scale bar applies to Figs. 21–26.



Figures 27-31. *Ceramium rintelsianum* sp. nov. holotype. Fig. 27. Habit, epiphytic on *Gelidiopsis*; Fig. 28. Detail of upright and development of stichidium-like tetrasporangial swellings; Fig. 29. Exploded view of node with periaxial cell and two acropetal cell rows; Fig. 30. Detail of tetrasporangial pair and involucres; Fig. 31. Detail of branch tip; scale as for Fig. 30.

HABITAT & REMARKS: Uncommon, epiphytic on *Sargassum* sp., on reef flat from low intertidal to 2 metres. This minute, distinctive *Ceramium* is readily recognized by its tetrasporangial stichidia, which clearly separate it from the other lightly corticated species with four periaxial cells (such as *Ceramium codii*) common in the tropical Pacific; it differs from *Ceramium procumbens* Setchell & Gardner by the lack of opposite branching, and in the arrangement of tetrasporangia in opposite pairs, not whorled. This species superficially resembles *Ceramium procumbens* Setchell & Gardner *prox* in Dawson (1954: 441, fig. 56, c-d; non *Ceramium procumbens* Setchell & Gardner 1924) from Viet Nam. It differs from *C. procumbens* by the lack of branching, and from *C. procumbens* and Dawson's Vietnamese material by the unique stichidium-like arrangement of the tetrasporangia.

PACIFIC ISLAND DISTRIBUTION: SAMOA

SPECIES OF CERAMIUM WITH MORE THAN FOUR PERIAXIAL CELLS

5. *CERAMIUM FLACCIDUM* (HARVEY EX KÜTZING) ARDISSONE

(Figs 32-39; 41-44)

Hormoceras flaccidum Kützing 1862: 21, pl. 69: figs a-d (type locality: Kilkee, County Clare, Ireland).

Ceramium flaccidum (Kützing) Ardissone 1871: 40.—Reinbold 1896: 271; Garrigue & Tsuda 1988: 64; N'Yeurt et al. 1996: 82 (including *Ceramium punctiforme*); N'Yeurt 1997: 281, fig. 253; 424; Payri & N'Yeurt 1997: 895; Skelton & South 1999: 12.

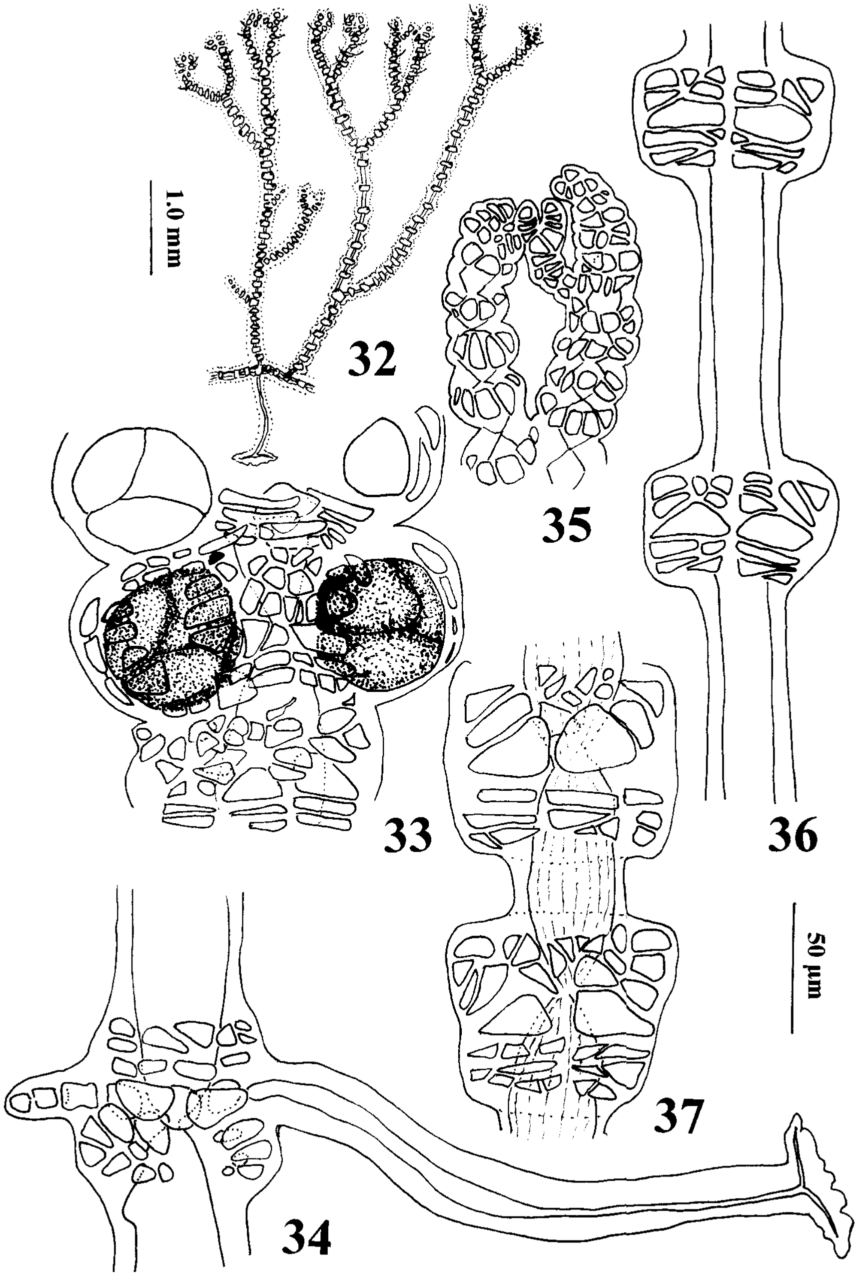
ADDITIONAL REFERENCES: Womersley 1978: 234-238, fig. 4; 1998: 410-411, figs 188E-H, 190A-D; Silva et al. 1987: 54; 1996: 397-398; 919-920; Millar, 1990: 395, figs 42A-E; 43C-E; Millar & Kraft, 1993: 38; Maggs & Hommersand 1993: 59, fig. 19A-G.

TAXONOMIC SYNONYM: *Ceramium byssoideum* Harvey 1853: 218 *nom. illeg*. (type locality: Key West, Florida, U.S.A.) (= *Gongroceras subtile* Kützing; see Weber-van Bosse 1923: 327).—Schmidt 1928: 75; Tokida 1939; Kanda, 1944: 272; Taylor 1950: 138; 39.

Ceramium gracillimum (Kützing) Griffiths & Harvey var. *byssoideum* Mazoyer 1938: 323.—Reinbold 1896: 271; Schmidt 1928: 75; Dawson 1954: 448, figs 55 e-f; 1956: 53; 1957: 122; 1962: 57, pl. 20: figs 2-3; pl. 21: figs 2-3; Gilmartin 1960: 215; Levring 1960: 123; May 1966; Tsuda & Trono 1968: 196; Trono 1969: 76; Womersley & Bailey 1970: 324; Abbott & Hollenberg 1976: 97, fig. 538; Womersley 1978: 234; Tsuda & Wray 1977: 104; Payri 1987; Silva et al. 1987: 55; 1996: 397; South 1991: 8; Garbary et al. 1991: 254; South & Kasahara 1992: 63; N'Yeurt et al. 1996: 82.

Ceramium byssoideum var. *alternatum* Ballantine & Humm 1975: 158, fig. 2; Womersley 1978: 234.

Ceramium masonii Dawson 1950: 126-127, pl. 2: figs 11, 12 (type locality: Cabeza Ballena, Baja California Sur, Mexico).—Womersley 1978: 234;



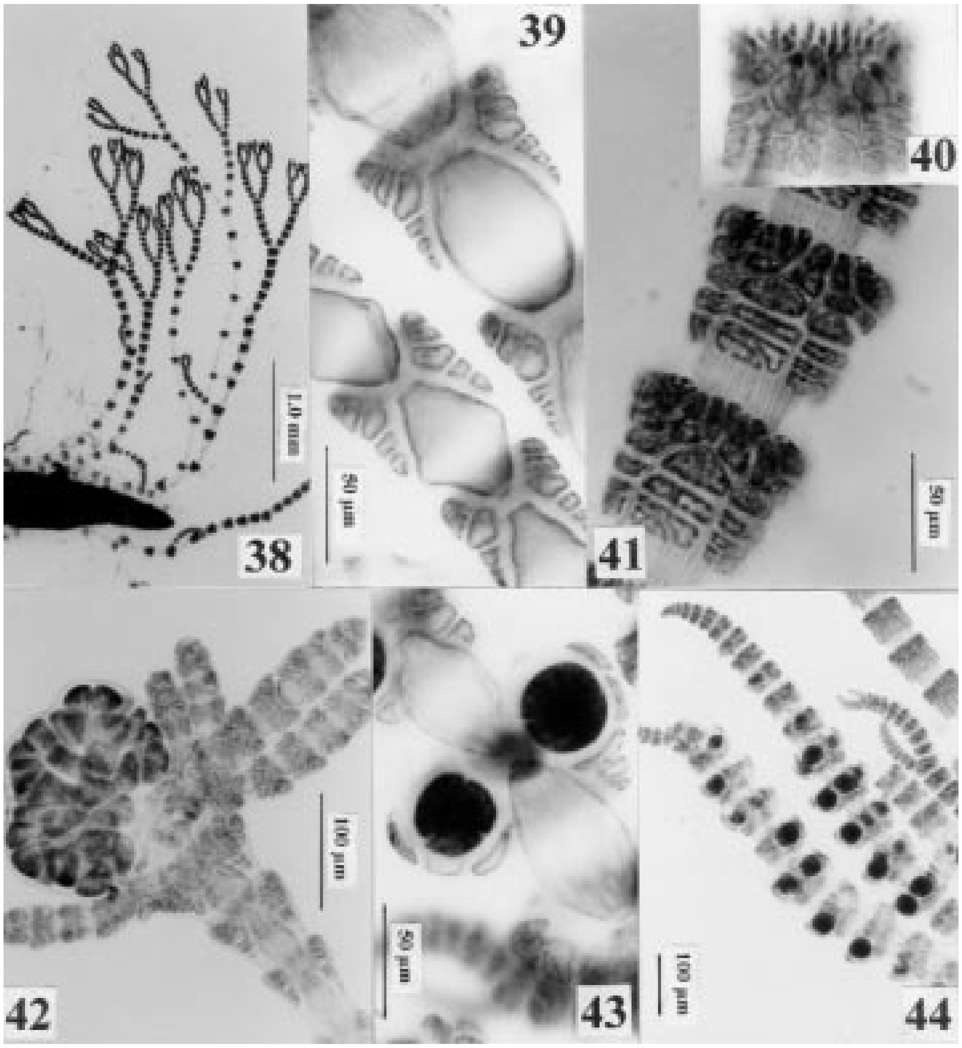
Figures 32-37. *Camera lucida* drawings of Ceramium flaccidum. Palolo Deep, Samoa July 1, 1998. Fig. 32. Habit; Fig. 33. Tetrasporangia with involucres; Fig. 34. Uniseriate rhizoid derived from periaxial cell of the prostrate node; Fig. 35. Apex with forcipate tips; Fig. 36. Weakly developed nodes and extended internodes; Fig. 37. Well developed node with greatly reduced internodes. Fifty micrometer scale bar applies to Figs. 33–37.

Kasahara 1985: 65; South 1991: 8; South & Kasahara 1992: 63.

DESCRIPTION: *Thallus* robust, to 6 mm high; axes prostrate, creeping, giving rise to erect branches; attached to substratum by unicellular, blind-ending or digitate rhizoids borne on periaxial cells; branches arising from axial cells before periaxial cells cut off; branching irregular to alternate, occasionally subdichotomous, every 4-6(-7) segments; branch apices slightly incurved, rarely straight, forcipate; periaxial cells 6(-7), initially triangular in outline, 20-30 μm long and 8-15 μm high, becoming large and rounded in mature nodes; each periaxial cell producing one transversely elongate, basipetal cortical cell, to 20-30 μm long and 10 mm wide; basipetal cells often undergoing further divisions, the lowermost of these splitting obliquely into two transversely aligned cells; each periaxial cell cutting off two cells acropetally and obliquely, these undergoing a further division to form a total of four acropetal cells in the shape of a 'V'; acropetal cells spherical or dome-shaped; pseudoperiaxial cells lacking; cortical nodes to 30-(44)65 μm long and 45-(63)80 μm in diameter; 'gland' cells produced to a greater or lesser extent on nodal bands; often small thin (1.0 μm diam.), hairs produced on acropetal cortical cells. *Tetrasporangia* tetrahedral, to 37.5-(51)-57.5 μm in diameter, borne on periaxial cells and covered by an involucral branch of two cells when mature; one or two sporangia formed per cortical node. *Cystocarps* to 125 μm diam., borne at the base of subdichotomy, often resulting in numerous adventitious branches arising from subdichotomous branches; carpospores polygonal shape but generally three sided, smooth to 25-45 μm wide X 15-25 μm high. *Spermatangia* arising from the corticating node.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton*, July 1, 1998: USP S19:1; *ibid*, September 17, 1998: USP S19:2; *Skelton & Faletoese*, July 2, 1998: July 2, 1998: USP S19:4; *ibid*, July 11, 1998: USP S19:3; *ibid*, September 16, 1998: USP S19:5; *Skelton & Afiti*, September 15, 1998: USP S18:12); Laucala Bay, Suva, Fiji (*South*, January 20, 1992: USP S8:6-7); Makaluva Island, Suva Reef, Fiji (*Keats*, August 11, 1994: USP S11:7; USP S11:8); Suva Barrier Reef, Fiji (*South*, May 6, 1993: USP S8:20); Deuba, Coral Coast, Fiji (*South & Skelton* February 28, 1999: USP S17:12). Korolevu, Fiji (*R.F. & C. Scagel*, July 27, 1980: UBC A32984; *ibid*. 24 August, 1980: UBC A15566); Korolevu Is., Fiji (*S. Villeneuve*, February 16, 1982: UBC A39805); Sawa-i-lau, Fiji (*S. Villeneuve*, February 6, 1982: UBC A 52008; *ibid* February 24, 1982: UBC A54136); Naikacuru, Fiji (*S. Villeneuve*, February 25, 1982: UBC A58394); Beachcomber Is., Fiji (*S. Villeneuve*, February 21, 1982: UBC A47418); Plantation Is., Fiji (*D.J. Garbary*, August 10, 1981: UBC A49558); Viti Levu (west), Fiji (*D.J. Garbary*, August, 1981: UBC A51998).

