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# Southern Australian Species of *Ceramium* Roth (Rhodophyta)

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#### Abstract

Fifteen species of *Ceramium* are recognized from the coast of southern Australia, and their distribution and ecology are outlined. Two species (*C. rubrum* and *C. flaccidum*) are of widespread distribution in other parts of the world, but the remaining species appear to be largely confined to southern Australia.

The species are separated mainly on the development of the nodal cortication from the ring of periaxial cells at the upper end of each axial cell; other useful taxonomic features are the dimensions of the filaments, the branching pattern, and the arrangement of the tetrasporangia.

The pattern of cortical development at the nodes is usually readily followed after aniline blue staining and mounting in corn syrup, since slight contraction of the cells in this process renders the pit-connections visible. Each periaxial cell typically cuts off two cells both acropetally and basipetally and in most species these branch further in a similar pattern; in some species three cells may occasionally be cut off, and in one species (*C. flaccidum*) only one cell is cut off basipetally. In a few species no cells (or only odd ones) are cut off basipetally, and in many species cortical development is greater acropetally than basipetally. The margin of the nodal cortication (whether straight through synchronous cell development or irregular) may be characteristic of certain species.

A variation giving a distinctive pattern in a few species is where the periaxial cells cut off one or two pseudoperiaxial cells which interpose in the periaxial ring (e.g. *C. shepherdii*, *C. australe* and *C. macilentum*).

In many species the cortical development is limited and soon reaches a stage which is then consistent throughout the thallus. In some species (e.g. *C. tasmanicum*) an extending cortex later develops which may largely or completely close the internodal space; in fully corticated species (*C. rubrum* and *C. pusillum*) the cortex extends from an early stage and maintains complete cover of the axial cell. Heavily corticated species usually have an outer cortex of small cells lying outside the larger inner cortical cells. Gland cells may be characteristic of certain species but are usually variable in frequency and not always present.

The nature of the branch apices, while characteristic in some species, depends on the activity of the apical growth. Carposporophytes and spermatangial plants provide little help in taxonomic distinctions.

The European species *C. gracillimum* sensu Harvey is now recognized as a very widely distributed species distinct from *C. gracillimum* Kuetzing. The oldest name is apparently *C. flaccidum* (Kuetzing) Ardissone, for which there are many synonyms. It is characterized by the formation of only a single cell basipetally from each of the periaxial cells and also by having unicellular rhizoids; the single basipetal cell may produce one or two further cells and commonly itself divides into 2–4 cells.

# Introduction

*Ceramium* Roth is a large genus with most coasts of the world having a few to many species; in very few places is *Ceramium* absent. Most of the species are small,

delicate plants, and in few published floras are the species well defined so that determinations can be made with confidence. Many of the species are regarded as variable and in some (e.g. *C. rubrum*) several varieties or forms have been described. The variation appears to be greater in areas of reduced salinity, such as the Baltic.

The widespread distribution and common occurrence of *Ceramium* results in some species being involved in nearly all ecological or environmental surveys, ranging from the lower intertidal and uppermost subtidal (where many species occur) to deep water. In many such accounts the species are not determined or the name used is doubtful, thus reducing the value of the work. This has certainly been true in accounts of southern Australian algae.

Dixon (1960*a*) discussed the taxonomic history of *Ceramium*, and gave a comprehensive account of the developmental morphology and reproduction of the genus, whilst Hommersand (1963) has described several species in detail. The following account of the generic features is given to assist understanding of the southern Australian species, some of which show features differing from the general statements of Dixon. In studying species of *Ceramium*, it is highly desirable to work with well preserved liquid material; dried specimens often do not show the cortical cell lineages and other features clearly.

The most important diagnostic feature in *Ceramium* is the pattern of cortical cell development from the periaxial cells (pericentral cells of most authors). The pitconnections between the cells must be observed and figured in face view; even when pit-connections are indistinct, the shape of adjacent cells often indicates their origin. Secondary pit-connections are generally absent in the genus. Since the excellent illustrations of Cramer (1864) which show clearly the pit-connections and cortical cell lineages in his *Herpoceras australe*, virtually no accounts of the species of *Ceramium* show adequately the pit-connections, and hence the pattern of the cortical development, until Dixon (1960a, 1960b), Hommersand (1963), and Simons (1966) who shows them in sectional view of the nodes, and recently Itono (1977). In fresh material, the cell lineages are not readily seen. However, in material stained in aniline blue, acidified, and mounted in corn (karo) syrup, the cells both shrink slightly (mainly due to the acid) thereby showing the pit-connections more clearly, and also the cortical cells tend to lie more in one layer (apart from outer cortical cells). The following descriptions and illustrations are based on material processed in this way.

