

## *Callidictyon abyssorum*, gen. et sp. nov. (Rhodophyta), A New Deep-water Net-forming Alga from Hawai'i<sup>1</sup>

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**ABSTRACT:** *Callidictyon abyssorum*, gen. et sp. nov., an unusual, net-forming red alga, is described from deep-water Pacific collections made from the research submersible *Makali'i* at 80-m depths on Penguin Bank, off the island of Moloka'i, Hawai'i. Though no reproductive structures were found, the new genus shares vegetative similarities with three tribes of the Ceramiaceae. The vegetative structure of *C. abyssorum* is similar to that of genera of the tribe Antithamnieae in having: (1) distinct basal cells on all primary lateral branches that are isodiametric and smaller than other cells of the primary laterals; (2) a central axis that is prostrate except for the portions near the apices of branches; and (3) axes that are completely without cortication. Some characters of *C. abyssorum* also suggest affinities to genera of the Callithamnieae, including: (1) the oblique apical cell division resulting in a strictly alternate branching pattern; (2) the absence of gland cells; and, (3) the presence of short, branching rhizoids on the basal cells of the primary lateral branches and long slender rhizoids on the main axial cells. Finally, the regularly alternate branching pattern, blunt apices, formation of anastomoses, and different types of rhizoidal filaments, all characteristics of *C. abyssorum*, are also features present in members of the Compsothamnieae. Based on vegetative features, *Callidictyon* is tentatively placed in the Ceramiaceae until reproductive structures are found.

SEVERAL FILAMENTOUS net-forming red algae are known among the Ceramiaceae Dumortier (1822). The membranous genus *Delesseriopsis* Okamura (1931), along with *Balliella* Itono & Tanaka (1973), is placed in the tribe Delesseriopsieae Itono & Tanaka (1973). *Haloplegma* Montagne (1842), a three-dimensional net-forming alga, and *Rhododictyon* W. Taylor (1961), a netlike alga, have been placed in the Compsothamnieae Schmitz (1889) by Itono (1977) and Schneider (1975), along with the genera *Pleonosporium* Nägeli (1862) and *Compsothamnionella* Itono (1977). Distinctions among the tribes of the Ceramiaceae are based on reproductive mor-

phology and ontogeny of the carposporangium (see, e.g., Feldmann-Mazoyer 1941, Hommersand 1963, Wollaston 1968, Gordon 1972, Itono 1977). Other net-forming red algae include *Martensia* Hering (1841) of the Delesseriaceae; *Halydictyon* Zanardini (1843), *Dictyurus* Bory (1834), and *Thuretia* Decaisne (1844) of the Dasyaceae; and *Mortensenia* Weber-van Bosse (1926) among the Ceramiaceae of uncertain position (Hommersand 1963).

From deep-water collections made using the research submersible *Makali'i*, a new genus and species of a net-forming red alga is described. Its affinities, based on vegetative characters, to other algae in the Ceramiaceae are considered.

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### MATERIALS AND METHODS

Specimens of benthic macroalgae were collected on Penguin Bank (21° 03' N, 157° 47' W), off the island of Moloka'i, using

the research submersible *Makali'i* of the Hawaiian Undersea Research Laboratory (HURL) (NOAA Program at the University of Hawai'i). The alga described in this study was found attached and growing prostrate on a large, loose carbonate boulder collected on *Makali'i* Dive no. 85–344 at a depth of 80 m.

Specimens were liquid-preserved in buffered 5% Formalin/seawater solution in the field. Light microscope studies and photomicrographs were made using a microscope (Zeiss Universal) on liquid-preserved specimens stained with 1% aniline blue, fixed in 1% HCl/distilled water, and mounted on microscope slides with 50% Karo (Best Foods, CPC International, Englewood Cliffs, New Jersey) clear corn syrup that had phenol added as a preservative (Tsuda and Abbott 1985). The holotype specimen and accompanying microscope slides are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution (US), and an isotype in the Bernice P. Bishop Museum, Honolulu, Hawai'i (BISH). Herbarium abbreviations are from Holmgren et al. (1990).

*Callidictyon* J. Norris & Abbott, gen. nov.  
Figures 1–8

Thallus uniaxialis monosiphonius axe centrale et axibus lateralibus alternatis. Axes laterales primarii cellulis basalibus distinctis isodiametricis vix majoribus quam cellulis ramulorum secundarium lateralium, rhizoidarum et cellulis ramorum saepe conjunctis in reticulum. Rhizoidea cellularum basalium brevia tenues pauce ramosa. Rhizoidea cellularum axialium longa pauce ramosa. Cellulae uninucleatae; cellulae glandulares nullae.

**DESCRIPTION:** Thallus uniaxial, monosiphonous, with a central axis and alternately formed laterals. Primary laterals with distinct basal cells that are isodiametric and only slightly larger than cells of the secondary lateral branches. Short, sparingly branched rhizoidal filaments, composed of small, slender segments, develop from basal cells of primary lateral branches near the base of the thallus. Long, sparingly branched rhizoidal filaments composed of slender segments develop on main axial cells throughout the thallus. Fu-

sions among cells of the lateral branches give the netlike appearance. Cells uninucleate; gland cells absent.

**GENERIC TYPE:** *Callidictyon abyssorum* J. Norris & Abbott (herein).

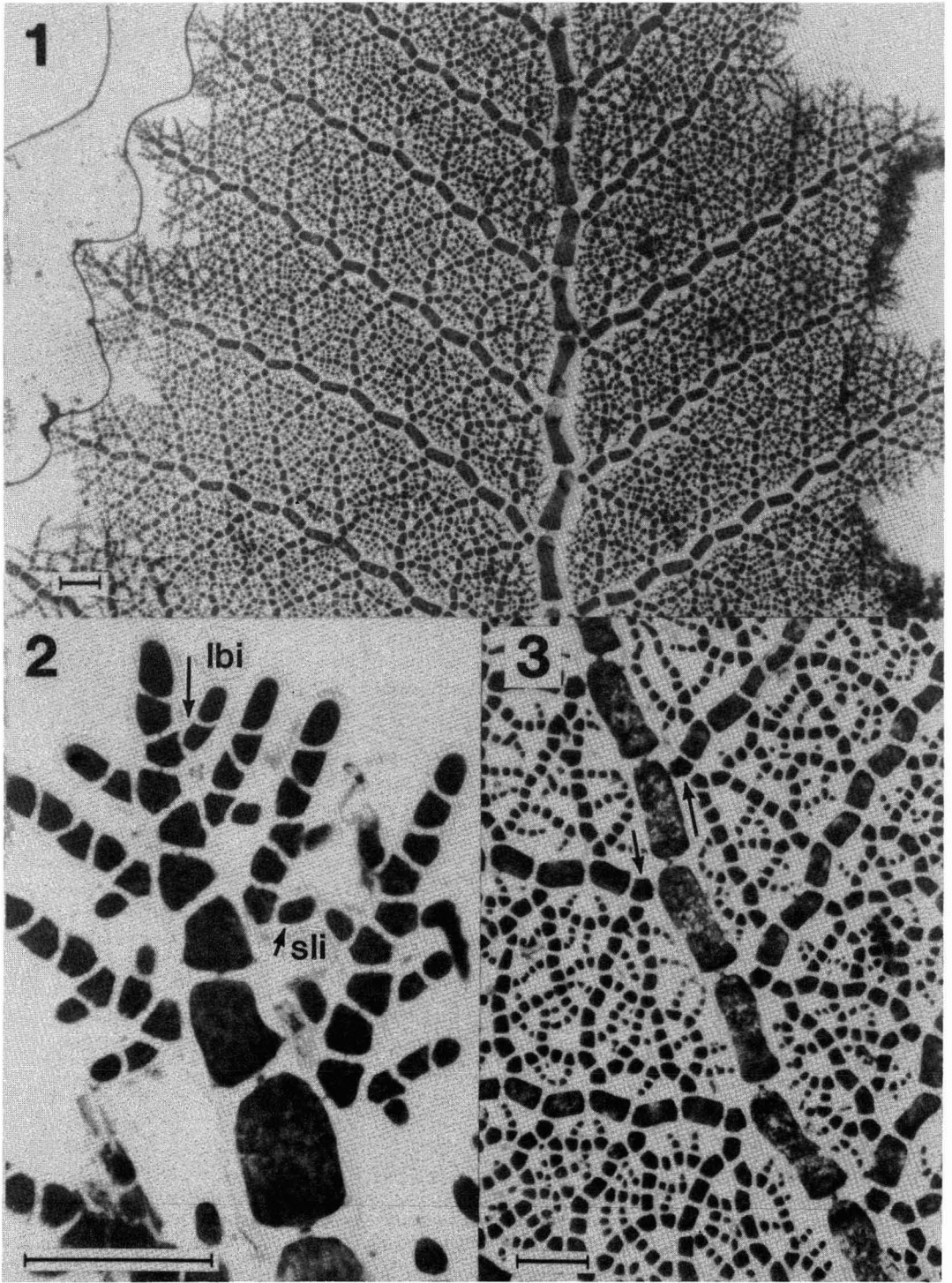
**ETYMOLOGY:** The generic name, *Callidictyon* ("beautiful net"), is neuter and derived from the Greek *callos* ("beauty") and *-dictyon* ("net") (Brown 1956).

*Callidictyon abyssorum* J. Norris & Abbott, sp. nov.

Figures 1–8

Thallus ab axe filamento lateraliter ramosus in apicem indeterminatus in ramosis et ramulis determinatus, marginis in partibus crenatis, cellulis terminalibus secundariis et tertiariis vel ordinis aliis inter ramos saepe anastomosis; cellulis inter ramos et axem aut inter ramos primarios non anastomosis; cellulis axialibus cylindricis in diametro 55–83  $\mu\text{m}$  ( $\bar{x} = 69 \pm 14 \mu\text{m}$ ) et 160–230  $\mu\text{m}$  longis ( $\bar{x} = 195 \pm 35 \mu\text{m}$ ) ( $\bar{x} \pm \text{SD}$ ,  $n = 25$ ); 2.5–3.5 longiores quam latiores; cellulae rhizoidorum ab cellulis basilaribus ramorum elongatae in diametro 10  $\mu\text{m}$  et 160  $\mu\text{m}$  longae. Structurae reproductivae ignotae.

**DESCRIPTION:** Thallus a filamentous network composed of a distinct indeterminate main axis with alternate determinate laterals that branch to three or more orders and fuse to form a monosiphonous net in one plane with crenate margins. Cells uninucleate; apical cells, with blunt apices, divide transversely. Main axial cells of mature thalli cylindrical, 55–83  $\mu\text{m}$  diameter ( $\bar{x} = 69 \pm 14 \mu\text{m}$ ) and 160–230  $\mu\text{m}$  long ( $\bar{x} = 195 \pm 35 \mu\text{m}$ ) ( $\bar{x} \pm \text{SD}$ ,  $n = 25$ ); axial cell 2.5–3.5 times longer than wide. Lateral branches alternately branch at each order of branching. Main axis indeterminate; primary, secondary, and higher orders of lateral branches determinate. Terminal cell of secondary and higher orders of lateral branches fuse here and there with each other to form a net. Anastomoses absent between lateral branches and main axis or primary lateral branches. Two kinds of rhizoidal filaments present: (1) short, branched filaments composed of small cells (ca. 5  $\mu\text{m}$  in diameter and 10  $\mu\text{m}$  long)



that originate from the basal cells of primary lateral branches; and (2) long, branched filaments composed of elongate cells (10  $\mu\text{m}$  in diameter and 160  $\mu\text{m}$  long) that develop from main axial cells. Reproductive structures not found.

**TYPE MATERIAL:** Holotype: *C.R. Agegian-127* (Alg. Coll. #us-162585), Penguin Bank (21° 03' N, 157° 47' W), off northwest end of the island of Moloka'i and to the southeast of the island of O'ahu, Hawai'i, 14 May 1985, NOAA/HURL Research Submersible *Makali'i* dive no. 85-344. Isotypes: BISH, US.

**HABITAT:** Incidental among crustose corallines; attached and growing prostrate on large, loose carbonate boulders scattered over the sand plain at 80 m depth. Temperature was 21°C at 80 m (range 24.8°–19°C between 45 and 100 m, and 17.3°C at 182 m). Salinity was 34.8 ppt vs 35.01 ppt at the surface. Light level at the surface was ca. 70  $\mu\text{Ein m}^{-2} \text{sec}^{-1}$ , with an average light attenuation coefficient  $k$  of 0.052  $\text{m}^{-1}$ ; calculated depth of the euphotic zone at 1% of surface radiation was 85 m.

**DISTRIBUTION:** Penguin Bank, Hawai'i.

**ETYMOLOGY:** The specific epithet, *abyssorum* ("of the depths") is the genitive plural of the Latin *abyssus* ("deep [sea]").

**COMMENTS:** The thallus of the alga is a filamentous network composed of a conspicuous indeterminate main axis and three or more orders of determinate lateral branches (Figure 1). The overall shape of the thallus is a defined, netlike frond formed in one plane, with crenate margins that give the appearance of a ragged edge. The apical cell (ca. 15  $\mu\text{m}$  long with very blunt apices) of the indeterminate axis divides by conspicuous, alternate oblique divisions (Figure 2). The high

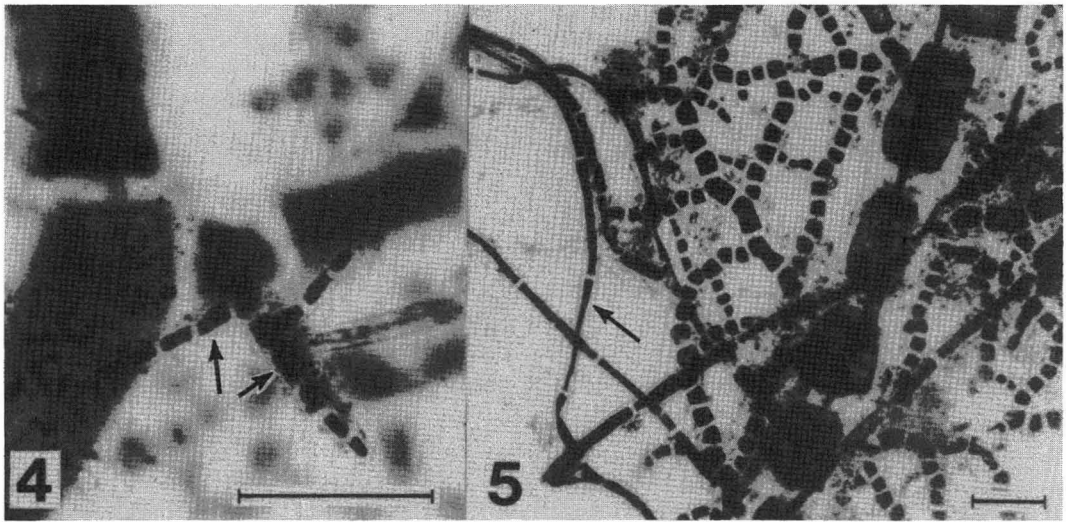
sides of the axial segments are arranged alternately to the right and left. The cells of the axial segments enlarge gradually and when mature are cylindrical, measuring 55–83  $\mu\text{m}$  in diameter ( $\bar{x} = 69 \pm 14 \mu\text{m}$ ), and are 2.5–3.5 times longer, 160–230  $\mu\text{m}$  in length ( $\bar{x} = 195 \pm 35 \mu\text{m}$ ) ( $\bar{x} \pm \text{SD}$ ;  $n = 25$ ).

The initial of a lateral branch, ca. 13  $\mu\text{m}$  long, originates as a protrusion near the apex from one side of an axial cell (Figure 2, arrow). The protrusions always develop on the high side of the axial cell, producing lateral branches that are arranged in an alternate, distichous manner on the axis. Each axial cell produces a single lateral branch, the primary lateral. The basal cell of the primary lateral branch remains small and nearly isodiametric (Figures 1, 3). Other cells in this branch elongate to about twice the length of the basal cell (Figure 3). Basal cell size is only slightly larger than cells of the secondary lateral branches, the first of which develops from this cell. Elongation of the cells of the primary lateral branches follows oblique divisions of a conspicuous apical cell. Regardless of the plane of division of the apical cell, an alternate branching pattern is regular throughout the branch orders.

Two kinds of rhizoidal filaments were observed, both with undifferentiated apices. One type was short, sparingly branched filaments composed of small, slender cells, mostly 5 by 10  $\mu\text{m}$ , which originate from basal cells of the primary lateral branches below the apex (Figure 4). The other was long, sparingly branched filaments composed of elongate cells, ca. 10 by 160  $\mu\text{m}$ , which originate from the main axial cells (Figure 5).

Beginning with the third to fourth lateral branch down from the apex of the main axis, the primary lateral cuts off the secondary lateral initial on the abaxial side of the basal cell (Figure 2, arrows). A second lateral ini-

FIGURES 1–3. *Callidictyon abyssorum* J. Norris & Abbott, sp. nov. 1, The holotype specimen (Alg. Coll. #us-162585) showing the characteristic filamentous network composed of an indeterminate main axis and three or more orders of determinate lateral branches. Scale = 100  $\mu\text{m}$ . 2, The apical cell of the indeterminate main axes divides by alternately oblique divisions, with lateral branch initial (lbi) originating near the apex from one side of an axial cell. The first secondary lateral initial (sli) is cut off near the apex on the abaxial side of the basal cell of a third or fourth primary lateral branch. Scale = 100  $\mu\text{m}$ . 3, The basal cell of the primary lateral branch is nearly isodiametric and remains small (arrow) with other cells of the branch elongating to about twice the length of the basal cell. Scale = 100  $\mu\text{m}$ .



FIGURES 4–5. *Callidictyon abyssorum* J. Norris & Abbott, sp. nov. 4, A short, sparingly branched filament (arrow) composed of small, slender cells, mostly 5 by 10  $\mu\text{m}$ , develops from the basal cells of the primary lateral branches. Scale = 100  $\mu\text{m}$ . 5, Long, sparingly branched filaments (arrow) composed of elongate cells, ca. 10 by 160  $\mu\text{m}$ , develop from the main axial cells. Scale = 100  $\mu\text{m}$ .

tial also forms on the abaxial side but on the third cell of the primary lateral branch. Secondary lateral initials are then added to the abaxial side of a lateral branch again, thus maintaining a regularly alternate branching pattern. Secondary lateral branches grow in length adaxially and abaxially until they meet at a distance about halfway between two axial cells. The apical cells of these secondary laterals fuse, effectively joining primary lateral branches on the same side of the main axis.

Tertiary lateral branches are produced alternately by transverse divisions and fuse with intercalary cells of secondary lateral branches as well as apical or intercalary cells of other tertiary lateral branches. Secondary and tertiary lateral branches were never observed fusing to cells on primary laterals or the main axis (Figure 6). The division patterns are sometimes variable in tertiary and higher-order lateral branchlets and eventually obscure their branching pattern, forming an intricate network of filaments.

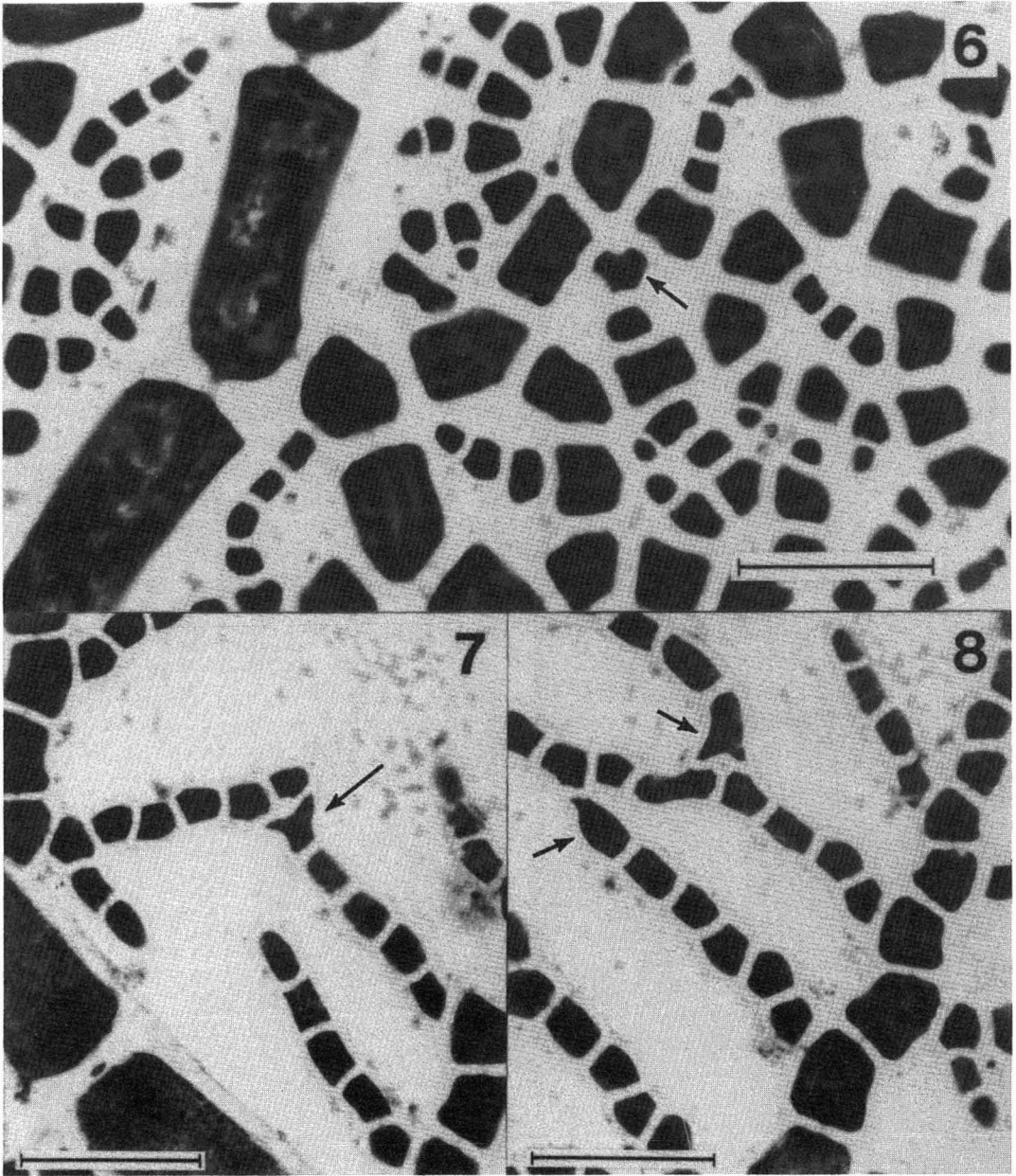
Two variations of cellular fusions were observed. Nodal fusions occur when an apical cell (contact cell) approaches and subse-

quently fuses with two intercalary cells (host cells) straddling the node (Figures 7, 8). Internodal fusions occur between two contact cells or between a contact cell and a host cell in a lateral filament (Figure 8). Secondary pit connections were formed in both fusion types. The contact cell in a nodal fusion formed two pit connections, one with each of the host cells.

In both of these variations the contact cell becomes distorted in shape. In an internodal fusion, the contact cell enlarges, becoming drawn out with a bulbous end that flattens upon contact. Occasionally, a large cell is formed from the fusion between two contact cells. This suggests that a fusion of the cell wall and intercytoplasmic exchange may occur. However, the latter events as well as the formation of a synapse have not been confirmed in *Callidictyon*.

#### DISCUSSION

In the absence of any reproductive structures, our placement of the new genus in the Ceramiaceae is based solely on its resem-



FIGURES 6-8. *Callidictyon abyssorum* J. Norris & Abbott, sp. nov. 6, Tertiary lateral branches are produced alternately by transverse divisions and fuse with intercalary cells of secondary lateral as well as apical or intercalary cells of other tertiary lateral branches (arrow). Scale = 100  $\mu$ m. 7, Two variations of cellular fusions. Nodal fusions of an apical contact cell (arrow) fused with two intercalary host cells straddling the node (seen also in Figure 8). Scale = 100  $\mu$ m. 8, Internodal fusions between a contact cell and a host cell in a lateral filament (arrows). Scale = 100  $\mu$ m.

blance to the vegetative structure of some members of the family. Further, based on vegetative characters *Callidictyon* cannot be satisfactorily assigned to any of the tribes in the Ceramiaceae (see Itono 1977). In fact, *Callidictyon* shows some of the features found in three of the tribes, the Antithamnieae Hommersand, Callithamnieae (Kützing) Schmitz, and Compsothamnieae Schmitz.

The alternate branching pattern and blunt apices of *Callidictyon* strongly resemble *Callithamnion*/*Aglaothamnion*-like plants with profuse secondary and tertiary alternate lateral branching. Alternate branching is a common feature of genera in the tribes Callithamnieae and Compsothamnieae, but is rare in the Antithamnieae and restricted to secondary lateral branches.

The prostrate habit and distinct basal cell on each primary lateral branch suggests an association with the Antithamnieae sensu Wollaston (1968). Determinate lateral branches and rhizoidal filaments are produced from the basal cell of *Callidictyon*. However, some members of both the Callithamnieae and Compsothamnieae have been described wherein the basal cells of primary lateral branches are distinct, either in shape or size, or both (e.g., *Callithamnion biseriatum* Kylin [1925], *Pleonosporium vancouverianum* [J. Agardh] J. Agardh [Abbott and Hollenberg 1976], and *Pleonosporium abyssicola* Dawson [1962]). The formation of simple, branched or unbranched rhizoidal processes (i.e., *Pleonosporium* sensu Itono 1971) is characteristic of the Compsothamnieae [note: Gordon-Mills and Wollaston (1990) suggested that *Pleonosporium* should be removed from this tribe and probably placed in the Spongoclonieae].

The form and position on thalli of gland cells are useful generic criteria of the Antithamnieae (Wollaston 1968). Gland cells are rarely seen in the other tribes of the Ceramiaceae, however, and are totally absent in *Callidictyon*.

An apparently uninucleate condition and the nature of cell fusions are confounding characteristics that make it difficult to further speculate on the taxonomic affinities of *Callidictyon* in the Ceramiaceae. Uninucleate cells are found throughout the members of

the Antithamnieae. However, they are also reported in only two genera of the Callithamnieae, *Aglaothamnion* Feldmann-Mazoyer (1941) and *Seirospora* Harvey (1846) (see also L'Hardy-Halos and Maggs 1991). All other genera in the Callithamnieae and those of the Compsothamnieae are multinucleate. Though Dixon and Price (1981) considered *Aglaothamnion* a taxonomic synonym of *Callithamnion* Lyngbye (1819), L'Hardy-Halos and Rueness (1990) and L'Hardy-Halos and Maggs (1991) more recently concluded that the nuclear condition is a valid generic character to separate the uninucleate *Aglaothamnion* from the multinucleate *Callithamnion*.

Previously described algae in the Ceramiaceae that form anastomoses are from the tribe Compsothamnieae and thus multinucleate. Anastomoses have been described for species of *Pleonosporium*, *Bornetia*, and *Griffithsia* (see L'Hardy-Halos 1969) and *Rhododictyon* (Taylor 1961), as well as the distinctive network of *Haloplegma* (see Børgesen 1919). *Rhododictyon* (Taylor 1961, Schneider 1975) forms a net from the anastomosing of a regular series of alternate lateral branches radiating near the outer margin, thus differing from *Callidictyon* in manner of branching pattern and net formation.

L'Hardy-Halos (1969) described fusion of indeterminate branches in *Pleonosporium* as a flattening of the encroaching contact cell, fusion of the contact cell with a host cell through the fusion of the cell wall to form an intermediate cell, and cell wall constriction into a partition resulting in a fusion cell.

The fusion of two apical cells or an apical cell with secondary or tertiary branch cell in *Callidictyon* (Figures 7–8) is similar to that described for *Pleonosporium* in that the apices of the approaching cell flatten in the process of contacting the other cell. It seems that a nuclear division would be required in an anastomosing uninucleated alga, an event that is not reported in the previously described genera. However, the details of this process require further elucidation.

*Callidictyon* and *Delesseriopsis* are similar in that both have uninucleate cells and form filamentous thalli. Vegetative features that distinguish *Delesseriopsis* from other genera

of the Ceramiaceae include (1) its erect and secondarily derived prostrate axes; (2) rhizoidal cortications of indeterminate axes; and (3) gland cells that are unique in position and form. However, although the reproductive morphology of *Delesseriopsis* suggests a close relationship to the Antithamnieae, its opposite branching pattern, presence of gland cells, and apparent absence of secondary pit connections suggest an even greater distinction from *Callidictyon* and the Antithamnieae.

The vegetative structure of *C. abyssorum* is characterized by a regularly alternate branching pattern, blunt apices, formation of anastomoses, and two kinds of rhizoidal filaments, all features represented in the Compsothamnieae. Elucidation of the process of formation of the anastomoses in this un-nucleated genus along with the finding and description of its reproductive structures are necessary to define the affinities of *Callidictyon* and resolve its tentative placement within the Ceramiaceae.

*Callidictyon* is the third net-forming red alga to be described from deep water. Two were described from dredged specimens, *Rhododictyon* (Taylor 1961) from 46–92 m depths in the tropical western Atlantic, and *Mortensenia* (Weber-van Bosse 1926) from 50 m in the tropical western Pacific.

In Hawai'i, Doty et al. (1974) reported 4 green, 5 brown, and 4 red algal species dredged from 70–164.6 m depths. From submersible collections on Penguin Bank, Agegian and Abbott (1986) reported 54 species of algae (15 greens, 7 browns, and 2 reds) beyond 55 m depths, with 11 of them occurring below 100 m. Most *Makali'i* algal collections from Penguin Bank were between 45 and 70 m. Occurring at 80 m depth, *C. abyssorum* was deeper than most of the deep-water algae, though crustose corallines were found from 50 to 182 m and species of *Codium* were abundant between 90 and 125 m. Among the Hawaiian deep-water (> 50 m) red algae are recently discovered species, such as *Ptilocladia yuenii* Abbott from 7 to 15 m and possibly from 75 to 90 m (Abbott and Norris 1993), and a new species of *Micropeuce* from 72 m.

Although not approaching the depth record for living benthic macrophytes, discovered

using a submersible at 268 m off San Salvador Island, Bahamas (Littler et al. 1985), *Callidictyon abyssorum* indicates that further deep-water exploration in the tropical Pacific may yield many interesting species. Submersibles give biologists access to greater depths, allow direct observation and collection, and will provide new data on the ecology and distribution of deep-water algae.

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