HABITAT & REMARKS: Common, epiphytic and epilithic, found in all habitats from intertidal to 25 m depth. The complex taxonomy and nomenclature of *C. flaccidum* is detailed in Silva et al. (1996: 919-920). The synonymy employed here largely follows Womersley (1978: 234-238), except for the exclusion of *Ceramium taylorii* Dawson (1950: 127-128, pl. 2: fig. 13, pl. 4: figs 31-33), and *Ceramium fimbriatum* Setchell & Gardner (1924: 777, pl. 26: figs 43, 44). We have examined isotype material of *C taylorii* from Cabeza Ballena, Baja California (BISH 498510), and find that the nodal structure (Fig. 40) is quite different from that included under *Ceramium flaccidum*. Silva et al. (1996: 396), Wynne (1995: 292) and Abbott (1999: 272, fig. 76A-C) maintain *Ceramium*



Figures 38-44. *Ceramium flaccidum* and *C. taylorii* [Fig. 40 only]. Fig. 38. Habit with regularly pseudodichotomously branched uprights, arising from the prostrate base [Palolo Deep, Samoa July 2, 1998]; Fig. 39. View of the axial cell and the periaxial band with 2-3 acropetal and 3 basipetal cell rows [*S. Villeneuve*, Sawa-i-lau, Fiji, February 6, 1982]; Fig. 40. Detail of the cortical band of the *Ceramium taylorii* isotype, to compare with *C. flaccidum*; scale as in Fig. 41; Fig. 41. Surface view of nodes of *C. flaccidum* with horizontally elongate basipetal cell rows; Fig. 42. Cystocarps; Fig. 43. Tetrasporangia with well developed involucres. Fig. 44. Tetrasporangial branch.

fimbriatum as a separate taxon. In the Indian Ocean Sundari et al. (1980) showed that *C. fimbriatum* has a chromosome number of 2n = 42, while *C. gracillimum* var. *byssoideum* has 2n = 84 or more. The inclusion of *Ceramium masonii* as a synonym is based on Dawson (1956: 53), who noted that variability in the presence of gland cells in Marshallese specimens (as *C. gracillimum* var. *byssoideum*) and the presence of whorled involucrate sporangia encompassed the description of *Ceramium masonii* from Pacific Mexico (Dawson 1950: 126, pl. 2: figs 11-12). Millar (1990: 396) remarked that *Ceramium flaccidum* is distinguished mainly by its triangular periaxial cells, transversely elongate basipetal cortical cells, and acropetal cells which grow in a 'V'-shaped pattern. He noted that in these features the Coffs Harbour material is wholly comparable to liquid-preserved material of *C. flaccidum* he had examined from the Atlantic Coast of Spain, *Ceramium taylorii* Dawson from the Gulf of California (Mexico), and *Ceramium byssoideum* Harvey from Key Largo (Florida), taxa he included in the synonymy of *C. flaccidum*. We have examined isotype material of *C. taylorii* (BISH 498510; Dawson No. 3393). The cortical bands are unlike those of *C. flaccidum*; the basipetal rows are in clear vertical series and the lowermost row lacks the horizontally elongate cells characteristic for *C. flaccidum* (see Abbott & Hollenberg 1976: fig. 541). In addition, the distal acropetal cell row comprises small, vertically elongate cells, quite unlike those in *C. flaccidum*. On the basis of this, the synonymy of *C. taylorii* under *C. flaccidum* appears to be unwarranted. *Ceramium punctiforme* Setchell also has transversely elongated basipetal cortical cells, but has only four periaxial cells per node, as opposed to 6(-7), and tetrasporangia that are cruciately, rather than tetrahedrally, divided. The regular arrangement of cortical cells in *C. flaccidum* appears to be its most diagnostic feature (Millar 1990: 396). Wynne (1995: 292) distinguished *C. fimbriatum* from the Seychelles by the presence of bulbous hairs arising from the upper nodal cells, one of the features also noted by Abbott (1999). This was not considered an important character by Womersley (1978). Buggeln & Tsuda (1966: 19; as *C. gracillimum* var. *byssoideum*) noted that the characteristic nodal cortication having the cortical bands divided into the lower one third composed of transversely elongated cells is indicative of this species. Tsuda & Trono (1968: 196) stated that male plants from Baker Island have spermatangia in between nodes, borne on the upper segments of the thallus. In material from Samoa, the spermatangial clusters are more or less continuous between one node and the next.

PACIFIC ISLAND DISTRIBUTION: FIJI, SAMOA, Marshall Islands, Palau, Kiribati, New Caledonia, Solomon Islands, French Polynesia.

WORLD DISTRIBUTION: Cosmopolitan in cold temperate to tropical seas.

6. *CERAMIUM KRAMERI* SP. NOV.

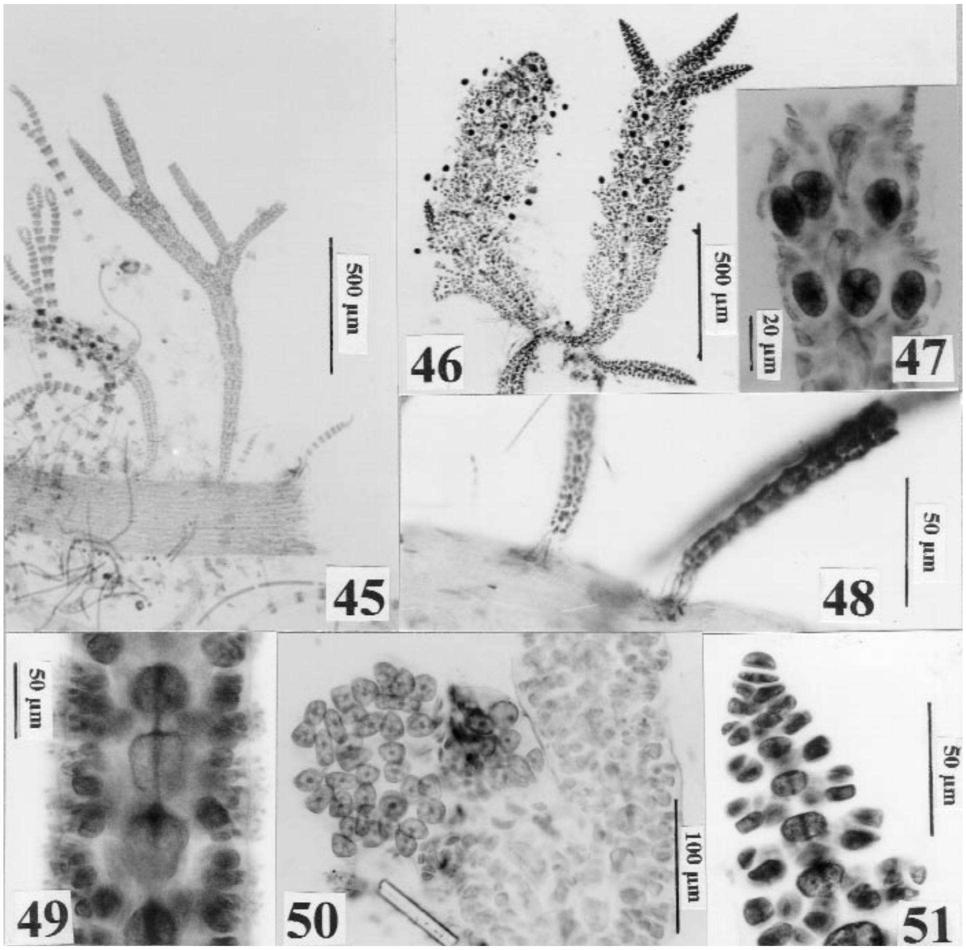
(Figs 45-51)

Ceramium krameri sp. nov. Type locality: Sawa-I-lau, Fiji.

HOLOTYPE: *S. Villeneuve* February 24, 1982: UBC A53213.

SYNONYM: *Ceramium* sp.—Garbary et al. 1991: 254, 256.

DIAGNOSIS: *Thallus ad 3.0 mm altus, solitarius, per rhizoidea unicellularia affixus; axes erecti simplices vel sparsim sympodialiter ramosi, ad 60 mm diametro, apicibus rectis; cellulae periaxiales 6, a cellulis corticaliibus vix distinguibiles, unam seriem irregularem cellularum corticalium acropetarum efferentes; vittae corticales commiscentes; internodi nudi absentes; tetrasporangia cruciatim divisa, ad 43 mm diametro, immersa; spermatangia e cellulis corticalibus evoluta; axes spermatangiales ad 70 mm diametro; cystocarpia globularia, nuda, terminalia vel subterminalia.*



Figures 45-51. *Ceramium krameri* sp. nov. Fig. 45. Habit of holotype, [UBC 53213. *S. Villeneuve* Sawa-i-lau, Fiji, February 24, 1982]; Fig. 46. Tetrasporangial plant habit [Palolo Deep, Samoa, September 15, 1998]; Fig. 47. Detail of whorled tetrasporangia [holotype]; Fig. 48. Solitary plants attached by rhizoids down-growing from the lowermost cortical cells; Fig. 49. Detail of spermatangial clusters [Palolo Deep, Samoa, September 15, 1998]; Fig. 50. Carposporangia developing laterally to the main upright [Palolo Deep, *ibid*]; Fig. 51. Detail of apical region and conspicuous apical cell [Palolo Deep, *ibid*].

Thallus to 3.0 mm tall, solitary, attached by unicellular rhizoids; erect axes simple or sparsely sympodially branched, to 60 µm in diameter, with straight apices; periaxial cells 6, scarcely distinguishable from cortical cells, giving rise to one irregular row of acropetal cortical cells; cortical bands merging, naked internodes lacking; tetrasporangia cruciately divided, to 43 µm diam., immersed; spermatangia developed from corticating cells, spermatangial axes to 70 µm diam.; cystocarps globular, naked, terminal or subterminal.

ETYMOLOGY: *Ceramium krameri* is named in honour of Dr Augustin Krämer, Surgeon Major of the Imperial German Navy, and scholar of Samoa.

DESCRIPTION: *Thalli* solitary, minute, to 3.0 mm tall, epiphytic, attached by unicellular rhizoids (15 µm diam.) that develop from the lowermost 2-3 rows of corticating cells; uprights terete, 25-(44)-100 µm broad; unbranched, or sparsely sympodially branched; apical cell prominent, to 10 µm diam.; axis tapering proximally and distally, to 60 µm diam.; tips straight, periaxial cells 6, scarcely differentiated from corticating cells, giving rise initially to one acropetal cell row; nodal bands barely discernible in the tip region, merged for most of the axis, the corticating cells not forming vertical or horizontal rows. *Tetrasporangia* cruciately divided, 27.5-(30)-42.5 µm diam., immersed in the tumid nodal cells; mature tetrasporangial sorus occupying up to three quarters the length of the thallus; *spermatangia* in tufts from the nodal cells, to 70 µm diam.; *cystocarp* terminal, globular, naked to 17.5 µm diam. Plants are epiphytic on *Gelidiopsis intricata* (C. Ag.) Vickers and *Coelothrix irregularis* (Harv.) Børg., from 1.5–25 m deep.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton & Faletoese*, September 18, 1998: USP 5024; USP S18: 11; *Skelton, Faletoese & Afiti*, September 18, 1998: USP S18: 2).

HABITAT & REMARKS: Frequent, epiphytic on *Gelidiopsis intricata* and *Coelothrix irregularis* and other macroalgae from the 1.5 to 25 m depth. The algal rim along the ‘deep’ at Palolo Deep Marine Reserve appears to be a favored habitat for this alga in Samoa. The Fijian and Samoan plants are identical. Garbary et al. (1991: 254, 256) commented that their specimens (as *Ceramium* sp., now designated as the holotype of *C. krameri*) resembled *Ceramium maryae*, and that they might represent a new species. Our examination of the type of *C. maryae* revealed that it does not at all match *C. krameri*.

PACIFIC ISLAND DISTRIBUTION: FIJI, SAMOA

7. *CERAMIUM MACILENTUM* J.AGARDH

(Figs 52-62)

Ceramium macilentum J. Agardh, 1894: 15 (type locality: Port Phillip, Victoria, Australia). Womersley 1978: 232, figs 3E, 14A-D; 1998: 408, figs 187E, 188A-D. Price & Scott 1992: 100, fig. 31; Millar & Kraft 1993: 39; Silva et al. 1996: 399.

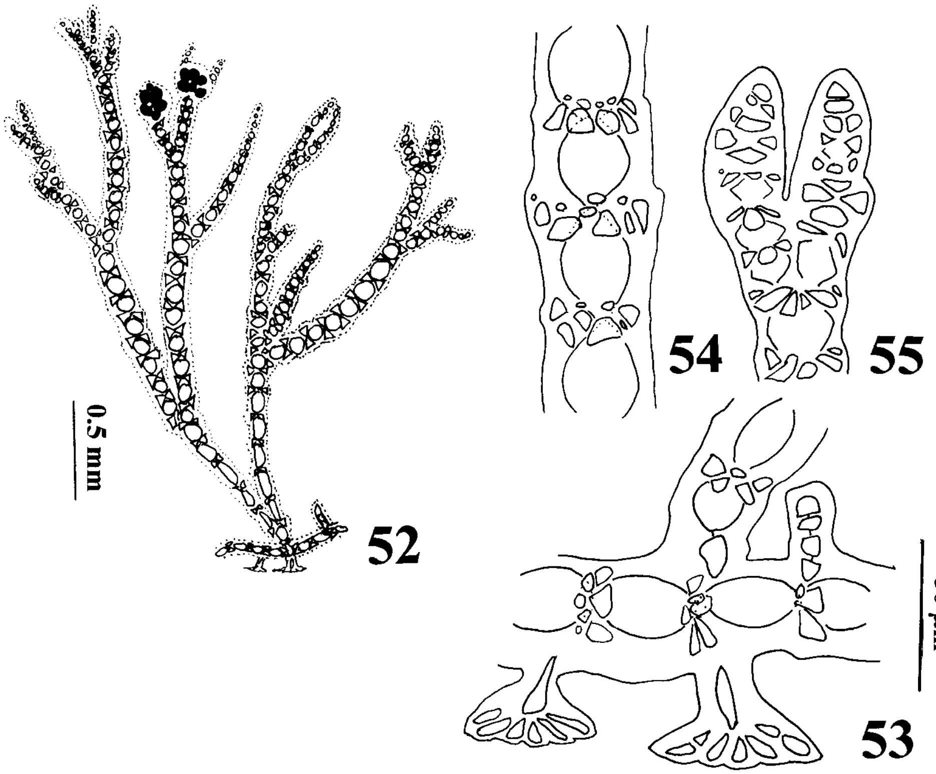
TYPE: Herb. Agardh, LD, 20616 (*fide* Womersley, 1978: 233).

TAXONOMIC SYNONYM: *Ceramium mazatlanense* Dawson 1950: 130, pl. 2: figs 14, 15 (type locality: Mazatlán, Sinaloa, Mexico).—Dawson 1954: 448, figs 55g-j; Dawson 1956: 53; 1957; 1962: 59, pl. 23: figs 1-2; Gilmartin 1960: 215 (as *Ceramium mazathanense*); Trono 1969: 74, pl. 10: figs 3, 8; Womersley & Bailey 1970: 324; Tsuda & Wray 1977: 104; Cribb, 1983: 85, pl. 62: figs 1-3; Payri 1987; Garbary et al. 1991 (as *Ceramium mazatlense*): 254; N'Yeurt 1993a: 177, figs. 190, 191, 199; 1993b: 9; 1996:422: figs 156,157, 165; South & Yen 1992: 129; South et al. 1993: 190; N'Yeurt et al. 1996: 82; Payri & N'Yeurt 1997: 895.

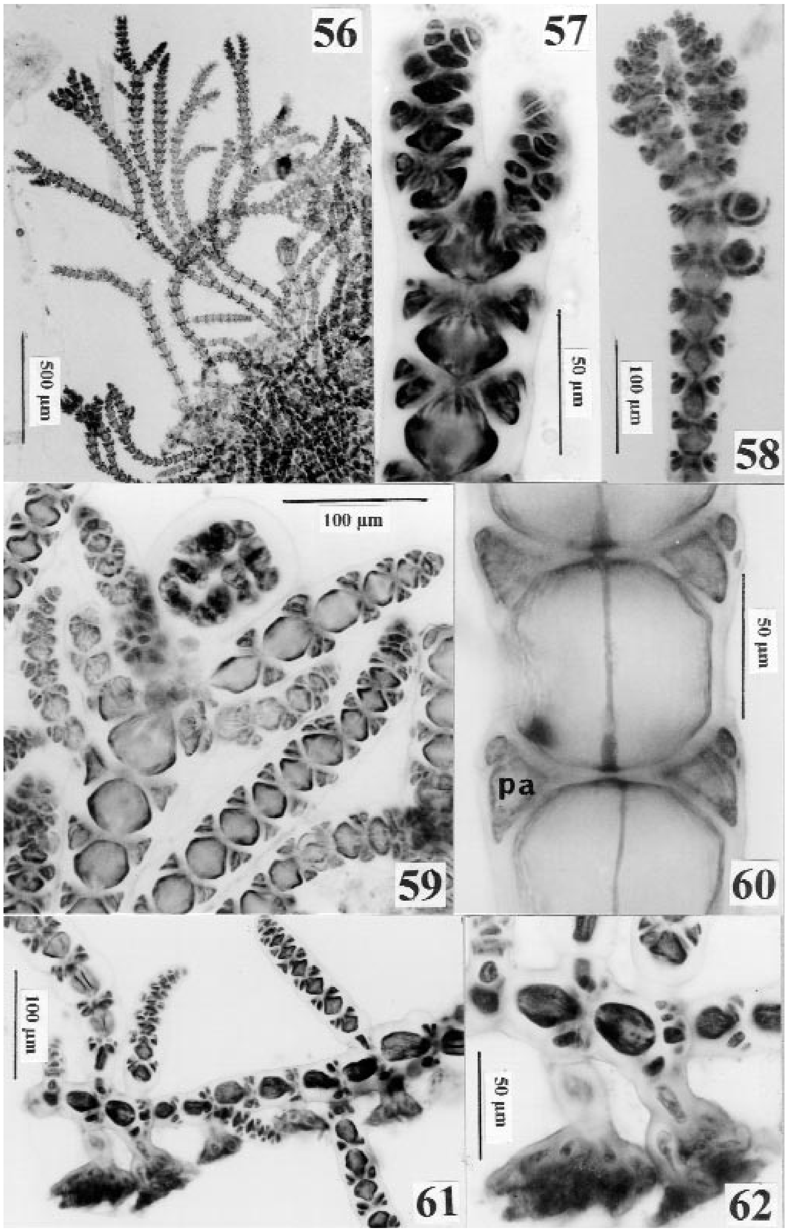
ADDITIONAL REFERENCES: Dawson 1954, fig. 55 g-j; Itono 1972: 82; Ngan & Price 1979: 14; Lewis 1984: 42; Silva et al. 1987: 55; 1996: 399; Tsuda 1991: 49.

TYPE: BISH 623184 (clastotype prepared by R.E. Norris from isotype UC 925467; Dawson No. 3603).

DESCRIPTION: *Thallus* light red, a few millimetres (Fijian and Samoan material) to 6 cm high, erect or often in tangled masses. Branching subdichotomous to



Figures 52-55. Camera lucida drawings of *Ceramium macilentum* [Palolo Deep, Samoa, September 18, 1998] Fig. 52. Habit of cystocarpic plant; Fig. 53. Detail of rhizoids with terminal multicellular attachment pad; Fig. 54. Node of upright with simple structure and absence of basipetal corticating cells; Fig. 55. Branch tip.



Figures 56-62. *Ceramium macilentum* [Palolo Deep, Samoa September 28th 1998; Deuba, Fiji, February 28, 1999 (Fig. 58 only)] Fig. 56. Habit; Fig. 57. Branch tip with pseudodichotomous branch and slightly forcipate tips; Fig. 58. Tetrasporangial branch with tetrasporangia abaxially arranged and with a well developed involucre; Fig. 59. Cystocarps, note enclosing sheath; Fig. 60. Exploded view of nodes showing single acropetal cell row arising from the periaxial cells (pa); Fig. 61. Prostrate base with rhizoids developing from most nodes; Fig. 62. Detail of rhizoids showing multicellular attachment pad.

alternate (often every 5-8 cells above) and sometimes tending to be somewhat complanate above, sparse in lower parts, with few if any proliferous branchlets. Attachment by rhizoids of 1-3 uniseriate cells with a multicellular pad, arising usually singly from a periaxial cell on each node of prostrate filaments. Branches 70-130 (-150) µm in diameter below, tapering often very slightly to 40-70 µm several cells below the (normally) involute apices. Axial cells L/D (0.5-)1-1.5 near apices, elongating in larger specimens to L/D 4-6, with a narrow cortical nodal band 30-50 µm long. Periaxial cells usually 6, most of which divide obliquely to form a wedge-shaped pseudoperiaxial cell which interposes between the periaxial cells to form a ring of 10-12 cells; each of these cells usually cuts off one or two cells acropetally, and in older parts these may cut off a further 1-2 cells; the node is thus 2-3 cells long, very occasional basipetal cells may be cut off from the periaxial cells but this is rarely found over several nodes or from more than one periaxial cell in a node. Slender hairs commonly present on cortical cells near apices. Rhodoplast discoid in corticating cells, ribbon-like and longitudinally arranged in axial cells. *Reproduction*. Gametophytes dioecious. *Carposporophytes* with 1-2 irregularly globular lobes, 100-200 µm across, subtended by 2-4 curved branchlets, carposporangia angular, 18-25 µm across. *Spermatangia* forming patches on the adaxial sides of nodes, later tending to spread around the node. *Tetrasporangia* in prominent, abaxial rows (very occasionally in adaxial rows or opposite), usually some distance below the apices, with 1-3 sporangia per node, derived from periaxial cells; tetrasporangia basally involucrate (to half the sporangium) by cortical filaments of a few cells, subspherical to ovoid, irregularly decussately to tetrahedrally divided, 40-75 µm in diameter, with a persistent sheath (adapted from Womersley 1998: 408; Dawson 1950: 130, pl. 2: figs 14, 15; Cribb 1983: 85, pl. 62: figs 1-3).

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton*, July 1, 1998: USP S17:14; *ibid*, September 18, 1998: USP S19:6; USP S19:8; *Skelton & Afiti*, September 15, 1998: USP S19: 7; *Skelton, Afiti & Faletoese*, September 18, 1998: USP S19:10); Deuba, Coral Coast, Fiji (*South & Skelton*, February 28, 1999: USP S17:10; USP S17:11; USP S19:9).

HABITAT & REMARKS: Common, epiphytic on macroalgae, on solid substrata, or on ascidians (not in Fiji or Samoa). Found from the reef flat to 25 m depth. Womersley (1998: 410) noted that *Ceramium macilentum* is a slender species which seems well marked by its nodal cortex, with the interposed pseudoperiaxial cells and the virtual absence of any basipetal derivatives of the periaxial cells. Price & Scott (1992: 102) note that plants assigned by Cribb (1983) to *Ceramium mazatlanense* Dawson strongly resemble their material of *Ceramium macilentum* and also conform closely with *Ceramium comptum* Børgesen. The isotype material of *C. mazatlanense* agrees with the description of this species in Cribb (1983: 85, pl 62, figs 1-3). A comparison of the description of *C. macilentum* in Price & Scott (1992: 100, fig. 31) and Womersley (1978: 232, figs 3E, 14 A-D) with the type of *C. mazatlanense* and with collections from Fiji and Samoa confirms that a single taxon is represented. We therefore place *C. mazatlanense* in synonymy with *C. macilentum*, which has priority. The Samoan plants are the lowest end of the size range for the species in Australia. The usual lack of basipetal derivatives from the periaxial cells and the interspersed pseudoperiaxial cells is also notable in the Samoan plants, together with the comparatively narrow uprights and the distinct ovoid shape of the axial cells, which stands out under low-power microscopic examination. In his original description of *C. mazatlanense* Dawson (1950: 132) noted that the species has a nodal structure suggestive of *Ceramium gardneri* Kylin, though the cortical bands are much shorter. He also noted variation in the nature of the tips and the arrangement of the tetrasporangia between specimens from Sinaloa and Salina, Mexico. Dawson later (1954: 448) noted that *Ceramium mazatlanense* is related to *Ceramium cruciatum* Collins & Hervey from Bermuda, which differs in having more elongate cortical cells and cruciate sporangia. We have examined type material of *C. cruciatum* (NY6237; Collins No. 7418a, Gibbet Is., Bermuda, January 16, 1913) and concur with the view of Dawson (1954). Womersley & Bailey (1970: 324) noted that Weber-van Bosse recorded *C. cruciatum* from Celebes, and her illustration agrees with the Solomon Island plants in nodal structure. Womersley & Bailey (1970) expressed the view that detailed comparisons may show that these taxa belong to one species, but the nodal structure and mainly tetrahedral sporangia may distinguish the Pacific Ocean plants. In her description of *C. mazatlanense* from Hawaii, Abbott (1999: 278, fig. 78C-D) describes the tetrasporangia as cruciately divided, unlike those from our collections, and with vegetative characters similar to those of *Ceramium vagans* The Hawaiian plants thus appear to be distinct from those described here, and would not warrant placement in synonymy with *C. macilentum*.

PACIFIC ISLANDS DISTRIBUTION: FIJI, SAMOA, Federated States of Micronesia, Nauru, Solomon Islands, French Polynesia.

WORLD DISTRIBUTION: Pan-tropical

8. *CERAMIUM* SP. AFF. *C. MARSHALLENSE* DAWSON *SENSU* PRICE & SCOTT 1992: 102, FIG. 32.

(Figs 63-71; 73)

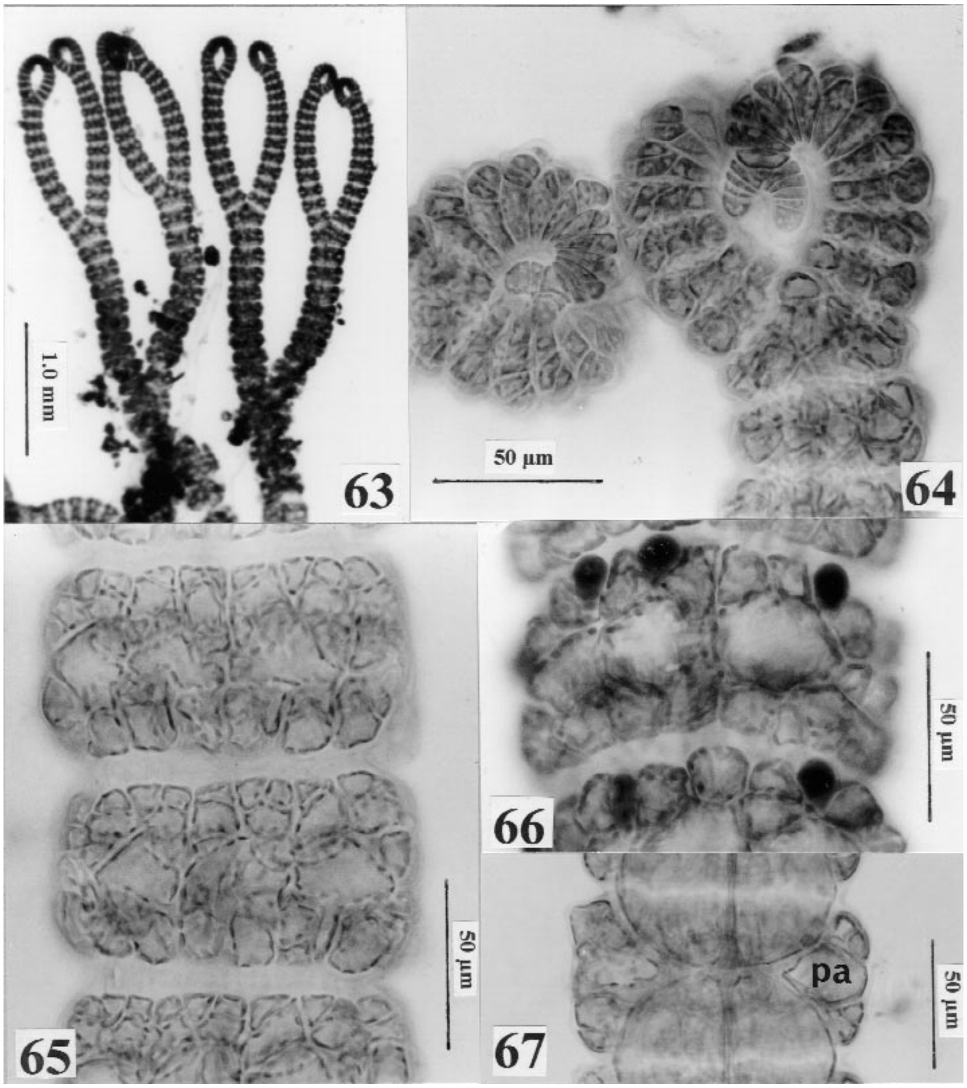
Ceramium marshallense Dawson 1957: 120–121, figs 27a-b (type locality: Rigili Island, Eniwetok, Marshall Islands).—Tsuda & Wray 1977: 104.

ADDITIONAL REFERENCES: Dawson 1957a: 21; Itono 1972: 82–83, fig. 12; Silva et al. 1987: 55; 1996: 399; Price & Scott 1992: 102, fig. 32 (as *Ceramium* sp. cf. *marshallense* Dawson); Wynne 1993: 14–15, figs 8–9; 1995: 294, figs 38–39.

TYPE: Dawson No. 14013 in BISH No. 500457

MISAPPLIED NAME: *Ceramium brevizonatum* H. Petersen 1918: 14, figs 8, 9 (syntype localities: Algiers, Algeria; Menton, France).—Kapraun & Bowden 1978: 201, fig. 20.

DESCRIPTION: *Thallus* pale red, epiphytic on larger algae, attached by elongate (up to 1.0 mm) multicellular rhizoids proximal cell occasionally bulbous to 55 µm diam., otherwise cells 13-20 µm diam., arising singly or in groups from periaxial cells of the prostrate system; free branches up to 6.6(-7.4)9.0 mm tall; branching primarily pseudo-dichotomous, sterile apices strongly forcipate and usually circinately in-rolled; main axes 55(-130)188 µm diam.; cortication consisting of nodal bands 25(-62)113 µm tall; cortical bands consisting of a central ring of 6-10 iso-



Figures 63-67. *Ceramium* sp. af. *C. marshallense* [Palolo Deep, Samoa, July 2, 1998] Fig. 63. Habit; Fig. 64. Detail of markedly circinate tips; Fig. 65. Surface view of nodes with two regularly arranged acropetal and basipetal cell rows partially obscuring the periaxial cells; Fig. 66. Surface view of node with gland cells; Fig. 67. Exploded view of node showing the double acropetal and basipetal cell rows derived from the periaxial cell (pa).

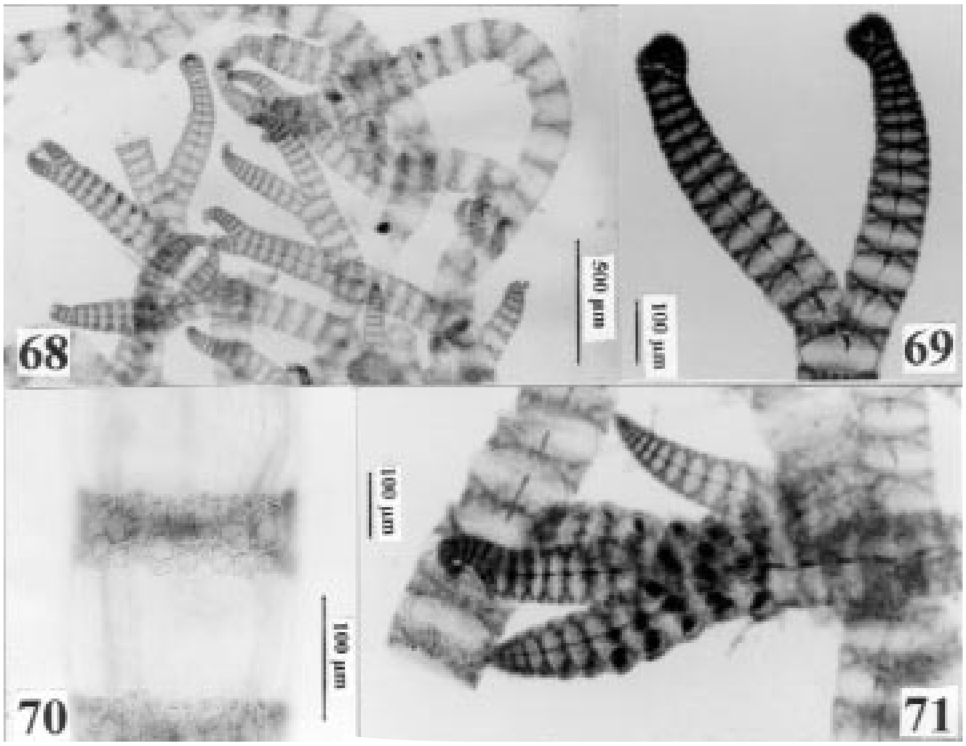
diametrical periaxial cells 30-45 µm in diameter with a single (double) row of corticating cells produced acro- and basipetally; internodes 8(-65)150 µm long; gland cells lacking to numerous, protruding from corticating cells, with 15->20 (local material) to 40-60 gland cells (type material) per node up to 13-20 µm diam.; *tetrasporangia* lacking in local material; *sexual reproduction* unknown.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton & Faletoese*, September 18, 1998: USP S17: 13; USP S17:16; *ibid*, 2 July, 1998: USP S17:10; USP S17:17; *Skelton & Afiti*, September 16, 1998: USP S17: 11; USP S17: 14; USP S17:15; *Skelton, Faletoese & Afiti*, 18 September, 1998: USP S17: 12).

HABITAT & REMARKS: Common, epiphytic, easily recognized in the field due to its conspicuous nodes, however, plants are fragile and easily break up; intertidal to 22 m depth. Our investigations have shown that the specimens collected from Fiji and Samoa are different from those occurring in Hawaii. Meneses (1995) and Abbott (1999: 269, fig. 79A-C) have placed Hawaian *C. marshallense* in synonymy with *Ceramium clarionensis* Setchell & Gardner. Meneses (1995: 170) has pointed out that *C. clarionensis* has been confused with *Ceramium aduncum* Nakamura) by Dawson (1950). Plants from Fiji and Samoa, however, most closely resemble those reported from the Great Barrier Reef in Price & Scott (1992:102, as *Ceramium* sp. aff. *C. marshallense*) and from Southern Japan in Itono (1972: 82-83) in which there are 6-8 periaxial cells giving rise to 1-2 basipetal and acropetal cell rows, and in which pseudoperiaxial cells are lacking. We have examined the type specimens of *C. marshallense* and *C. clarionensis* and agree with earlier authors that they are identical in vegetative structure. Both possess 6-8 periaxial cells and an equal number of pseudoperiaxial cells. Price & Scott (1992:102) added that in both their material and the type specimens of *C. marshallense* small, mostly triangular cells are occasionally cut off at the surface of the cortical bands. Dawson (1950) had noted that small angular cells formed a continuous outermost cortical layer in *C. clarionensis*, but added that the layer was poorly developed in some specimens. Gland cells are present in the type material of *C. marshallense*, a feature in common with plants from Fiji and Samoa, although not previously reported. In comparison with the type material and the original description in Dawson (1957: 120-121), tetrasporangia in Australian material project strongly from the cortical band, and are surrounded by a distinct involucre composed of branched filaments. We have been unable to confirm this since reproductive plants are absent from our collections. He also emphasized the production of emergent tetrasporangia lacking an involucre in that species. Cribb (1983) recorded *C. clarionensis* from the southern Great Barrier Reef, and also suggested that it did not differ vegetatively from *C. marshallense*. Our conclusion is that the plants from Fiji and Samoa, as well as those from the Great Barrier Reef, are probably a new species.

PACIFIC ISLAND DISTRIBUTION: FIJI, SAMOA, Marshall Islands

WORLD DISTRIBUTION: Maldives, (?Seychelles), Southern Japan, Pacific Costa Rica, Philippines, (?Australia: Qld.)



Figures 68-71. *Ceramium marshallense* holotype Fig. 68. Habit; Fig. 69. Forcipate, circinate tips with pseudodichotomous branching; Fig. 70. Surface cell rows; Fig. 71. Tetrasporangial branch with whorled, immersed tetrasporangia.

9. *CERAMIUM SUBDICHOTOMUM* WEBER-VAN BOSSE
(Figs 74-79)

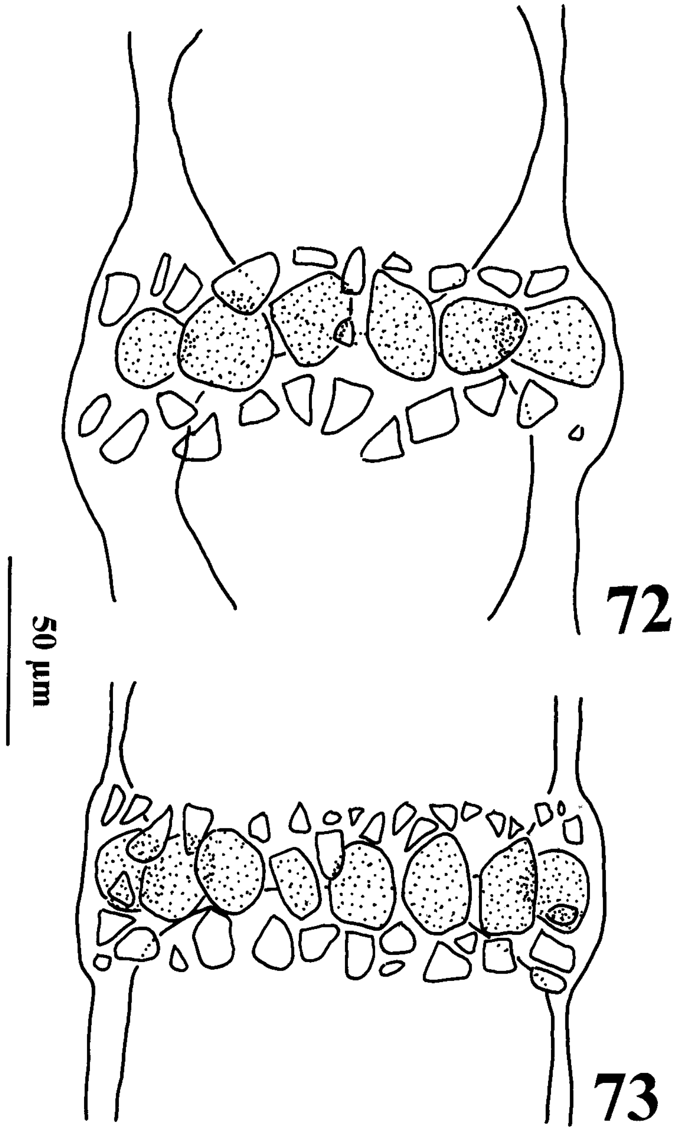
Ceramium subdichotomum Weber-van Bosse 1923: 333-335, fig. 125 (type locality Muaras).—Wynne 1995: 296, fig. 44, 45; 1999: 195, figs. 8, 9.

TYPE: Weber-van Bosse specimens of this species are not types; the type may be lost (Prud'homme van Reine, pers. com.).

TAXONOMIC SYNONYM: *Ceramium sympodiale* Dawson 1957: 121, figs 27c,d (type locality: Rigili Island, Eniwetok, Marshall Islands).—Womersley & Bailey 1970: 324; Tsuda & Wray 1977: 104; Payri & N'Yeurt 1997: 895.

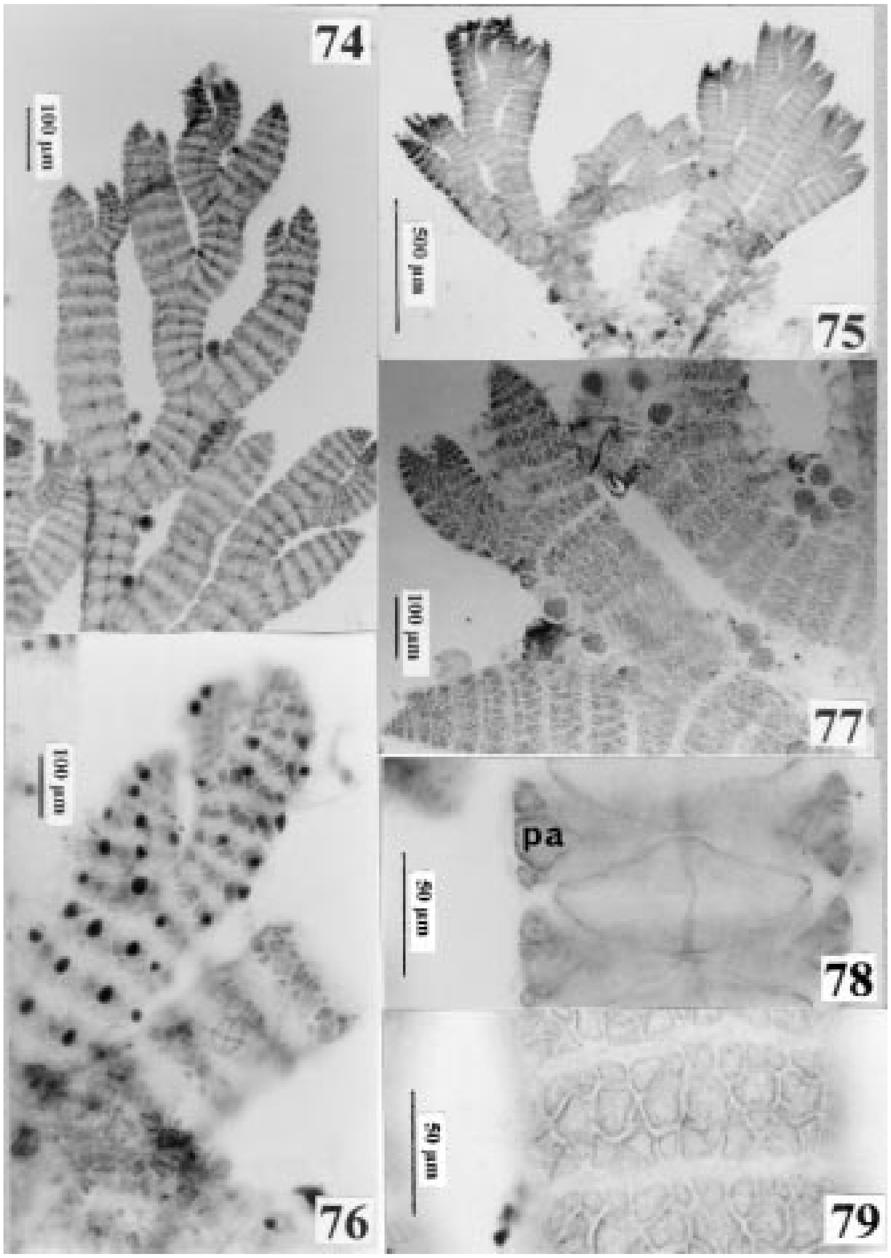
TYPE: BISH 500458. Holotype, Dawson No. 14014.

DESCRIPTION: *Thallus* pale red, minute, 3.5-5.5 mm tall, epiphytic, the base creeping, prostrate, attached by unicellular rhizoids; rhizoids formed opposite uprights, to 100 µm long × 25 µm diam. terminating in a plate-like attachment; uprights arising from each 1-2 prostrate nodes or from assurgent branch tips, 100 µm diam.; branching sympodial – sub-dichotomous, more or less distichous, with short, adventitious laterals arising at irregular intervals; periaxial cells 6-8, cells angular, to 25 µm diam, dividing further to form 2 acropetal and 2 basipetal cell



Figures 72-73. *Ceramium clarionensis* & *C. marshallense*. Details of nodal structure of *Ceramium clarionensis* [holotype] Fig. 72, and *Ceramium marshallense* [holotype] Fig. 73, emphasizing their close similarity.

layers; nodes to 58 µm wide × 105 µm high (2 L/B), the internodes 62.5 µm apart in the lower region, reduced in the upper region; apices straight or slightly forcipate; apical cell conspicuous, dome-shaped, 17.5 µm diam. × 12.5 µm long; simple hairs frequent near the apices, formed from the upper acropetal cortical cells, and soon shed. Gland cells numerous, developing from the acropetal nodal cells.



Figures 74-79. *Ceramium subdichotomum* [Palolo Deep, Samoa, September 15, 1998] & *C. sympodiale* [holotype]. Fig. 74. *C. sympodiale* habit; Fig. 75. *C. subdichotomum* habit; Fig. 76. *C. sympodiale* branch tip with numerous gland cells; Fig. 77. *C. subdichotomum* with emergent tetraspores on the adaxial surface of the nodes; Fig. 78. *C. subdichotomum*, exploded view of the nodal band showing single acropetal and basipetal cell rows; Fig. 79. *C. subdichotomum* surface view of nodal band.

Tetrasporangia tetrahedrally divided, 25-30 µm diam. (excluding hyaline sheath), emergent, lacking an involucre, borne single adaxially on the upper branches. Sexual stages not seen.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton & Afiti*, July 4, 1998: USP S17:19; *ibid*, September 15, 1998: USP S19:12-14).

HABITAT & REMARKS: Fairly common, epiphytic on various macroalgae, in calm locations from intertidal to 25 m depth. Our examination of the type of *C. sympodiale* Dawson and comparisons of this species with the original description of *Ceramium subdichotomum* in Weber-van Bosse (1923: 333-335), confirms our placement of *C. sympodiale* in synonymy with *C. subdichotomum*. The description of *C. subdichotomum* from Oman in Wynne (1999: 195, figs 8, 9) also strongly indicates its conspecificity with *C. sympodiale*. It is remarkable that Dawson (1957: 121) and others (e.g., Price & Scott 1992: 109-110) do not refer to *C. subdichotomum* in their descriptions of *C. sympodiale*, since the species appear to be identical. Our description closely follows the original description of *C. sympodiale* in Dawson (1957: 121). Womersley & Bailey (1970: 324) reported this species (as *C. sympodiale*) on *Acropora* coral and epiphytic on *Chondria* near a surge channel, under strong wave action. They described it as a small, slightly iridescent species with prostrate filaments attached by rhizoids, producing erect, pseudo-sympodial branches lying in one plane. The apices are straight, not involute, with nodes of fairly uniform small cells, and numerous gland cells in most, but not all, specimens. The only reproductive structures seen were spermatangia, formed densely around the nodal cortical cells. They noted that the Solomon Islands material agrees well with Dawson's description of *C. sympodiale*, though he did not observe gland cells. They also noted that the apices are not truly sympodial since the apex continues growth, cutting off laterals alternately on two sides, as illustrated here. The synonymy given here is different from that in Meneses (1995) and Abbott (1999), who place *C. sympodiale* in synonymy with *Ceramium borneense* Weber-van Bosse (1923: 329). This difference is unlikely to be resolved until all the relevant type material has been found and compared with collections from throughout the distribution range.

PACIFIC ISLAND DISTRIBUTION: SAMOA, Marshall Islands, Solomon Islands, French Polynesia

WORLD DISTRIBUTION: Indonesia, Oman, South Pacific Ocean

10. *CERAMIUM UPOLENSE* SP. NOV.

(Figs 80-88)

Ceramium upolense sp. nov. (type locality: Palolo Deep Marine Reserve, Upolu Island, Samoa).

TYPE: *Skelton, Tombleson & Tuivaiti*, July 11, 1998: SUVA (USP) 5024.

SYNONYM: *Ceramium* sp. in Price & Scott 1992: 112, fig. 32 A-E.

DIAGNOSIS: *Thalli prostrati, ad 3 mm alti; rami erecti simplices vel parce ramosi, apicibus rectis; cellulae periaxiales 5-7; vitta nodalis aequaliter evoluta, seriebus duabus cellularum corticalium acropetarum et isdem cellularum* *basipetarum; cellulae duae conspicuae curvatae basipetae corticales saepe praesentes; tetrasporangia ellipsoidea cruciatim divisa, in verticillos disposita, partim protrudentia; spermagantia in superficie tota vittae corticalis evoluta; carposporophyta ignota.*

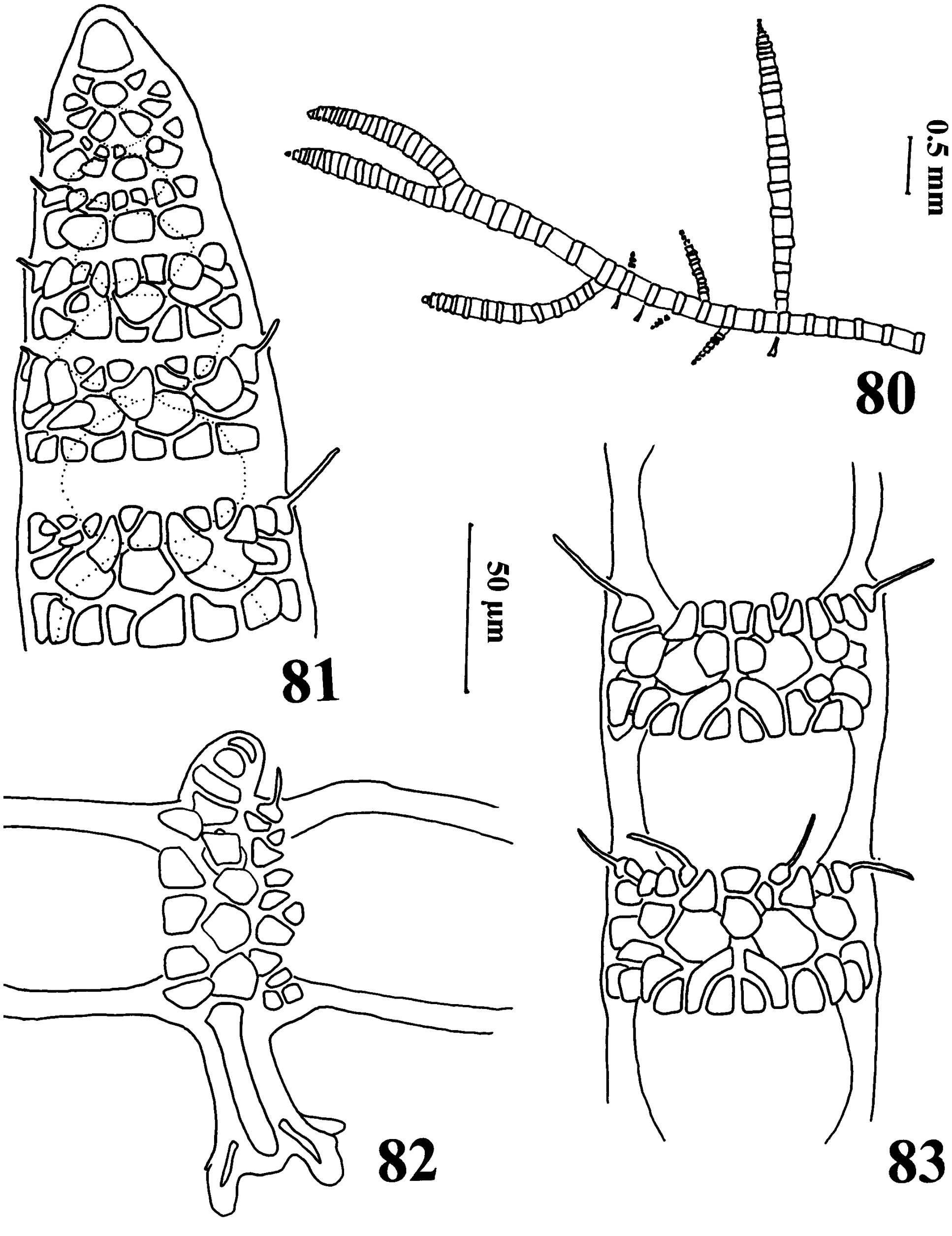
Thalli prostrate, to 3 mm tall; erect branches simple or sparingly branched, with erect apices; periaxial cells 5-7, nodal band evenly developed, with two rows of acropetal cortical cells and the same of basipetal cells; two conspicuous curved basipetal cortical cells frequently present; tetrasporangia ellipsoidal, cruciately divided, in whorls, partly protruding; spermatangia developed over entire surface of cortical band; carposporophytes not known.

ETYMOLOGY: *Ceramium upolense* is named after the island of Upolu, Samoa.

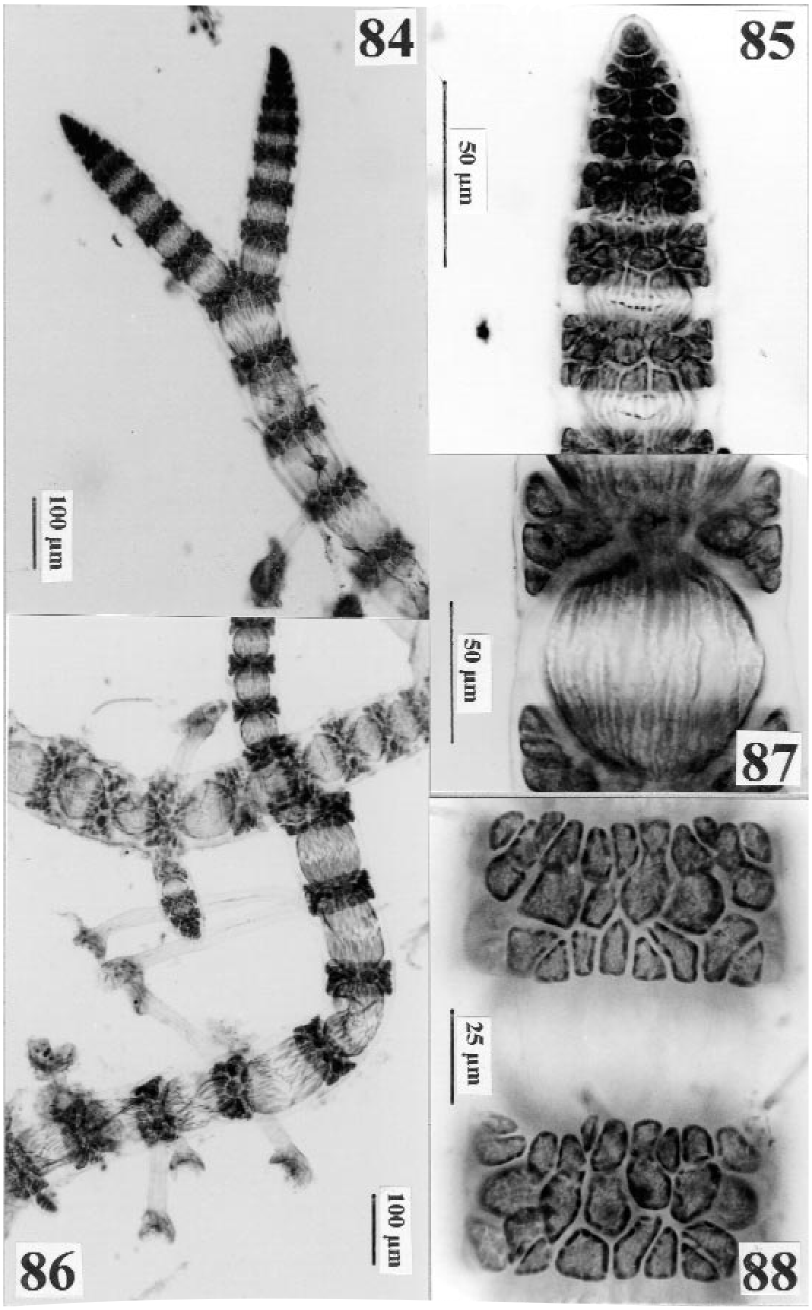
DESCRIPTION: Plants from Samoa agree with the description of *Ceramium* sp. in Price & Scott (1992: 112). *Thalli* to 3 mm tall, arising from branched prostrate axes bearing simple erect branches with more or less straight tips; attachment is by unicellular rhizoids. Mature segments (75-)90-110(-120) µm diam., 80-125(-200) µm long with L/D1-2(-2-3). Cortical bands symmetrical, the acropetal and basipetal margins straight, with 4-5 (up to 6) cell rows. Axial cells ellipsoidal, 55-115 µm diam.; periaxial cells (5-)6-7, rounded to polygonal, 12-17.5 µm diam. × 20-30 µm long; pseudoperiaxial cells lacking. Each periaxial cell cutting 2 (often unequal) acropetal and 2 basipetal cortical initials, which in turn cut off 1-2 acropetal and basipetal cortical cells respectively, resulting in 5 cell rows including the periaxials; surface cells triangular to polygonal in surface views, 5-12 µm diam., 10-18 µm long. Two large, curved basipetal cortical cells are often a conspicuous feature of the nodal band. Slender hairs are frequently produced by the acropetal cortical tissue. *Tetrasporangia* ellipsoidal, 25-40 µm diam., 30-40 µm long, cruciate, borne in whorls of (1-)5-6(-11) in successive swollen cortical bands, usually near tips of branches. Sporangia partly protruding from more strongly developed acropetal tissue; cortical bands bearing sporangia 150-220 µm diam. *Sexual stages* were not seem on Samoan material. Price & Scott (1992) described them as follows: *Spermatangia* formed in dense patches, developing over entire surface of cortical band. *Carposporophtyes* not known.

REPRESENTATIVE MATERIAL: Palolo Deep, Samoa (*South*, 1 July, 1998: USP S19:20; *Skelton* 17 September 1998: USP S17:20; *ibid*, 1 July, 1998: USP S19:11; USP S20:1).

HABITAT & REMARKS: Rare, epiphytic on *Halimeda opuntia* (L.) Lamour., intertidal and shallow subtidal. The most distinctive features of this species are the even development of the cortical bands, and the frequent presence of two large, curving basipetal cells. Samoan plants are epiphytic on *Sargassum* in shallow water on the lagoon flat. Price & Scott (1992: 112) noted that their material occurs on the reef crest or, in winter, on the reef flat. Their material resembles that from the southern Great Barrier Reef referred by Cribb (1983) to *Ceramium camouii*, although pseudodichotomous branching and forcipate tips were not observed, and cortical band development is not as extensive as described by



Figures 80-83. *Ceramium upolense* sp. nov. Camera lucida drawings of the holotype. Fig. 80. Habit; Fig. 81. Branch tip with conspicuous apical cell and cauducous hair cells arising from the acropetal cell row; Fig. 82. Rhizoid, terminating in a multicellular attachment pad; Fig. 83. Details of nodal bands with the characteristic curved basipetal cells.



Figures 84-88. *Ceramium upolense* sp. nov. holotype. Fig. 84. Habit; Fig. 85. Detail of branch tip with conspicuous apical cell. Fig. 86. Development of paired uniseriate rhizoids; Fig. 87. Exploded view of node showing single acropetal and basipetal cell rows developed from the periaxial cells; Fig. 88. Surface view of node showing characteristically curved basipetal cells.

Cribb. Price & Scott (1992: 113) examined the holotype material of *C. camouii* and confirmed Dawson's (1944) original description with slender branches (30-40 µm diam.) and simple nodal bands composed of only 2-3 cell rows.
PACIFIC ISLAND DISTRIBUTION: SAMOA.
WORLD DISTRIBUTION: Australia (Qld.).

11. *CERAMIUM VAGANS* P. SILVA
(Figs 89-93)

Ceramium vagabundum Dawson 1957: 121, fig. 27e ('*vagabunde*') (type locality: Parry Island, Eniwetok Atoll, Marshall Islands).—Buggeln & Tsuda 1966: 20; Dawson 1962: 66, pl. 27: fig. 5; Trono 1969: 75, pl. 10: figs 1-2; Tsuda & Wray 1977: 104; Kapraun & Bowden 1978: 18-19; Payri 1987; South & Kasahara 1992: 63; Millar & Kraft 1993: 39.

Ceramium vagans P. Silva in P. Silva, Meñez & Moe, 1987: 56.—N'Yeurt 1993a: 178, figs 188, 192, 193, 196; 1993b: 9; 1996: 423, figs 154, 158, 162; 1997: 424

ADDITIONAL REFERENCES: Wynne 1995: 296: figs. 46-47; Silva et al. 1996: 404.

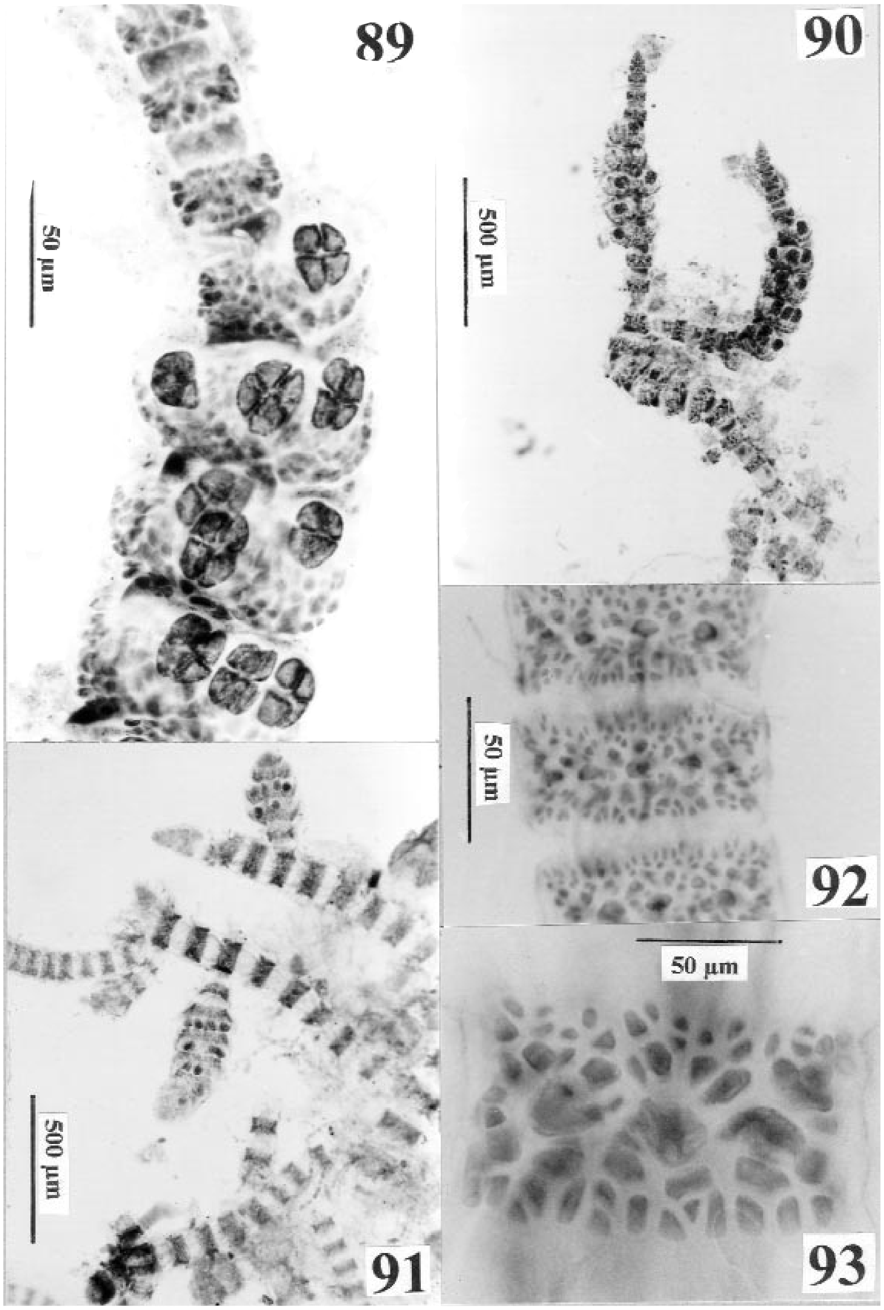
NOTE: *Ceramium vagans* is a substitute name for *C. vagabundum* Dawson, a later homonym of *C. vagabundum* (Linnaeus) Roth (1800: 465) = *Cladophora vagabunda* (Linnaeus) van den Hoek, 1963:144.

TYPE: Dawson 13620a; BISH 500455.

DESCRIPTION: Plants from Fiji and Samoa closely match the description of this species in Dawson (1957: 121-122) and the type material. *Thalli* minute, 3-5 mm high, growing among other tufted algae, consisting of a creeping, semi-prostrate basal filament provided with numerous ventral rhizoids from the nodes, giving rise to irregularly and sparsely branched erect branches with blunt, non-forcipate tips; erect axes 80-140 µm in diameter, incompletely corticated, the internodes spaced at intervals of 30-70 µm in middle and lower parts; cortical bands narrow, 1 ½-2 times as broad as tall, without secondary growth above or below, the margins even, especially the lower ones, consisting of a narrow inner ring of larger cells and on either side of an outer ring or irregularly arranged small angular cells less than 10 mm in maximum diameter; *tetrasporangia* cruciate, ovate-pyriform, 28-45 µm in length, borne verticillately within prominently swollen involucres which develop acropetally from the closely juxtaposed distal nodal bands of the erect axes; terminal fertile areas to 163-315 µm in diameter, resembling those of *Equisetum* in form.

REPRESENTATIVE MATERIAL: Palolo Deep Marine Reserve, Samoa (*Skelton*, September 18, 1998: USP S19: 16-17). Deuba, Coral Coast, Fiji (*South & Skelton*, February 28, 1999: USP S19: 18).

HABITAT & REMARKS: Uncommon, epiphytic on various macroalgae, from reef crest to reef flat. Dawson (1950) noted that this species is closest to *Ceramium nakamurai* Dawson from Garanbi, Taiwan (*Ceramium equisetoides* Nakamura), but is not dichotomously branched. He also stated that it is identical



Figures 89-93. *Ceramium vagans* Fig. 89. Detail of whorled cruciate tetrasporangia with partial involucres [Deuba, Fiji, February 28, 1999]; Fig. 90. Habit of tetrasporangial plants [Deuba, ibid]; Fig. 91. Habit of tetrasporophyte [Palolo Deep, Samoa, September 18, 1998]; Figs 92 & 93. Variation in the nodal structure [holotype].

with tetrasporangial specimens cited and illustrated as an undescribed species from Isla San Benedicto, Mexico [Dawson, 1954: 6, pl. 4: fig. 2 (as *Ceramium* sp.)]. Wynne (1995: 296) confirmed that Seychellois plants agree closely with Dawson's (1957) description. He noted that the thallus is essentially creeping, and gives rise to sparsely branched erect branches with blunt tips; branching is non-dichotomous; the branches may arise uni- or bilaterally at right angles to the parent axis. He described the cortical bands as having even margins, consisting of an inner ring of larger cells with usually two irregular rows of small angular cells to either side. Wynne (1995) also stated that the exerted whorled tetrasporangia with their prominent involucres, the more developed cortication, and the erect apices in *C. vagans* distinguish it from *C. marshallense* which has whorled tetrasporangia surrounded by a tumid cortication, strongly forcipate apices, and narrower cortical bands.

PACIFIC ISLAND DISTRIBUTION: FIJI, SAMOA, Marshall Islands, Johnston Atoll, French Polynesia

WORLD DISTRIBUTION: Pacific Mexico, Seychelles, Philippines

DOUBTFUL SPECIES

12. *CERAMIUM ZACAE* SETCHELL & GARDNER

Ceramium zacae Setchell & Gardner 1937: 89, pl. 8: figs 22a-c [type locality: Bahia San Bartolomé (Bahía Tortugas), Baja California Sur, Mexico].—Dawson 1950: 134, pl. 3: figs 27-28; Dawson 1962: 67-68, pl. 26: figs 4-6; N'Yeurt 1993a: 179, figs 186, 187, 198; 1993b: 9; 1996: 423, figs 152, 153, 164; 1997: 283, fig. 251; N'Yeurt et al. 1996: 83; South et al. 1993: 190.

ADDITIONAL REFERENCES: Abbott & Hollenberg 1976: 598, fig. 542; Fortes & Trono 1979: 60, fig. 11; Silva et al. 1987: 56.

TYPE: The type specimens are lost (P.C. Silva, pers. comm.).

DESCRIPTION: *Thalli* epiphytic up to 5 mm high and 90-100 µm diam. arising from prostrate filaments adhering by rhizoids from ventral nodal surfaces. Branching dichotomous, with forcipate apices. Cortical band 57-60 µm in diameter and 4-5 rows wide, smooth at the margins and somewhat elongated and irregular acropetally; truncate basipetally. Axial cells ovoid, internodal areas 97-100 µm long. Periaxial cells 6-8, giving rise acropetally to 2 rows of progressively smaller derivatives and basipetally to 1-2 rows of triangular to subrectangular derivatives. *Tetrasporangia* arranged in two regular rows, one on each side of the upper dichotomies, or whorled in groups of three or more at a node. *Sexual stages* not observed. (after Dawson 1950: 134; N'Yeurt, 1997: 283).

REMARKS: In the absence of type specimens, it has not been possible to compare our collections or to verify the only previous records of this species from Fiji (N'Yeurt 1996: 423, figs 152, 153, 164). In his review of *Ceramium* along the Pacific Coast of North America, Dawson (1950) stated that *Ceramium avalonae* shows considerable superficial, microscopic resemblance to *Ceramium zacae*, and has a similar tetrasporangial arrangement. He noted, however, that the

branching habit and the structure of the nodal cortication, were distinct. The disposition of the large cells in the lower part of the node, cutting off smaller cells above and toward the outside is a character, which persists in older parts of the filaments. The outer cortical cells of *C. zacae* are irregularly arranged. In it the larger cells lie interior to the smaller ones and are ordinarily situated in the middle of the nodes rather than in the lower part. *C. zacae* is more abundantly branched above than *C. avalonae* and the older nodes are not tumid as in the latter. The lower internodes of *C. zacae* are relatively shorter than in *C. avalonae*, being less than as long as wide, rather than 1.5 times as long as wide or more. Tetrasporangia of *C. avalonae* are not necessarily solitary at the nodes as originally described, though the abaxial arrangement is maintained even then two or more tetrasporangia are produced at a node. Dawson later (1962: 53) merged *Ceramium avalonae* with *Ceramium caudatum* Setchell & Gardner (1924: 776), but Womersley (1978: 232) maintained it as a separate species, which he regarded as most closely related to *Ceramium cupulatum* Womersley (1978: 231-232). Likewise, Silva et al. (1996: 390) maintained *Ceramium avalonae* as an independent species. Trono (1971: 55) described *Ceramium kororensis* from Koror, Palau, a species previously reported by him (Trono 1969: 78) as *Ceramium* sp. The material on which the type description is based is sterile, but has some similarity to figures 4-6 in Dawson (1962) for *Ceramium zacae*. The regularity and precise arrangements of the cells at the nodal cortication is very distinctive of this species. Trono (1971: 55) also commented that this species is nearest to *Ceramium vagabunde* described by Dawson (1957) from Eniwetok Atoll, Marshall Islands in regards to the nature of the nodal cortication but differs from that species in having a dichotomous type of branching and forcipate apices in the filaments.
PACIFIC ISLAND DISTRIBUTION: questionable for FIJI
WORLD DISTRIBUTION: Philippines, Mexico

13. *CERAMIUM CAMOUII* DAWSON

Ceramium camouii Dawson 1944: 319-320, pl. 51: figs. 2, 3 (type locality: Isla Turners, Baja California, Mexico).—Dawson 1956: 53, fig. 52; 1962: 52; Tsuda & Wray 1977: 104; Garbary et al. 1991: 254; N'Yeurt et al. 1996: 82; Silva et al. 1996: 391.

ADDITIONAL REFERENCES: Abbott & Hollenberg 1976: 594, fig. 533; Jaasund 1976: 107, figs 218A-B; Cribb 1983: 78-79, Pl. 27: figs 5-6; pl. 58: figs 1-4; Stegenga et al. 1997: 414, fig. 155.

TYPE: E.Y. Dawson 737: BISH 623179 (fragment from the holotype at HAHF prepared and verified by R.E. Norris, June 1992)

DESCRIPTION: *Thalli* pale pink to greyish, minute, to 8 mm tall; prostrate axis well developed, giving rise to erect branches at every other node or irregularly; erect branches 0.8 to 1.5 mm high, simple or with irregularly arranged adventitious branches, or pseudodichotomous with the apices slightly incurved or almost straight; erect and adventitious branches distinctly narrower than the parent branch; periaxial cells 5-(6)-7, polygonal, to 12-18 μm diam.; giving rise to

2 cell rows acropetally and basipetally; in poorly developed nodes, periaxial cells each cutting off two acropetal cells partly covering the periaxial cells to produce a nodal band two cells high including the periaxial cells; in fully developed nodes with three, exceptionally four generations of cells both basipetally and acropetally, and sometimes with both the basipetal and acropetal primary cortical cells cutting off 1-2 cells towards the central part of the node but the periaxial cells never completely obscured; in the fully developed nodal bands the cells angular, mostly 6-15 µm diam., irregularly arranged, the band almost symmetrical but often cells of the upper border slightly smaller than those of the lower border; nodal bands slightly protruding, 50-150 µm diam., (20) 30-100 µm high, mostly 2 L/B; internodal bare area 1-3.5 (4) times as long as adjacent nodal bands; central cell 75-200 (280) µm long; *tetrasporangia* cruciately divided, occasionally single or in unilateral groups of 2–3, or in whorls of up to 7; tetrasporangia obovoid to spherical, to 15 µm diam., × 56 µm long; strongly protruding, with involucral cells extending to or almost to the level of the top of the sporangia, with nodal diameter at the sporangial whorls 120–160 µm. (from Cribb 1983: 78-79).

REPRESENTATIVE MATERIAL: Sawa-i-lau, Fiji (*S. Villeneuve*, February 24, 1982: UBC A54138).

HABITAT & REMARKS: The Fiji specimen examined more or less matches the type, but the characteristic arrangement of tetrasporangia was not seen. We are therefore reluctant to confirm this solitary record. The type material is a confusing mixture of a number of microscopic algae, including more than one species of *Ceramium*. Type specimens were determined by matching them with the original illustrations. Millar (1990: 395) notes the similarity in the cortical cell development between *Ceramium filicum* Womersley, *Ceramium avalonae* Dawson and *Ceramium camouii* Dawson, but added that neither displays the diamond-shaped axial cells of *C. filicum*. He also noted that some Coffs Harbour (northern New South Wales, Australia) specimens of *C. filicum* are similar to *Ceramium marshallense* Dawson, but differ in details such as rhizoids, axial cell dimensions, and the predominant pattern of cortical cell development. In their description of *Ceramium camouii* from the South African West Coast, Stegenga et al. (1997: 414) state that the plants are up to 10cm long, and dichotomously branched at 10-20 (or more) segments; they thus differ significantly from the circumscription of this species from the tropical South Pacific. Cribb (1983: 79) stated that *C. camouii* shows considerable variation, often on different parts of the same filament, of the degree of cortical development and filament diameter. This is also true for the type specimens. He noted that the plants with poorly developed bands most closely fit Dawson’s (1944) description and figures of the type specimens, while the more robust specimens more closely fit the interpretation of this species by Feldmann-Mazoyer in Børgesen (1952). Cribb (1983: 79) also noted that the Queensland specimens of *C. camouii* appear to approach *Ceramium vagabunde* Dawson (= *Ceramium vagans* P. Silva), suggesting that the latter species may be a synonym of *C. camouii*.

PACIFIC ISLAND DISTRIBUTION: Questionable for FIJI, SAMOA; probable for Marshall Islands.

WORLD DISTRIBUTION: California, Baja California, Kenya, Mauritius, South Africa, Tanzania, Australia (Qld).

14. *CERAMIUM CLARIONENSIS* SETCHELL & GARDNER

Ceramium clarionensis Setchell & Gardner, 1930: 170, pl. 7: figs 25-27 (type locality: Isla Clarión, Revillagigedo Archipelago, Mexico).—Dawson 1950: 134, pl. 4: fig. 29 ("*clarionense*"); Dawson 1956: 54; 1957: 119; Tsuda & Wray 1977: 104; Garbary et al. 1991: 254; N'Yeurt et al. 1996: 82; Payri & N'Yeurt 1997: 894.

NOTE Dawson (1950 et seq.) used the spelling "*clarionense*", which has perpetuated since then. He also confused this species with *Ceramium aduncum* Nakamura (Meneses 1995: 166).

ADDITIONAL REFERENCES: Dawson 1950: 134, pl. 4: fig. 29; 1954: 448, fig. 55k; 1962: 53-54, pl. 18: figs 5-6; Abbott & Hollenberg 1976: 595, fig. 535.

TYPE: CAS in UC 173620, on *Codium*. Herbert L. Mason No. 75.

DESCRIPTION: *Thalli* to 3 mm to 1.0 cm tall producing a green iridescence in life; partially creeping and attached by unicellular rhizoids, 25 µm X 275 µm long; erect parts 160-250 µm diam., regularly pseudo-dichotomously branched with strongly circinate apices; axial cells slightly longer than broad below, diminishing in length upward; cortication of variable extent, the internodes sometimes so narrow above as to be little more than lines, commonly 18-60 µm above, lengthening to 150-200 µm below; cortical bands usually a little more than ½ as long as wide, truncate above, and below, sometimes becoming tumid in lower parts, consisting of 10-12 rotund periaxial cells 15-18 µm diam., and an outer layer of irregularly arranged, more or less angular cells mostly about 10 µm in maximum dimension, provided, external to the cortical cells, with small deeply staining globules ("gland cells") and sometimes also with short hairs; tetrasporangia numerous, emergent, usually naked, scattered adaxially or all the way around the node without cortical modification; spermatangia surrounding the nodes, 1.5 µm diam.; *cystocarps* borne in the axils of the pseudodichotomies, naked, variously lobed. (from Dawson, 1962: 53).

REMARKS: Meneses (1995) and Abbott (1999) include *C. marshallense* in synoymy with *C. clarionensis* in Hawaii. We have examined the only collection of this species from Fiji (Garbary et al. 1991: 254). The specimen does not match the type of *Ceramium clarionensis* on the basis of its nodal structure, and in the absence of tetrasporangia (the authors had misinterpreted the numerous gland cells as tetrasporangia). In light of this, we have been unable to confirm the occurrence of *C. clarionensis* in Fiji or Samoa.

PACIFIC ISLAND DISTRIBUTION: Questionable for FIJI, probable for Marshall Islands, French Polynesia,

WORLD DISTRIBUTION: California, Mexico

15. *CERAMIUM SUBVERTICILLATUM* (GRUNOW) WEBER-VAN BOSSE

Ceramium kützingianum Grunow var. *subverticellatam* (sic) Grunow 1874: 31 (type locality: Ovalau, Fiji).—Garrigue & Tsuda 1988: 64.

Ceramium subverticillatum (Grunow) Weber-van Bosse 1923: 327, figs 119, 120.—Chapman 1971: 170; N'Yeurt et al. 1996: 82; Silva et al. 1996: 403; Skelton & South 1999: 12.

Non Gongroceras subtile Kützing, 1863 (= *Ceramium byssoideum* Harvey).

DESCRIPTION: *Thalli* minute, to 3 mm tall, branching dichotomous, axis 60-100 µm diam., nodes close at the apex and becoming elongated below, to a maximum length of 200 µm. Periaxial cells pyriform, rounded or angular, cortical cells formed both acropetally and basipetally. *Tetrasporangia* emergent, in whorls, non-involucrate, to 44 µm diam., tetrahedrally divided; "gland" cells frequent at the tips. (*fide* Weber-van Bosse, 1923: 327).

REMARKS: The type of this species has been lost, and we are unaware of any isotype material, so it has been impossible to verify the occurrence of this species in Fiji. Weber-van Bosse (1923: 327, figs 119, 120) noted that the nodal structure in this species differs significantly from that of *Ceramium byssoideum*. The plants resemble *Ceramium macilentum* and *Ceramium leptozonum* Howe; they differ from the former by the narrow filaments, and the naked tetrasporangia, and from the latter by the nodal band comprising three rows of cells in the fertile region, and more variable in the sterile specimens, and by the forcipate tips. The main species, which bears sparser tetrasporangia, was collected by Veillard on *Galaxaura tomentosa* in New Caledonia.

WORLD DISTRIBUTION: Bahrain, Saudi Arabia, Seychelles, Somalia

PACIFIC ISLAND DISTRIBUTION: FIJI, questionable for SAMOA, New Caledonia

Acknowledgements

We are grateful to the Canada-South Pacific Ocean Development Program, Phase II (Projects USP01 and 02) and the Government of Japan for financial support. We thank the Division of Environment and Conservation, Department of Lands, Surveys and Environment, and Siaki and Leuka Laban, for access to the Palolo Deep Marine Reserve, Samoa. Field support was provided by Amanda Tombleson, 'Max' Rintels Tuivaiti, David Faletoese and Talauati Afiti. Diving assistance was from MOANA Divers, under the management of Foua and Logo Toloa. We greatly appreciate the help of Dr Carolyn Bird in the provision of the Latin diagnoses and for her insightful comments on our descriptions. The location and loan of type material was made possible by Dr Paul Silva (PC), Dr Chris Puttock (BISH), Dr Willem Prud'homme van Reine (L), Ms Julie Oliveira (UBC) and the curators of NY and W; we thank them all for their assistance.

References

Abbott, I.A. 1999. Marine Red Algae of the Hawaiian Islands. Bishop Museum Press, Honolulu. Xv + 477 pp.

Abbott, I.A. & G.J. Hollenberg. 1976. Marine Algae of California. Stanford University Press, Stanford. xii + 827 pp.

Agardh, J.G. 1894. Analecta algologica. Continuatio II. Lunds Universitets Års-Skrift, Andra Afdelningen, Kongl. Fysiografiska Sällskapets i Lund Handlingar 30(7): 98 pp., [I] pl.

Ardissone, F. 1871. Revista dei Ceramii della flora italiana. Nuovo Giornale Botanico Italiano 3: 32–50.

Ballantine, H. & H.J. Humm. 1975. Benthic algae of the Anclote Estuary. I. Epiphytes of seagrass leaves. Florida Scientist 38: 150–162.

Børgesen, F. 1952. Some marine algae from Mauritius. Additions to the parts previously published, IV. Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser 18: (19): 1–72, pls 1–5.

Buggeln, R.G. & R.T. Tsuda. 1996. A preliminary marine algal flora from selected habitats on Johnston Atoll. University of Hawaii, Hawaii Institute of Marine Biology Technical Report 9: 1–29.

Chapman, V.J. 1971. The marine algae of Fiji. Revue Algologique 2: 164–171.

Collins, F.S. & A.B. Hervey. 1917. The algae of Bermuda. Proceedings of the American Academy of Arts & Science 53: 1–195.

Cribb, A.B. 1983. Marine Algae of the Southern Great Barrier Reef. Part I. Rhodophyta. Australian Coral Reef Society: Brisbane. Handbook No. 2: 173 + [2] pp., 71 pls.

Dawson, E.Y. 1944. The marine algae of the Gulf of California. Allan Hancock Expeditions 3: [i - v] + 189–453, including pls. 31–77.

Dawson, E.Y. 1950. A review of *Ceramium* along the Pacific Coast of North America with special reference to its Mexican representatives. Farlowia 4: 113–138.

Dawson, E.Y. 1954. Marine plants in the vicinity of the Institut Océographique de Nha Trang, Viêt Nam. Pacific Science 8: 373–469.

Dawson, E.Y. 1956. Some marine algae of the southern Marshall Islands. Pacific Science 10: 25–66.

Dawson, E.Y. 1957. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. Pacific Science 11: 92–132.

Dawson, E.Y. 1957a. Marine algae from the Pacific Costa Rican Gulfs. Los Angeles County Museum Contributions in Science 15: 1–28.

Dawson, E.Y. 1962. Marine red algae of Pacific Mexico. Part 7. Ceramiales, Ceramiaceae, Delesseriaceae. Allan Hancock Pacific Expedition 26(1): 1–208.

Dawson, E.Y. 1963. New records of marine algae from the Galapagos Islands. Pacific Naturalist 4(1): 1–23.

Dixon, P.S. 1958. *Ceramium codii* (Richards) Mazoyer: an addition to the British marine algal flora. Annual Magazine of Natural History ser. 13(1): 14–16.

Dixon, P.S. 1960. Studies on marine algae of the British Isles: the genus *Ceramium*. Journal of the Marine Biological Association of the United Kingdom 39: 331–374.

Edwards, P. 1973. Life history studies of selected British *Ceramium* species. Journal of Phycology 9(2): 181–184.

Evans C.M.B. C. Maggs, M.J. Stanhope & M. Hommersand. 1999. A taxonomic reevaluation of the genera *Microcladia*, *Campylaephora* and *Ceramium* in the tribe Ceramieae (Rhodophyta). The Phycologist 52 (Supplement). Abstracts of Presentations from the Annual Winter Meeting, University of Dundee, 4–7 January, 1999). p.7.

Feldmann, J. 1942. Les algues marines de la côte des Albères. IV. Rhodophycées (fin). Revue Algologique 13: 29–113.

Feldmann-Mazoyer, G. 1941. *Recherches sur les Céramiacées le la Mediterranée occidentale*. Algiers, 510 pp.

Feldmann-Mazoyer, G. 1952. *Ceramium*. *In* F. Børgesen, Some marine algae from Mauritius. Additions to the parts previously published. IV. Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser 18(19): 40–51, figs. 20–25.

Fortes, M.D. & G.C.Trono, Jr. 1979. Marine algal microphytes new to the Philippines. Kalikasan, Philippines Journal of Biology 8: 51–68.

Funk, G. 1955. Beiträge zur Kenntnis der Meeresalgen von Neapel zugleich mikrophotographischer Atlas. Pubbl. Stn. Zool. Napoli 25 (suppl.) x + 178 pp, 30 pls.

Garbary, D. 1988. Interoceanic hybridization in fully corticated Ceramium isolates (Rhodophyta) from Nova Scotia and Washington. The Korean Journal of Phycology 3: 89–93.

Garbary, J.W.D. 1975. The Genus *Ceramium*: Taxonomic, Morphological and Cultural Investigations. M.Sc. Thesis, Acadia University. Abstract. v pp.

Garbary, D.J., D. Grund & J. McLachlan. 1978. The taxonomic status of *Ceramium rubrum* (Huds.) C.Ag. (Ceramiales, Rhodophyceae) based on culture experiments. Phycologia 17(1): 85–94.

Garbary, D.J., D. Grund & J. McLachlan. 1980. Branching patterns and life history stages in *Ceramium rubrum* (Huds.) C.Ag. Nova Hedwigia 33: 249–260.

Garbary, D.J., J.C. Oliveira, R.F. Scagel & S. Villeneuve. 1991. Notes and distribution records for the marine algae of Fiji. Micronesica 24: 289–260.

Garrigue, C. & R.T. Tsuda. 1988. Catalog of marine benthic algae from New Caledonia. Micronesica 21: 53–70.

Gilmartin, M. 1960. The ecological distribution of the deep water algae of Eniwetok Atoll. Ecology 41(1): 210–221.

Grunow, A. 1874. Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. Journal des Museums Godeffroy [Hamburg] 3: 23–50.

Harvey, W.H. 1853. Nereis boreali-Americana…Part II. Rhodospermae. Smithsonian Contributions to Knowledge 5(5): 258 pp., pls. XIII - XXXVI.

Hoek, C. van den. 1963. Revision of the European Species of *Cladophora*. Proefschrift….Rijksuniversiteit te Leiden. Leiden: E.J. Brill. XI + 248 pp., 1 fig., 51 pls., 18 maps.

Howe, M.A. 1918. Class 3. Algae. *In* Britton, N.L., Flora of Bermuda (Illustrated). pp. 489–590. New York.

Itono, H. 1972. The genus *Ceramium* (Ceramiaceae, Rhodophyta) in southern Japan. Botanica Marina 15: 74–86.

Itono, H. 1977. Studies on the ceramiaceous algae (Rhodophyta) from southern parts of Japan. Bibliotheca Phycologica 35: 1–499.

Jaasund, E. 1976. Intertidal Seaweeds in Tanzania. University of Tromsø. [III+] 160 pp.

Kajimura, M. 1972. Comparison of *Ceramothamnion* and *Ceramium*. Proceedings of the International Seaweed Symposium 7: 136–141.

Kanda, C. 1944. Ecological notes on the marine algae from Kororu and adjacent islands in the South Sea Islands. Palao Tropical Biological Station Studies 2(4): 737–800.

Kapraun, D.F. & W.A. Bowden. 1978. Additions to the benthic marine algal flora of Fiji. Micronesica 14: 199–207.

Kasahara, H. 1985. Marine Green and Red Algae collected at Viti Levu and Ndravuni Islands of Fiji. M.Ag. Thesis, Kagoshima University. 83 pp.

Kützing, F.T. 1842. Ueber *Ceramium* Ag. Linnaea 15: 727–746.

Kützing, F.T. 1863. Diagnosen under Bemerkungen zu drei und siebenzig neuen algenspecies. *In* Zu der öffentlichen Prüfung sämmtlicher Klassen der Realschule zu Nordhausen….[1863]. Nordhausen. Pp. 1–19. [Reprinted Hedwigia 2: 86–95, 1863.]

Kylin, H. 1956. Die Gattungen der Rhodophyceen. C.W.K. Gleerups Förlag: Lund. xv + 673 pp.

Lewis, J.A. 1984. Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. I. Rhodophyta. Department of Defence, Defence Science and Technology Organisation Materials Research Laboratories Report MRL-R-912. Melbourne.

Levring, T. 1960. A list of marine algae from Rennell Island. The Natural History of Rennell Island, British Solomon Islands 3: 121–125.

Maggs, C.A. & M.H. Hommersand. 1993. Seaweeds of the British Isles. Vol. 1 Rhodophyta. Part 3A Ceramiales. The Natural History Museum, London. xv + 444 pp.

May, V. 1966. Algae of the Gilbert Islands. Contributions of the New South Wales National Herbarium 4: 14–16.

Mazoyer, G. 1938. Les Céramiacées de l’Afrique du Nord. Bulletin de la Société de l’Histoire Naturelle de l’Afrique du nord. 29: 317–331.

Meneses, I. 1995. Notes on *Ceramium* (Rhodophyta, Ceramiales) from the Hawiian Islands. Pacific Science 49: 165–174.

Millar, A.J.K. 1990. Marine red algae of the Coffs Harbour region, northern New South Wales. Australian Systematic Botany 3: 293–593.

Millar, A.J.K. & G.T. Kraft. 1993. Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, South-western Pacific. Australian Systematic Botany 6: 1–90.

Nakamura, Y. 1954. The structure and reproduction of the genera *Ceramium* and *Campylaephora* in Japan with special reference to criteria for classification. Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido Imperial University 4: 15–62.

Nakamura, Y. 1965. Species of the genera *Ceramium* and *Campylaephora*, especially those of northern Japan. Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University. 5: 119–180.

Ngan, Y. & I.R. Price. 1979. The intertidal algae of the mainland coast in the vicinity of Townsville, Queensland. Atoll Research Bulletin 237: 1–29.

Norris, R.E. & I.A. Abbott. 1992. New taxa of Ceramieae (Rhodophyta) from Hawaii. Pacific Science 46: 453–465.

N'Yeurt, A.D.R. 1993a. A Floristic Survey of the Intertidal and Shallow Benthic Marine Algae of Rotuma. M.Sc. Thesis, The University of the South Pacific, Suva. 1 –258 + pls.

N'Yeurt, A.D.R. 1993b. A preliminary checklist of the marine benthic macroalgae of Rotuma. The University of the South Pacific Marine Studies Programme Technical Reports 1993(2): 1–14.

N'Yeurt, A.D.R. 1996. A preliminary floristic survey of the benthic marine algae of Rotuma Island. Australian Systematic Botany 9: 361–490.

N'Yeurt, A.D.R. 1997. A Floristic and Taxonomic Study of the Benthic Intertidal and Subtidal Marine Algae of the Suva Lagoon and Reef, Fiji. Ph.D. Thesis, The University of the South Pacific, Suva. vi + 446 pp., 334 figs. & 1 pl.

N'Yeurt, A.D.R., G.R. South & D.W. Keats. 1996. A revised checklist of the benthic marine algae of Fiji (including the island of Rotuma). Micronesica 29: 49–96.

Payri, C.E. 1987. Variabilité Spatiale et Temporelle de la Communauté des Macrophytes des Récifs Coralliens de Moorea (Polynésie française). Contribution des Algues au Métabolisme du carbone de l'Ecosystème Récifal. Thèse d"Etat. (Université des Sciences et des Techniques du Languedoc: Montpellier) [Not seen by the authors].

Payri, C.E. & A.D.R. N'Yeurt. 1997. A revised checklist of Polynesian benthic marine algae. Australian Systematic Botany 10: 867–910.

Peterson, H.E. 1918. Algae (excl. calcareous algae). *In* J. Schmidt (ed.), Report on the Danish Oceanographical Expeditions 1908 - 1910 to the Mediterranean and adjacent seas. Vol. II. Biology. København. [Art.] K.3. 20 pp., 10 figs.

Price, I.R. & F.J. Scott. 1992. The Turf Algal Flora of the Great Barrier Reef. Part I Rhodophyta. James Cook University of North Queensland, Townsville. xii + 266 pp. 81 figs.

Reinbold, T. 1896. Meeresalgen (Schizophyceae, Chlorophyceae, Rhodophyceae). *In* F. Reineke, Die Flora der Samoa-Inseln. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 23: 266–275.

Richards, H.M. 1901. *Ceramothamnion codii*, a new rhodophyceous alga. Bulletin of the Torrey Botanical Club 28: 257–265, pls. 21, 22.

Rosenvinge, L.K. 1924. The marine algae of Denmark. Contributions to their natural history. Part III. Rhodophyceae III (Ceramiales). Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Raekke, Naturvidenskabelig og Mathematisk Afdeling 7: 285–487, figs. 202–453, pls V–VII, [2] maps.

Roth, A.W. 1800. Tentamen florae germanicae. Vol. 3, part 1. Lipsiae [Leipzig]. vii + 578 pp.

Schiller, J. 1911. Botanische Beobachten, IV, Jahresberichte Ver. Förd. Naturwiss. Erforsch. Adria 6: 89–91.

Schmidt, O.C. 1928. Verzeichnis der Meeresalgen von Neu-Guinea und dem westlichen Oceanien. Hedwigia 68: 19–86.

Setchell, W.A. 1924. American Samoa: Part I. Vegetation of Tutuila Island. Part II. Ethnobotany of the Samoans. Part III. Vegetation of Rose Atoll. Publications of the Carnegie Institution of Washington 341. VI + 275 pp., 57 figs., 37 pls., 3 tables.

Setchell, W.A. 1926. Tahitian algae collected by W.A.Setchell, C.B. Setchell, and H.E. Parks. University of California Publications in Botany 12: 61–142, pls. 7–22.

Setchell, W.A. & N.L. Gardner. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The marine algae. Proceedings of the California Academy of Sciences, ser. 4, 12: 695–949, including pls. 12–88, folded map.

Setchell, W.A. & N.L. Gardner. 1930. Marine algae of the Revillagigedo Islands Expedition in 1925. Proceedings of the California Academy of Sciences, ser. 4, 19: 109–215, including pls 4–15.

Setchell, W.A. & N.L. Gardner. 1937. The Templeton Crocker Expedition of the California Academy of Sciences 1932, No. 31. A preliminary report of the algae. Proceedings of the California Academy of Sciences 4: 22-65-98. 1 fig., pls 3–25.

Skelton, P.A. & G.R. South. 1999. A preliminary checklist of the benthic marine algae of the Samoan Archipelago. The University of the South Pacific Marine Studies Programme Technical Report 1999(1): 1–30.

Silva, P.C., E.G. Meñez & R.L. Moe. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contributions to the Marine Sciences 27: iv + 179 pp., 2 figs., 1 table.

Silva, P.C., P.W. Basson & R.L. Moe 1996. Catalog of the benthic marine algae of the Indian Ocean. University of California Publications in Botany 79: I-xiv + 1–1259.

Simons, R.H. 1966. The genus *Ceramium* in South Africa. Bothalia 9: 153–156.

South, G.R. 1991. Benthic marine algae from Dravuni Island, Astrolabe Islands, Kadavu, Fiji. The University of the South Pacific Marine Studies Programme Technical Report 1991(5): 1–13.

South, G.R. & H. Kasahara. 1992. A preliminary checklist of the benthic marine algae of the Fiji Islands, South Pacific. Micronesica 25: 41–70.

South, G.R., A.D.R. N'Yeurt & R.A. Raj-Prasad. 1993. Additions and amendments to the benthic marine algal flora of Fiji, including the island of Rotuma. Micronesica 26: 177–198.

South G.R. & S. Yen. 1992. Notes on the benthic marine algae of Nauru, Central Pacific. Micronesica 25: 123–131.

Stegenga, H., J.J. Bolton & R.J. Anderson. 1997. Seaweeds of the South African west coast. Contributions from the Bolus Herbarium 18: 1–655.

Sundari, M., B.G.S. Rao & M. Umamaheswara Rao. 1980. Cytotaxonomic studies on some *Ceramium* species of Visakhapatnam coast. *In* T.V. Desikachary & V.N. Raja Rao (eds.), Taxonomy of Algae. University of Madras. Pp. 305–314, III pls.

Taylor, W.R. 1945. Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. Allan Hancock Pacific Expeditions 12: 1–528.

Taylor, W.R. 1950. Plants of Bikini and other Marshall Islands. Ann Arbor: University of Michigan Press. xv + 227 pp., 79 pls.

Tokida, S. 1939. A list of marine algae from Micronesia. Kagaku Nanyu 2(1): 16–26.

Trono, G.C. Jr. 1969. The marine benthic algae of the Caroline Islands, II. Phaeophyta and Rhodophyta. Micronesica 5: 25–119.

Trono, G.C. Jr. 1971. Some new species of marine benthic algae from the Caroline Islands. Micronesica 7: 45–78.

Tsuda, R.T. 1964. Floristic report on the marine benthic algae of selected islands in the Gilbert Group. Atoll Research Bulletin 105: 1–13.

Tsuda, R.T. 1991. Catalog of the marine benthic algae from the Ryukyu Islands, Japan. Galaxea 10: 35–64.

Tsuda, R.T. & G. Trono Jr. 1968. Marine benthic algae from Howland Island and Baker Island, Central Pacific. Pacific Science 22: 194–197.

Tsuda, R.T. & F.O. Wray. 1977. Bibliography of marine benthic algae in Micronesia. Micronesica 13: 85–120.

Weber-van Bosse, A. 1923. Liste des algues du Siboga. III. Rhodophyceae. Seconde partie. Ceramiales. Siboga-Expeditie Monographie 59c. Leiden. Pp. 311-392, figs. 110–142, pls. IX, X.

Wells, S.M. & M.D. Jenkins 1988. Coral Reefs of the World. Volume 3, Western and Central Pacific: pp. 323–329: Western Samoa. United Nations Environment Programme. International Union for Conservation of Nature and Natural Resources.

Womersley, H.B.S. 1978. Southern Australian species of *Ceramium* Roth (Rhodophyta). Australian Journal of Marine and Freshwater Research 29: 205–257.

Womersley, H.B.S. 1998. The Marine Benthic Flora of Southern Australia. Part IIIC. Ceramiales - Ceramiaceae, Dasyaceae. State Herbarium of South Australia. 535pp.

Womersley, H.B.S. & A. Bailey. 1970. Marine algae of the Solomon Islands. Philosophical Transactions of the Royal Society of London B. Biological Sciences 259: 257–232, 26 figs in text and pls. 24–27.

Wynne, M.J. 1993. Benthic marine algae from the Maldives collected during the RV *Te Vega* Expedition. Contributions to the University of Michigan Herbarium 19: 5–30.

Wynne M.J. 1995. Benthic marine algae from the Seychelles collected during the R/V *Te Vega* Indian Ocean Expedition. Contributions from the University of Michigan Herbarium 20: 261–346.

Wynne M.J. 1999. New records of benthic marine algae from the Sultanate of Oman. Contributions of the University of Michigan Herbarium 22: 189–208.

Received 10 Aug. 1999, revised 7 Dec.

Index