Since nearly all previous descriptions of species of *Ceramium* do not show adequately the cortical pattern, comparisons of southern Australian species with those described from elsewhere are difficult. While most southern Australian species appear to be distinct from northern hemisphere species, a more thorough analysis of the latter may show that some names are synonyms.

Very few southern Australian specimens have been seen which do not agree with one of the species described below. Two collections, however, almost certainly represent an undescribed species, but the dried material is inadequate for proper description of the cortical cell lineages and other details. The two specimens are from Port Phillip Heads, Vic. (*Wilson*, 4.ii.1889; MEL 45466, slide under ADU, A48121) and Western Port, Vic. (*Wilson*, 8.i.1885; MEL 45467). They have a branching pattern similar to *C. filiculum* but appear to have single rhizoids and the tetrasporangia are entirely naked and scattered over the nodes; clear internodal spaces are present throughout, but the nodal cortication appears more extensive than in *C. filiculum*. The species has been provisionally designated as *C. wilsonii* for curating purposes.

#### **Diagnostic Features of Ceramium**

Species of *Ceramium* are usually readily recognized by the filamentous branched thallus with axial cells bearing bands of nodal cortical cells which in most species are separated by non-corticated 'internodal spaces'; in some species (e.g. *C. rubrum*) the nodal cortication is closed virtually completely from the apex down. The branching of many species is pseudodichotomous, arising from more active development of a lateral apical cell cut off from the subapical cell of a filament; in other species the lateral development is delayed and the branching is clearly alternate or irregular.

Most species of *Ceramium* have more or less complanate branching in young actively growing parts, due to the lateral apical cell being cut off on the outer face of the subapical cell relative to the previous subdichotomy (Dixon 1960*a*, p. 340). This complanate branching is maintained indefinitely in some species, but in others becomes distorted and is further modified in some profusely branched species where many of the lateral branches arise adventitiously (usually originating from periaxial cells).

Filaments of *Ceramium* are attached to their substrate or host by rhizoids developed from the periaxial and often cortical cells of the nodes. In some species the base of the main axis is erect or virtually so, with loosely aggregated rhizoids from the basal node or from several lower nodes descending to form a relatively massive holdfast. In *C. filiculum*, and to a lesser extent in *C. cupulatum*, prostrate axes are attached by holdfasts formed of numerous tightly clumped rhizoids, with splayed-out ends. In other species the prostrate filaments are attached by one or more rhizoids from the lower cells of each or occasional nodes. In all but one of the southern Australian species, the rhizoids consist of a uniseriate row or two to several cells, attached by a digitate or discoid pad which becomes multicellular. The exception is *C. flaccidum*, where the whole rhizoid consists of a single cell.

The periaxial cells [used in the sense of Womersley and Cartledge (1975) in describing species of *Spyridia*] are cut off from the upper end of each axial cell and form a ring covering the region of union of two axial cells. Between 3 and 10 periaxial cells are formed in different species, and the number normally does not vary by more than one. The periaxial cells are formed in an alternating sequence [Dixon (1960*a*, p. 337), and apparently in most southern Australian species], with the first formed lying on the outer face relative to the previous pseudodichotomy or lateral branch. Associated with this, the actively growing apices in most species are involute, often markedly so, but if growth is slow or has ceased the apices may become almost straight; in some species the apices are rarely more than slightly curved. Hence the curvature of the apices must be used with caution as a taxonomic character.

Filament thickness in most species increases from branch apices to the lower main axes which may be more robust than the basal parts. These dimensions vary considerably in most species, but are often taxonomically useful.

By far the most important features to characterize the species lie in the development of the nodal cortex. Staining with aniline blue and mounting in corn syrup (and probably also in other media) renders visible the pit-connections and the cell lineages can be determined. Secondary pit-connections in species of *Ceramium* probably do not occur; if they do, they are certainly rare.

Each of the periaxial cells typically cuts off two cells acropetally and also two basipetally, and in many species these continue to divide in a similar pattern, with successively smaller cells. Occasionally three cells are cut off or more often only one, this probably being dependent on the space available around the axial cell. Usually the acropetal development tends to be slightly more extensive than the basipetal, but in some species (e.g. *C. cupulatum*) there are no basipetal cells and in others (e.g. *C. macilentum*) they are rare. In some species, the first cortical derivatives may cut off occasional cells in the reverse direction; these usually lie partly over the periaxial cells.

In many species, cortical development ceases after two or three successive divisions in each direction, and the nodes remain constant in structure throughout the thallus. In others (e.g. typical *C. rubrum*) the cortex extends continuously as the axial cells enlarge and no internodal space is present anywhere in the thallus. While in most southern Australian species there is normally (at least in the early stages) a developmental relationship between the enlargement of the axial cells and the growth of the cortex, the length and proportion of the internodal space is often variable in species where it occurs.

A distinctive variation on the normal acropetal and basipetal formation of cortical cells directly from periaxial cells occurs in *C. australe, C. macilentum* and *C. shepherdii*. In these species the periaxial cells cut off laterally one or two 'pseudoperiaxial' cells which interpose (completely in *C. australe* and *C. shepherdii*, largely in *C. macilentum*) between the periaxial cells giving a ring of two or three times as many cells. The further nodal cortex may be distinctive, as in *C. australe* where single acropetal and basipetal cortical cells are cut off from the pseudoperiaxial cells, but only acropetally from the true periaxial cells.

Some species (e.g. *C. isogonum*) have a very well defined margin to the nodal cortication, due to synchronous divisions of the cortical cells. In others this is less distinct, and in species such as *C. tasmanicum* the usually well defined cortex in young branches later initiates further growth and extends in an irregular manner to almost close the internodal space in old branches.

In slender species with a relatively short nodal cortex, the cortical cells usually all lie essentially on the surface of the axial cells. In more robust species an outer layer of smaller cells ('outer cortex') is usually cut off, mainly from the edges or corners of the inner cortical (and periaxial) cells as seen in face view. This pattern is more easily observed when stained and mounted as described above. Both the periaxial and inner cortical cells may enlarge considerably and the outer cortical cells often form rosettes around the inner cells as seen in face view. In some species, small darkly staining cells ('gland cells') form in the outer cortex. In certain species (e.g. *C. isogonum* and *C. flaccidum*) these are usually present, but some otherwise identical specimens lack them and their diagnostic value must be regarded with caution.

Virtually all species produce long, slender, caducous hairs from cortical cells near the apices of actively growing branches. Such hairs are easily lost and often not seen in dried or poorly preserved specimens. *C. flaccidum* also forms much broader, clavate 'hairs', but these are very variable in occurrence within the species and only of taxonomic value when present.

Some of the most easily recognized species of *Ceramium* are those which form spines or comparable outgrowths from the cortical cells. *C. monacanthum* and *C. puberulum* both form acute multicellular spines, in the latter from cortical cells of older parts of the thallus as well as near the apices. *C. shepherdii* provides a distinctive variation in the presence on the cortical cells of whorls of multicellular, outwardly projecting filaments with rounded ends to the terminal cells. Spines occur on species with significantly different cortical structure and the spinous species do not form a natural group. It is, however, convenient to key them out together because of this conspicuous feature.

# Reproductive Features

Development of the female reproductive system has not been followed in detail in southern Australian species, but appears to conform with that described by Dixon (1960*a*, p. 353). The carposporophyte (usually with successive gonimolobes) and its subtending branches do not often provide characters of real taxonomic value. Similarly male plants are relatively uniform, with the spermatangial sori often spreading from an initially adaxial position to later cover the nodes.

Tetrasporangia, however, do offer useful taxonomic characters in many species. In species with restricted cortical development, tetrasporangia usually originate only from the periaxial cells, and the degree of involucral protection by the cortical filaments varies in different species from very slight (e.g. *C. cliftonianum*), to the lower half or so of the sporangium (e.g. *C. cupulatum*), to almost complete cover (e.g. *C. flaccidum*). In *C. isogonum*, tetrasporangia originate mainly from the first cortical derivatives of the periaxial cells. In more heavily corticated species (e.g. *C. pusillum*), tetrasporangia may originate from cortical cells also, but initially they are formed from periaxial cells. In species with complete (or almost so) cortication (inner and outer cortex) the tetrasporangia are usually immersed within the cortex and become scattered in older parts as they are later formed from inner cortical as well as periaxial cells. In *C. isogonum* the tetrasporangia are completely naked.

In some slender species (e.g. C. macilentum and C. cliftonianum) the tetrasporangia are normally in unilateral, abaxial rows, and in others (e.g. C. filiculum) they are opposite in the plane of branching. While these are distinctive features in some species, in others (e.g. C. cupulatum) the early tetrasporangia may be unilateral, and in C. flaccidum opposite, but they soon become verticillate. Opposite tetrasporangia are often found on older branches of species which otherwise bear unilateral ones. These variations negate the value of the basic separation of groups of Ceramium by J. G. Agardh (1894).

Mature (i.e. divided) tetrasporangia can vary considerably in size within a species, and also in the type of division. In many species divisions vary from tetrahedral to cruciate, though in most cases they are probably basically of the tetrahedral type.

No strong evidence for reproductive seasonality is apparent for any southern Australian species; tetrasporangial plants are usually most frequent, and male plants most rarely seen.

Paraspores or 'galls' occur in C. *pusillum*, appearing very similar to those described for European species. Dixon (1960*a*, p. 348) considered them as galls and not as reproductive structures, but Rueness (1973) has shown that paraspores in C. *strictum* Harvey in the Oslofjord are reproductive spores which give rise to new parasporangium-bearing plants.

### Comparisons with Species from Other Regions

Comparisons of southern Australian species with those from other countries are very difficult in the absence of detailed illustrations of the cortical cell lineages in the latter; very few accounts are adequate for satisfactory comparisons. In view of the large number of poorly described species of *Ceramium*, especially from the Adriatic and eastern Mediterranean, earlier names for some of the southern Australian species may well eventuate. Recognition of two species (*C. rubrum* and *C. flaccidum*) common to northern hemisphere localities and to southern Australia is based on comparison of numerous collections by the author, as is maintenance of the other species as taxa endemic to southern Australia.

Recent studies (e.g. Garbary 1974) have shown that *C. rubrum* on the Atlantic coast of North America can vary considerably in the development of the cortical bands and degree of presence of the internodal space, depending on both day length and temperature. Such experimental evidence will be most valuable if it can be correlated with field recognition of taxa. The southern Australian species appear to be relatively stable in their morphology under field conditions, but experimental studies on their variation are clearly desirable.

# Segregate Genera from Ceramium

*Ceramium* is a well defined genus, and since its establishment there have been few groups segregated from it. Of several genera distinguished by Kuetzing (1841, 1849), only *Centroceras* has been generally accepted. The morphology and reproduction of this genus has been reviewed by Hommersand (1963, p. 241) who discussed the distinctive features of the cortical development and the spermatangial groups. Other related genera (Kylin 1956, pp. 369, 377-80) include *Microcladia* Greville (1830, p. 99), *Carpoblepharis* Kuetzing (1843, p. 449) and *Campylaephora* J. Agardh (1851, p. 149). These genera are generally more robust than species of *Ceramium*, with a thicker cortex of several layers, and in *Campylaephora* (Kylin 1956, p. 380; Nakamura 1965, p. 163; Itono 1977, p. 320) there is considerable rhizoidal development between the axial cells and the cortical cells. A species of *Microcladia* and the type species of *Carpoblepharis* have been described in detail by Hommersand (1963). The relationship of these genera with *Ceramium*, based on the type species, needs further study.

Another segregate genus from *Ceramium* is *Reinboldiella* De Toni (1895) from Japan, the type species of which [*R. schmitziana* (Reinbold) De Toni] appears distinct from *Ceramium* (Hommersand 1963, p. 233; Itono 1977, pp. 24, 84, 320). Two other species placed in *Reinboldiella* were referred to *Ceramium* by Hommersand (1963, p. 225), but Itono (1977, pp. 25, 26) has described two new species of *Reinboldiella*. Hommersand also refers *Ceramiella* Boergesen (1953, p. 47) to *Ceramium*, and notes (as have earlier authors) that *Ceramothamnion* Richards (1901) is not generically distinct. *Ceramiella* is maintained by Joly and Ugadim (1963) and Diaz-Piferrer (1968), but some of the supposed generic distinctions (e.g. 'stichidia') are shown to a greater or lesser extent by southern Australian species of *Ceramium*. Egerod (1971, p. 135) also discusses *Ceramiella*. *Corallophila* W. v. Bosse (1923, p. 339) from Sumatra also needs detailed comparison with *Ceramium*.

# Key to Southern Australian Species of Ceramium

- 1. Cortical cells not bearing spinous or tapering filaments (excluding slender, caducous hairs).....4

- 3. Spines one to several per node near apices, to 4 cells long, relatively slender; cortical cells on older branches with numerous 1-3 celled spines; internodal space present on young branches, closing on older parts; tetrasporangia mostly abaxial, largely enveloped by small cells; usually epiphytic on seagrasses (*Posidonia*, sometimes *Amphibolis*).....C. puberulum Sonder (p. 216)

\*Proportion of length to breadth equals 3-5.

9.	Thallus over 200 $\mu$ m thick below, usually strictly dichotomous, fastigiate; tetrasporangia naked or very slightly involucrate		
9.	Thal spor 10.	lus rarely over 200 $\mu$ m thick, irregularly subdichotomous to laterally branched; tetra- angia with a slight to extensive involucre	
	10.	Periaxial cells 6–7, each cutting off laterally two pseudoperiaxial cells thus forming a ring of 18–21 cells at the node, from which cortical cells develop acropetally and basipetally; gland cells occasionally present; outer cortex absent; tetrasporangia slightly involucrate, produced from the true periaxial cells, at first abaxially and later around the node	
11.	Cort	ical cells developing acropetally only (rarely single basipetal cells) from the periaxial	
	cells		
11.	Cort peria	ortical cells developing acropetally and basipetally (rarely few in <i>C. cliftonianum</i> ) from the eriaxial cells1	
	12.	Periaxial cells producing acropetally branched chains of 4–5 cortical cells, progressively smaller, forming a cupulate node; tetrasporangia becoming verticillate	
	12.	Periaxial cells each cutting off laterally a wedge-shaped pseudoperiaxial cell which largely interposes in the periaxial ring (then of 10–12 cells), each then cutting off 1 or 2 cells acropetally giving a node 2–3 cells long; basipetal cells rare; tetrasporangia abaxial $C$ macilentum L Agardh (p. 232)	
13.	Periaxial cells each cutting off two cells acropetally but only a single laterally elongate cell basipetally; the latter may cut off a further single cell, or two cells, and may itself divide laterally into 2-4 smaller cells; tetrasporangia whorled, largely involucrate; rhizoids unicellular		
13.	Peria tetra uniso 14.	axial cells each cutting off 2(-3) isodiametric cells acropetally and usually basipetally; sporangia opposite and largely involucrate, or unilateral and partly involucrate; rhizoids eriate-celled with multicellular pads	
	14.	Thallus on rock, epiphytic or epizoic, irregularly branched, subcomplanate above, branched at intervals of 4 or more axial cells; internodal spaces usually becoming several times as	

long as cortical bands; tetrasporangia unilateral and abaxial, partly involucrate...... C. cliftonianum J. Agardh (p. 240)

Ceramium shepherdii, sp. nov.

# Figs 1A-B, 5A-C

Thallus grey-red to red, to 12 mm high, epiphytic on Amphibolis, Posidonia or on algae associated with these seagrasses; basal filaments prostrate, attached by rhizoids from periaxial cells or their derivatives, 1–3 cells long and with multicellular pads. Branching of erect filaments sparsely subdichotomous or lateral.

Branches 100–150  $\mu$ m in diameter, tapering only slightly above, with relatively straight apices (Fig. 5B). Axial cells usually L/B  $\frac{3}{4}-1\frac{1}{2}(-2)$ , with narrow nodal bands 2 cells long and internodal spaces 3–6 times as long as nodal bands (Figs 1A, 5A, B). Rhodoplasts linear, traversing half or more of the length of the axial cells. Periaxial cells usually 6, each cutting off laterally one (occasionally 2, rarely none) pseudoperiaxial cell which lies in the periaxial ring (Fig. 1A, B), and each cell of this ring then cutting off acropetally a single cortical cell, thus forming a nodal band 2 cells

long\* (Figs 1A, 5A-C). Each direct derivative of the true periaxial cells producing a short tapering filament (to 100  $\mu$ m long) of 3-6(-7) cells (with a rounded apex) which projects outwardly and forward from the axis (Figs 1A, B, 5A-C); the true periaxial



Fig. 1. C. shepherdii. A, Part of branch showing periaxial (stippled) and pseudoperiaxial cells, acropetal cortical cells, tapering filaments and tetrasporangia (A47850). B, Cross section of node, showing 6 periaxial cells (stippled), pseudoperiaxial cells and their tapering filaments (dotted), and tapering filaments from acropetal cortical cells (clear) (A47850).

C. monacanthum. C, Spine near branch apex. D, Nodal cortication showing cell lineages from periaxial cells (both A42260).

C. puberulum. E, Node near apex of branch with primary spine. F, Older nodal cortication, with two primary spines and several hairs (both A46416).

\* The length of the nodal band in all species is taken in the same direction as the length of the whole filament or of the axial cells, and the number of cells long is based on the successive acropetal and basipetal derivatives from and including the periaxial cell; outer cortical cells or cells cut off in reverse directions are thus not included.

cells usually do not produce such a filament, though both they and the acropetal derivatives of the pseudoperiaxial cells may do so. Slender terminal hairs often present on these filaments.

Carposporophytes (Fig. 5A) globular, 120–180(–200)  $\mu$ m across, subtended by 1–3 short branchlets.

Spermatangial masses (Fig. 5B) cut off first from adaxial nodal cells, later developing all around the nodes.

*Tetrasporangia* (Figs 1*A*, *B*, 5*C*) cut off from enlarged periaxial cells, usually single per node and abaxial, often with further sporangia formed later from adjacent cells, protected by slightly greater development of nodal filaments (some basally dichotomous) than in sterile plants; tetrasporangia about  $60(-70) \mu m$  in diameter, tetrahedrally divided.

Diagnosis.- Thallus ad 12 mm altus, epiphyticus saepe in Amphibole et Posidonia, filamentis erectis nunc rare subdichotomis nunc latere ramosis. Rami 100-150  $\mu$ m diam., cellulae axiales  $\frac{3}{4}-1\frac{1}{2}(-2)$  plo longiores latitudine; cortex ad nodos ad 2 cellulas longas, et spatium inter nodos 3-6 plo longius nodis. Cellulae periaxiales sex in quaque 1(-2) cellula pseudoperiaxialis cellulam singularem acropetam corticalem portans. Filum verticale breve angustatumque ad 3-6(-7) cellulas in margine cellularum periaxialium nascitur. Tetrasporangia plerumque singula per nodum, abaxialia, tetraedrice divisa.

Type locality.- 4 km S. of Redcliff Point, northern Spencer Gulf, S.A.; on Posidonia australis, 10 m deep (J. Johnson, 10.i.1977).

Holotype.- ADU, A47850.

Distribution.- Known from Port Denison, W.A. (Kraft, 14.xii.1971; ADU, A41279) and from Coffin Bay, Tipara reef and near Redcliff in Spencer Gulf, Aldinga to Seacliff in St Vincent Gulf, from Kingston, S.A. (Lewis, 28.xi.1972; ADU, A42881), and from Snowy R. mouth, Vic. (F. Mueller, Feb. 1855; MEL 45455). At Redcliff, it occurs 2-10 m deep on Posidonia, throughout the year but most commonly in summer and autumn (December-June) and least in spring.

All collections (except MEL 45455, probably drift) have been associated with seagrass beds, between 2.5 and 12 m deep, in areas of moderate water movement.

C. shepherdii is a distinctive species, named after Scoresby A. Shepherd whose subtidal SCUBA studies have contributed greatly to knowledge of the southern Australian algal flora.

C. shepherdii is well marked by the irregular double whorls of filaments at the nodes and the pattern of nodal cell development. In forming pseudoperiaxial cells it shows similarity to C. australe, which is otherwise quite distinct. The blunt apices of the filaments separate C. shepherdii from C. monacanthum and C. puberulum and from the numerous extra-Australian species with acute spines, none of which are similar in their nodal development.

Ceramium monacanthum J. Agardh 1894: 29. De Toni 1903: 1468. Dixon 1960a: 345;

1960b: 382, 384, 389, fig. 5. Guiler 1952: 98. Lucas 1909: 53; 1929a: 26.

C. paniculatum sensu Cribb 1954: 8, 35 (NON Okamura 1896: 36).

# Figs 1C, D, 5D-G

Thallus (Fig. 5D) dark red, mostly erect, to 1.5 cm high, usually epiphytic on Codium fragile and Corallina, attached by tufts of rhizoids from the base of erect

axes or from short horizontal filaments; rhizoids arising from periaxial cells, uniseriate, simple or sparingly branched on *Codium*, sometimes with a multicellular attachment pad on *Corallina*. *Branching* dense, subcomplanate near apices, usually becoming more irregular below, alternate (to subdichotomous), 3–8 axial cells apart.

Branches 200-300  $\mu$ m in diameter below, tapering slightly to 100-150  $\mu$ m near the involute apices. Axial cells (Fig. 5E) more or less isodiametric, slightly shorter than broad in younger parts and slightly longer than broad in lower parts, with internodal spaces throughout. Periaxial cells 7-8, each cutting off 2(-3) smaller cortical cells acropetally and basipetally to form the nodal bands (Figs 1D, 5E) 4-6 cells long when young and bearing relatively coarse spines (Fig. 5F, G); node extending by fairly synchronous growth (Fig. 5E) but short internodal spaces present throughout the thallus, usually with long internodes in basal filaments. Spines usually single at each node, occasionally less common, abaxial, with a multicellular base and 3-6 cells (30-100  $\mu$ m) long (Figs 1C, 5G), usually lost from older parts of thallus.

Carposporophytes globular, about 250  $\mu$ m across, borne on upper branches and usually subtended by lateral branchlets.

Spermatangia (Fig. 5F) in dense patches covering the adaxial side of the nodal band, later spreading around the node.

*Tetrasporangia* (Fig. 5G) cut off from periaxial cells, at first single and abaxial, with later sporangia arising near the first and sometimes extending around the node, partly to largely involucrate by the cortical cells,  $35-45 \mu m$  in diameter, tetrahedrally divided.

Type locality.- Georgetown, Tas. (Gunn), on Codium.

Type.- Herb. Agardh, LD (21162).

Distribution.- Known from Cape Willoughby, Kangaroo I. and Robe in South Australia; Bridgewater Bay, Vic., and around Tasmania. Usually epiphytic on Codium fragile and Corallina.

Selected specimens studied.- Robe, S.A., on Corallina, low eulittoral pool edges inside point (*Womersley*, 9.ix.1968; ADU, A32694). Robe, S.A., on Codium fragile, pools on slipway reef (*Womersley*, 13.v.1972; ADU, A42260). Bridgewater Bay, Vic., on Codium fragile, low eulittoral (*Womersley*, 25.i.1967; ADU, A31784).

C. monacanthum is a distinctive species in south-eastern Australia, and most records are epiphytic on Codium fragile or Corallina, at a low eulittoral or uppermost sublittoral level. It differs from C. puberulum, the only other spinous southern Australian species, in having only a single, usually massive, spine at each node and in the internodal spaces remaining distinct throughout the thallus. The form of the rhizoids depends on the host: on Codium the rhizoids form a dense tuft, often branched but with simple ends, penetrating between the utricles, but multicellular pads are often formed on Corallina.

C. monacanthum is closely related to C. shuttleworthianum (Kuetz.) Silva (see Dixon 1960b), but differs in habit, in having shorter axial cells and internodal spaces in lower parts, in the presence of only a single spine at each node, and in the more completely covered tetrasporangia than in the latter. It is more closely related to C. paniculatum Okamura (1896, p. 36), which was recorded from Port Arthur, Tas., by Cribb (1954); Cribb's specimens (127.7 on Corallina, and 160.19) are C. monacanthum. C. paniculatum, as judged by the illustrations of Okamura (1921, p. 114, pl. 179 figs 8–16), Nakamura (1965, p. 145, figs 9, 10, pl. 2 fig. 5), Itono (1977, pp. 32, 101, figs 13D, 59F), and a specimen from Shinori, Japan (Taniguchi, 22.x.1968; ADU,

A47800), differs in habit, in being slenderer with longer internodal spaces below, and in having more emergent tetrasporangia; it should be carefully compared with *C. shuttleworthianum* to clarify differences. Specimens from Cape Willoughby, Kangaroo I. (*Womersley*, 8.i.1950; ADU, A12942) are much slenderer than normal in *C. monacanthum* and in this respect similar to *C. paniculatum*. They are sterile and represent the western limit of *C. monacanthum* to which they are referred provisionally pending study of further collections.

Ceramium puberulum Sonder 1845: 52; 1848: 167; 1853: 676. J. Agardh 1876: 102; 1894: 17. De Toni 1896: 229; 1903: 1452. Dixon 1960a: 345, 347. Guiler 1952: 98. Harvey 1855: 557; 1859: 330; 1863, synop.: 48. Lucas 1909: 53; 1929a: 26; 1929b: 53. Lucas and Perrin 1947: 367. Mazza 1912: 589. Reinbold 1897: 61; 1898: 51; 1899: 51. Tisdall 1898: 503. Wilson 1892: 185. Womersley 1950: 180.

C. puberulum ∝ crassior J. Agardh 1876: 102.

C. puberulum f. spinosissima Reinbold 1898: 51.

C. monile Hooker and Harvey 1847: 410. J. Agardh 1851: 132. Sonder 1853: 676.

C. monile β crassior J. Agardh 1851: 132.
C. puberulum β monile J. Agardh 1876: 102.

Celeceras monile (Hook. and Harv.) Kuetzing 1849: 684; 1862: 29, pl. 95.

# Figs 1*E*, *F*, 6

*Thallus* (Fig. 6A) light red to dark red-brown, erect, much branched in various planes, to 10 cm high, usually epiphytic on sea grasses (usually on *Posidonia* but also on *Amphibolis*), attached by numerous, branched, uniseriate-celled rhizoids originating from periaxial cells for several segments above the base of the erect axis, descending within the cortex and forming a compact discoid holdfast. *Branching* irregular, lateral to subdichotomous, sometimes with proliferations from older axes.

Branches up to 1 mm in diameter near the base, mid parts 100–250  $\mu$ m, upper parts 75–125  $\mu$ m in diameter. Axial cells L/B (1–)1 $\frac{1}{4}$ –2 below, upper L/B 1 $\frac{1}{2}$ –4. Periaxial cells 7(–8), each cutting off 2(–3) smaller cortical cells acropetally and basipetally (Fig. 1*E*, *F*) which further divide to form nodes (6–)8–12 cells long in upper parts,  $\frac{1}{5}-\frac{1}{2}(-1)$  times as long as internodal spaces, with the nodal cortication extending on older parts to become continuous near the thallus base; many plants showing moniliform lower branches due to constriction of axial cells between the nodal cortication. Outer cortex (Fig. 1*F*) forming a more-or-less continuous layer of small cells overlying the larger elongate inner cortical cells. Spines (primary) one to several per node near apices (Fig. 1*E*, *F*), 30–40(–60)  $\mu$ m and up to 4 cells long, usually relatively slender; primary spines usually soon lost but cortex of lower segments becoming covered with numerous short slender secondary spines (1–)2(–3) cells long (Fig. 6*B*) arising from the outer cortical cells; spines which arise near the apices always larger than later formed spines. Numerous fine hairs up to 250  $\mu$ m long arising from nodal cortical cells in some plants.

Carposporophytes globular,  $150-350 \,\mu\text{m}$  across, borne on upper branches and surrounded by several small, lateral, involucral branchlets.

Spermatangia (Fig. 6C) in dense patches covering the nodal cells of upper branches.

*Tetrasporangia* (Fig. 6D, E) at first single per node, later several, cut off from one or more periaxial cells usually abaxially, up to  $100 \,\mu\text{m}$  in diameter, prominent but usually becoming entirely enveloped by small involucral cells (some bearing spines);

the several tetrasporangia within the involucre form prominent, often scattered, enlarged nodes along the branches (Fig. 6D), though less so in young, slender plants (Fig. 6E).

Type locality.- Western Australia.

Type.- Isotypes in TCD and LD (20753). No specimen located in MEL.

*Distribution.*- From Dongarra, W.A., around southern Australia to Wilson's Promontory, Vic., and northern Tasmania; one record in BM from Cole's Bay, Oyster Bay, west coast of Tasmania (*Perrin* and *Lucas*, March 1934 on *Zostera*).

Selected specimens studied.- Point Peron, W.A., reef pools (Mitchell, 22.ix.1966; ADU, A30747). Redcliff Point, Spencer Gulf, S.A., on Posidonia, 7 m deep (Johnson, 5.ii.1975; ADU, A47826). Aldinga, S.A., on Posidonia, 7 m deep (Johnson, 7.vii.1973; ADU, A43888). American River inlet, Kangaroo I., S.A., on Posidonia, 2-3 m deep (Kraft et al. 16.iv.1973; ADU, A43754). