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Morphological study of *Ceramium clarionense* (Ceramiaceae, Rhodophyta) in the Atlantic Ocean

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Abstract – *Ceramium clarionense* Setchell *et* Gardner is a typical member of the genus characterized by having barrel-shaped axial cells incompletely covered by cortical cells and by pseudodichotomous branching. The apices are slightly incurved, causing a forcipate appearance of the branch tips. The axial cells cut off seven to eight periaxial cells, each one laterally producing a pseudoperiaxial cell. The cortication is formed by the development of cells originating from both periaxial and pseudoperiaxial cells. The pattern of cortication of the nodes, considering the number of periaxial cells, presence of pseudoperiaxial cells and its derivatives, is the main taxonomic characteristic of this species and differentiates it from all related species.

Brazil / *Ceramium clarionense* / Ceramiaceae / Rhodophyta / taxonomy

Résumé – Etude morphologique de *Ceramium clarionense* (Ceramiaceae, Rhodophyta) dans l'Océan atlantique. *Ceramium clarionense* Setchell *et* Gardner est un membre typique du genre qui se caractérise végétativement par un axe de cellules cylindriques couvert partiellement par des cellules corticales et par une ramification pseudodichotomique. Les extrémités du thalle sont légèrement incurvées donnant un aspect de forceps. La cellule axiale est divisée en huit cellules périaxiales et chaque cellule produit latéralement une cellule pseudopériaxiale. La cortication est formée par le développement des cellules périaxiales et pseudopériaxiales. Le modèle de la cortication des nœuds, c'est-à-dire le nombre de cellules périaxiales, la présence de cellules pseudopériaxiales et de leurs dérivées, est la principale caractéristique de cette espèce et la différentie des espèces proches.

Brésil / *Ceramium clarionense* / Ceramiaceae / Rhodophyta / taxonomie

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INTRODUCTION

Ceramium Roth is a large genus of marine red algae with about 191 species recorded worldwide (Boo & Lee, 1994; Lewis & Mei-Lan, 1996). The genus is common in the intertidal as well as subtidal, either growing as luxuriant tufts or epiphytic on various macroalgae. *Ceramium* is readily recognized by its monosiphonous branched thalli with periaxial cells producing corticating filaments covering the axial cells only at the nodes or completely through the thallus. Subdichotomous branching with forcipate apices is the more common habit, although other kinds of branching and apices also occur.

Species of the genus *Ceramium* are morphologically variable (Meneses, 1992). The most important diagnostic feature in the genus is the pattern of development of the corticating filaments allied to the presence or absence of pseudoperiaxial cells (Dixon, 1960; Womersley, 1978; Cribb, 1983; Millar, 1990; Barreto & Yoneshigue-Valentin, 2001). The dimensions of the filaments, the branching pattern, and the arrangement of the tetrasporangia are also considered important in distinguishing species. Gametangial structures have limited value in delimiting species (Womersley, 1978 & Maggs & Hommersand, 1993).

In Brazil, 15 taxa of *Ceramium* are reported (Horta *et al.*, 2001; Barreto & YoneshigueValentin, 2001 & Fujii *et al.*, 2001). The cortex development in these taxa is restricted to the nodes except in *C. nitens* (C. Agardh) J. Agardh (Fujii *et al.*, 2001) and *C. rubrum* (Hudson) C. Agardh (Williams & Blomquist, 1947), which have cortication extended through the thallus. The taxa with an incomplete cortex development can be grouped by the number of cortical initials per periaxial cell (Lewis & Mei-Lan, 1996) and the presence of pseudoperiaxial cells that cut off laterally from the periaxial cell.

Among the *Ceramium* species recorded hitherto from Brazil, only *C. tenerrimum* (Martens) Okamura and *C. brevizonatum* Petersen var. *caraibicum* Petersen *et* Børgesen have pseudoperiaxial cells. In this paper, we present a detailed account of the cortical development of a morphologically variable species, *C. clarionense* Setchell *et* Gardner.

Many authors have commented on the difficulties in delimitation of *Ceramium clarionense*. Dawson (1954) and Abbott (1999) discussed its resemblance with *Ceramium aduncum* Nakamura and *C. mazatlanense* Dawson and its close similarity of the vegetative thallus with *C. marshallense* Dawson (Cribb, 1983; South & Skelton, 2000). Abbott (1999) regards *C. marshallense* as a synonym of *C. clarionense*, however specimens of *C. marshallense* collected from Fiji and Samoa Islands are different from the Hawaian samples (South & Skelton, 2000).

Ceramium clarionense was originally described by Setchell & Gardner (1930) from Clarion Island, Revillagigedo Archipelago, in the Mexican Pacific Ocean. This species has to date been reported under this name only from the Pacific Ocean and Indian Ocean. Some authors misidentified this species under different names as *C. brevizonatum* var. *caraibicum* from the Caribbean region (Littler & Littler, 2000) and *C. brasiliense* from Santa Catarina State in Brazil (Cordeiro-Marino, 1978).

MATERIALS AND METHODS

Specimens were collected in various localities of the states of Espírito Santo, Rio de Janeiro and São Paulo (Fig. 1). Morphological studies are based on samples preserved in 4% Formalin seawater solution. Transverse sections for anatomical observation were hand-cut by a razor-blade. All observations were made by stereo and optical microscope from material stained with 1% aqueous aniline blue acidified with diluted HCl 1N. Line drawings were made with the aid of a camera lucida attached to a Zeiss Universal light microscope. Our collections were compared with the holotype of *Ceramium marshallense* Dawson (BISH). All algal material used in this study is deposited in the herbarium of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (RB), Rio de Janeiro, Brazil, and herbarium of the Instituto de Botânica (SP), São Paulo, Brazil.

RESULTS

***Ceramium clarionense* Setchell *et* Gardner** (1930, 19:170, pl. 7, figs 25-27)
= *C. marshallense* Dawson (1957, 11:120-121 figs 27 a-b).

Thalli 5-15 mm high, consisting of turfs or irregularly shaped tufts of one to several erect axes; attached by multicellular rhizoidal filaments, 10-54 µm in diameter and 120-640 µm long; nodes 80-286 µm in diameter and 70-106 µm high; internodes 134-256 µm in diameter and 40-130 µm high in lower parts (Figs 2, 5-6).

Main axes with forcipate to strongly involute apices; branching pseudodichotomous at intervals of 7-13 segments; adventitious branches frequent in young and old axes; nodes 140-250 µm in diameter and 48-90 µm high; internodes 130-220 µm in diameter and 40-160 µm high between the fourth and the fifth dichotomy (Figs 2-4).

The apical cell **(ap)** divides by means of a concavo-convex septum, resulting in the axial cell **(ax)**. An oblique division of the axial cell results in the first periaxial cell (**p**), always placed towards the outside of the forcipate apex. The axial cell divides in an alternating sequence forming 7-8 periaxial cells. Each of the them gives rise to 2 acropetal cells $\mathbf{a}^{1}$ and $\mathbf{a}^{2}$, then they cut off a single pseudoperiaxial cell laterally **(ps)** which interposes between the periaxial cells thus producing a ring of 14-16 cells. Each acropetal cell gives rise to 2 acropetal daughter cells $\mathbf{a}^{1.1}$, $\mathbf{a}^{1.2}$, $\mathbf{a}^{2.1}$ and $\mathbf{a}^{2.2}$. The pseudoperiaxial cells also cut off acropetally a cell $\mathbf{aps}^{1}$ and divides again to produce $\mathbf{aps}^{1.1}$. Finally the periaxial cell gives rise to 2 basipetal cells $\mathbf{b}_{1}$ and $\mathbf{b}_{2}$. Those cells sometimes give rise to 2 basipetal daughter cells $\mathbf{b}_{1.1}$, $\mathbf{b}_{1.2}$, $\mathbf{b}_{2.1}$ and $\mathbf{b}_{2.2}$. Each pseudoperiaxial cell gives rise to a single pseudobasipetal cell $\mathbf{bps}_{1}$. The cortical band, thus, consists of 2 rows of acropetal long cells, 6-22 µm high, one median row of longer cells 22-44 µm high and 1-2 rows of basipetal cells, 16-26 µm high (Figs 4-5, 7-8).

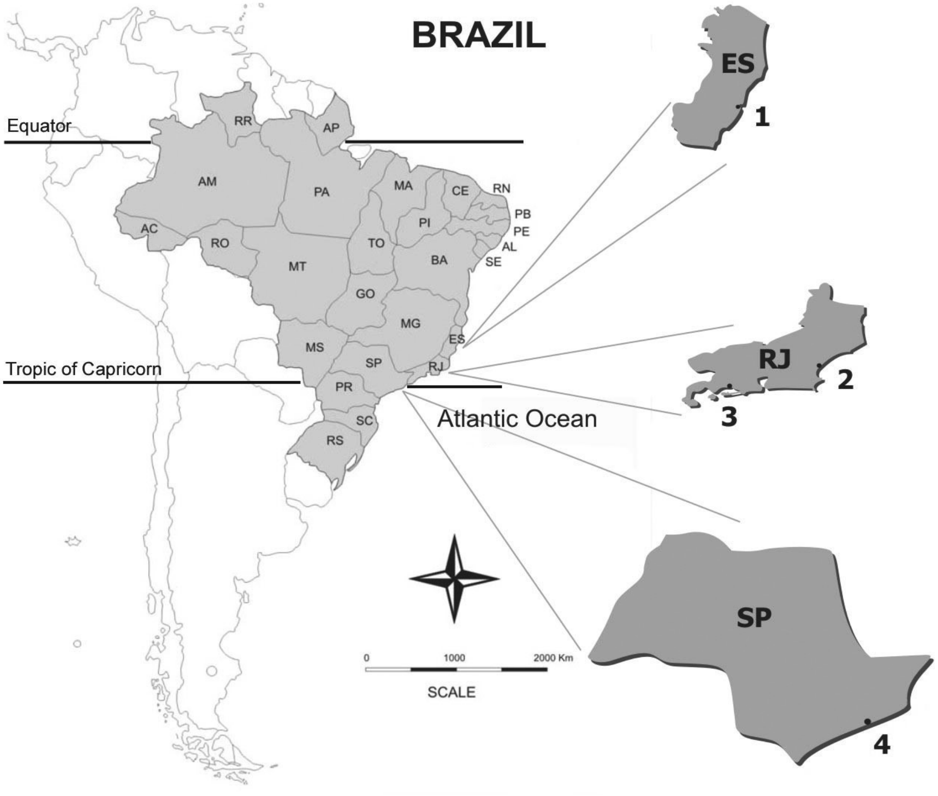


Fig. 1. Sampling sites: **1.** Frade Island and Boi Island, Vitória, ES; **2.** Rasa Beach, Armação dos Búzios, RJ; **3.** Grande Beach and Kutuka Beach, Sepetiba Bay, RJ; **4.** Laje de Santos, Santos, SP.

Tetrasporangia are borne singly or in whorls of 3 in subapical segments or in adventitious branches, on the abaxial side of the nodes, protruding laterally and being partially covered by corticating cells, spherical to ellipsoidal, 44-90 µm high. The tetrasporangia are tetrahedrally divided (Figs 9-14). Despite extensive collections, reproductive thalli bearing cystocarps or spermatangia were not found.

Habitat: Turf collected at the intertidal zone and at the infralittoral growing on rocks, next to *Ceramium brevizonatum* H. Petersen var. *caraibicum* H. Petersen *et* Børgesen and *C. tenerrimum* (Martens) Okamura, as well as on other algae. Tetrasporangial plants were collected in the summer, winter and spring time.

Representative specimens examined: Brazil, Rio de Janeiro, Rasa Beach, 24.i.1994 (RB 313.338) and 04.xi.1994 (RB 313.367); Rio de Janeiro, Itacuruça Island, Grande Beach, 28.vi.1994 (RB 313.374); Rio de Janeiro, Marambaia Island, Kutuca Beach 06.iv.1999 (RB 340390, RB 340391). São Paulo, Santos, Laje de Santos, 20.x.2001 (SP 355928). Espírito Santo, Vitória, Ilha do Frade, 18.v.1999 (SP 356107).

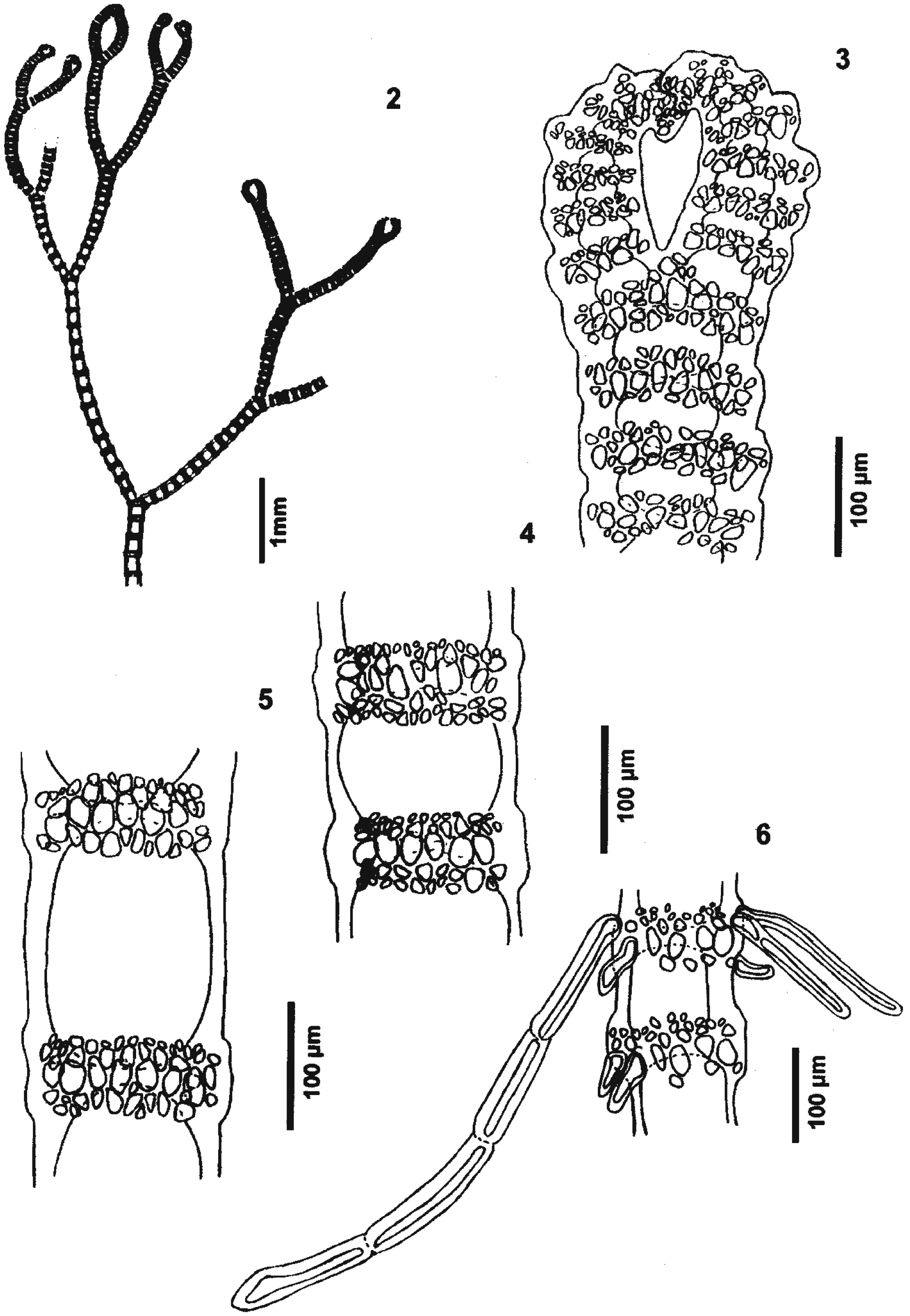
DISCUSSION

The main taxonomic characteristics of *Ceramium* are the branching pattern, tetrasporangial features and the pattern of cortication of the nodes, in particular the number of periaxial cells and their derivatives. A relevant feature of some species is the production of pseudoperiaxial cells originating from lateral divisions of the periaxial cells (Womersley, 1998; Abbott, 1999; Cho *et al.*, 2002). *Ceramium australe* Sonder, *C. borneense* Weber-van Bosse, *C. brevizonatum* var. *caraibicum, C. hamatispinun* Dawson, *C. macilentum* J. Agardh, *C. mazatlanense* Dawson, *C. recticortum* Dawson, *C. shepherdii* Womersley and *C. tenerrimum* share with *C. clarionense* the presence of pseudoperiaxial cells. In the specimens studied, the periaxial cells, which cut off 2 acropetal and 2 basipetal cells, also divide laterally, forming pseudoperiaxial cells that interpose between the periaxial cells. The pseudoperiaxial cells also cut off cells acropetally and basipetally, contributing to the cortex.

Ceramium clarionense differs from *C. hamatispinun* and *C. shepherdii* by the absence of spines or filaments growing from the nodes, which are characteristic of both species. *Ceramium hamatispinun* produces acute, recurved spines of 2-5 cells from the true acropetal cells while *C. shepherdii* forms short filaments of 3-6 cells from either the true acropetal cells, rarely from the periaxial cells and sometimes from the pseudoperiaxial cells and their acropetal cells. *Ceramium borneense, C. mazatlanense* and *C. recticortum* have fewer periaxial cells (4-5) than *C. clarionense*. *Ceramium macilentum* lacks basipetal cells formed from pseudoperiaxial cells and produces one periaxial cell less than *C. clarionense*. *Ceramium clarionense* can be distinguished from *C. australe* by forming only one pseudoperiaxial cell per periaxial cell and by cutting off acropetal and basipetal cells. *Ceramium australe*, on the other hand, is characterized by 2 pseudoperiaxial cells on each side of the periaxial cell and the periaxial cell itself forming only acropetal filaments. *Ceramium brevizonatum* var. *caraibicum* and *C. tenerrimum* differ from *C. clarionense* by the lack of basipetal cortical filaments and the absence of acropetal cells produced from the pseudoperiaxial cells (Table 1). *Ceramium aduncum* Nakamura from Hawaii (Abbott, 1999) and *C. marshallense* from Fiji, Samoa Islands and the Great Barrier Reef (Price & Scott, 1992; South & Skelton, 2000) resemble *C. clarionense* in their general habit, size and branching pattern, but can be distinguished from the latter by the lack of pseudoperiaxial cells.

Our studies, including verification of literature reports and herbarium material, have shown that specimens collected from Brazil are referable to *C. clarionense*. However, the Brazilian and Hawaiian plants differ in a number of respects. The Brazilian specimens are characterized by each periaxial cell producing two acropetal cells, and the pseudoperiaxial cell forming only one acropetal cell, while in the Hawaiian material the periaxial cell produces only one acropetal cell, and the pseudoperiaxial cell forms two acropetal cells. Abbott (1999) describes tetrasporangia as cruciately divided in *C. clarionense* from Hawaii while they are tetrahedrally divided in Brazilian specimens as showed in figure 27 of the original description of Setchell & Gardner (1930).

In the Brazilian specimens of *C. clarionense*, only tetrasporophytes were observed. Gametophytes of this species are described by Setchell & Gardner (1930), Abbott & Hollemberg (1976) and Abbott (1999), with spermatangia forming in continuous, colourless clusters at nodes, 1.5 µm in diameter, and cystocarps with 2-3 gonimolobes in subterminal axils of branches, surrounded by 6 sterile branches.



Figs 2-6. *Ceramium clarionense* Setchell *et* Gardner. **2.** Habit of vegetative plant. **3.** Apical part of the branch. **4.** Nodal cortication. **5.** Nodal cortication of basal portion. **6.** Rhizoidal part.

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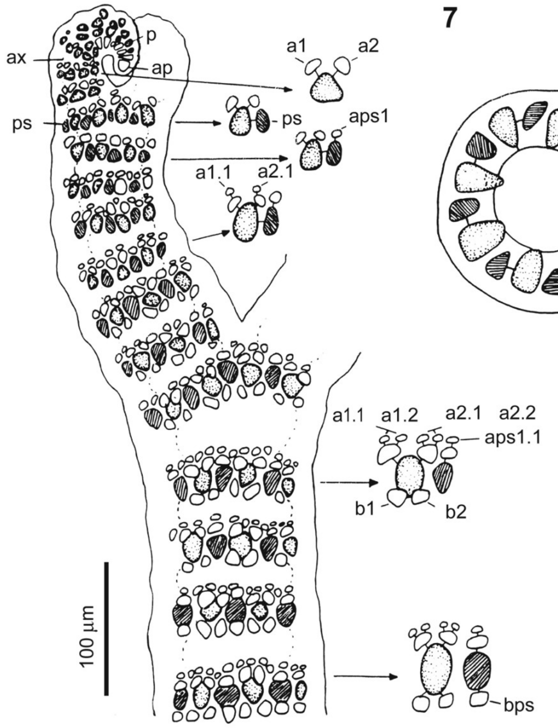

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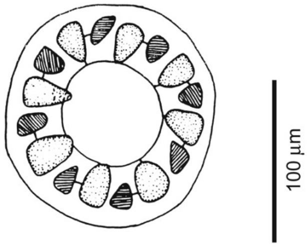

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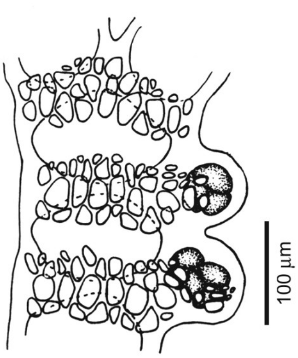

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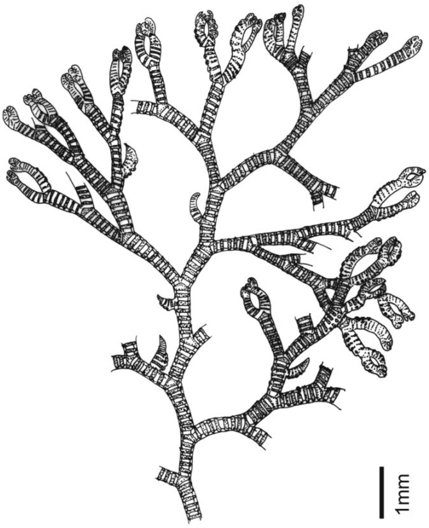
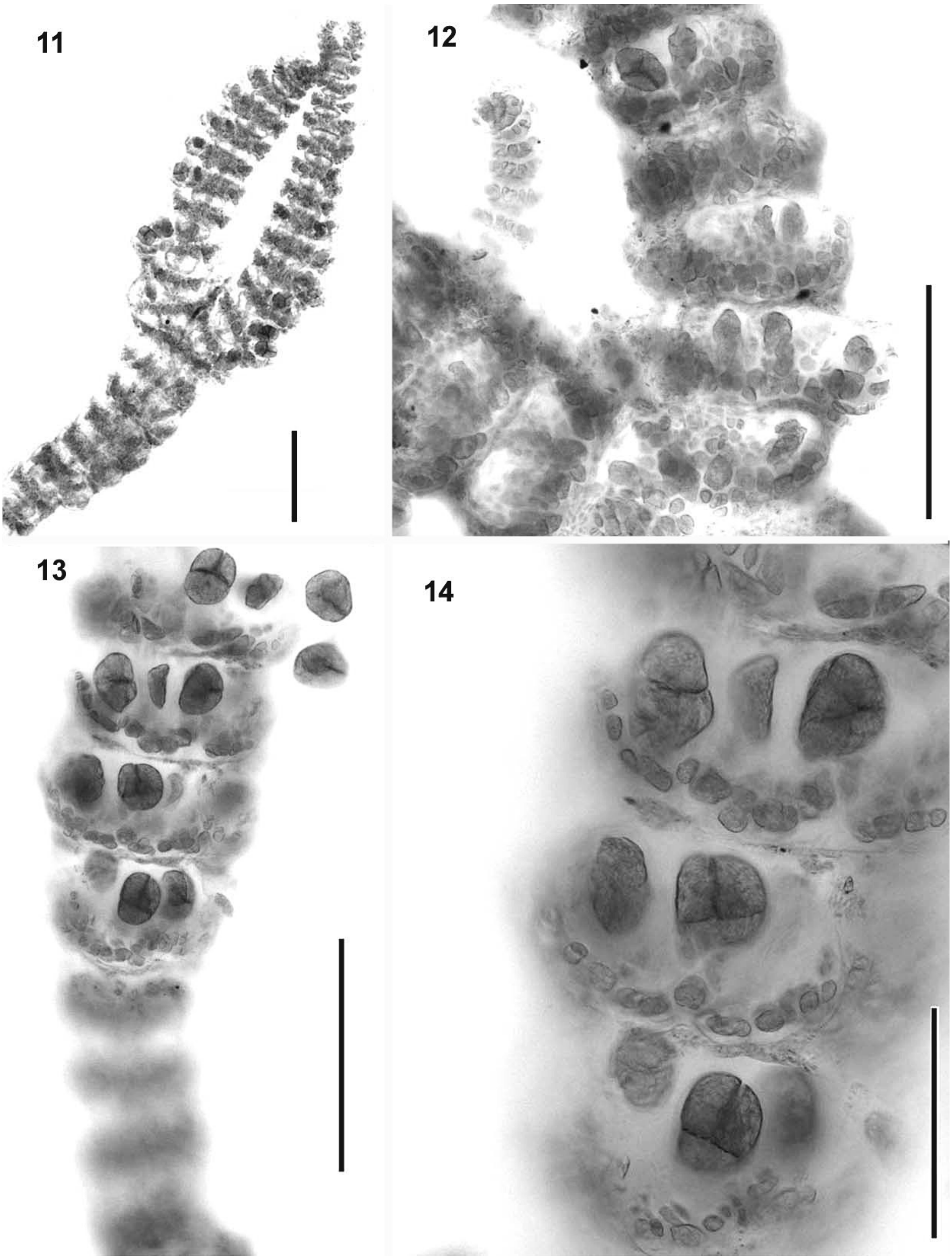


Figs 7-10. *Ceramium clarionense* Setchell *et* Gardner. **7.** Nodal development showing apicl cell (ap), periaxial cells (p), axial cell (ax), pseudoperiaxial cells (ps), acropetal cells (a), basipetal cells (b), pseudoacropetal cells (aps), and pseudobasipetal cells (bps). **8.** Cross section of the node showing periaxial and pseudoperiaxial cells. **9.** Tetrasporangial thallus with unilaterally arranged tetrasporangia. **10.** Tetrasporangia arranged tetrahedrically.



Figs 11-14. *Ceramium clarionense* Setchell *et* Gardner. **11.** Apical branch showing unilaterally tetrasporangia. Scale = 20 µm. **12.** Branches showing tetrasporangia in a whorl at each node. Scale = 20 µm. **13.** Apical portion showing a whorl of tetrasporangia. Scale = 20 µm. **14.** Tetrahedally arranged tetrasporangia. Scale = 10 µm.

Table 1. Characteristics of *Ceramium clarionense* and related species.

Taxa	*Cortical cell rows*	*No. of periaxial cells*	*No. of acropetal/ periaxial cells*	*No. of basipetal/ periaxial cells*	*No. of pseudoperiaxial cells*	*No. of acropetal/ pseudo periaxial cells*	*No. of basipetal/ pseudoperiaxial cells*	*Geographic Distribution*	*References*
C. australe	5-7	6-7	1	–	12-14	1	1	Western Pacific, Indian	Womersley, 1978, 1998
C. borneense	3-4	5	1	2-3	5	2	1	Pacific	Abbott, 1999
C. brevizonatum var. *caraibicum*	2-3	8-9	2	–	10-11	–	1 (occasionally)	Atlantic, Pacific, Indian	Barreto & Yoneshigue-Valentin, 2001
C. hamatispinum	3-5	6-7	1	2	6-7 (sometimes lack)	2	1	Pacific	Dawson, 1950; Abbott, 1999
C. macilentum	2-3	6	1-2	(occasionally)	5-6	1-2	–	Western Pacific, Indian	Womersley, 1978, 1998
C. mazatlanense	2-3	5	1	–	5	1	1	Pacific	Dawson, 1950, 1954; Jaasund, 1970; Itono, 1972; Abbott, 1999
C. recticorticum	4-5	4-5	1	1	4-6	1	1	Pacific, Indian	Dawson, 1950; Cho *et al.*, 2002
C. shepherdii	2	6	1	–	5-9 (rarely none)	1	–	Western Pacific, Indian	Womersley, 1978, 1998
C. tenerrimum	3-4	7-8	2	–	7-8	–	1	Atlantic, Pacific, Indian	Barreto & Yoneshigue-Valentin, 2001
C. clarionense	3-5	7-8	1-2	2	7-8	1-2	1-2	Atlantic, Pacific, Indian	Setchell & Gardner, 1930; Abbott, 1999; this study

Ceramium brevizonatum var. *caraibicum* and *C. tenerrimum* have a wide geographical distribution, being reported from all tropical oceans. All the other species with pseudoperiaxial cells have been reported only from the Pacific and Indian Ocean (Table 1). Up to now, species under the name *C. clarionense* had only been found in the Indo-Pacific: USA and Mexico (Dawson, 1950, 1957); Costa Rica (Dawson, 1957); Hawaiian Islands (Abbott, 1999); Marshall Islands (Dawson, 1956, 1957); Fiji and Samoa Islands (South & Skelton, 2000); Vietnam (Dawson, 1954); Philippines (Silva *et al.*, 1987), Australia (Cribb, 1983; Millar & Kraft, 1993); Maldives Islands (Wynne, 1993; Silva *et al.*, 1996) and Seychelles Islands (Silva *et al.*, 1996). The record from Japan (Itono, 1972) was later regarded as uncertain because of the lack of reproductive organs (Itono, 1977).

The morphology of *C. clarionense* is strongly affected by growing conditions and by sexual stages (Meneses, 1992). This susceptibility of morphological characters changeability often led to misidentification of this species. In Brazil, some records of this species were found under the name *C. brasiliense* Joly (e.g. Cordeiro-Marino, 1978, p. 202, figs 225, 228; and the exsiccate SPF3451 from São Paulo State). Also *C. brevizonatum* var. *caraibicum* from the Caribbean region seems to be referable to *C. clarionense*, based on the description and illustrations of Littler & Littler (2000, p. 146-147, figs 1-3).

The detailed study of this taxon corroborates the presence of *C. clarionense* in the Atlantic Ocean.

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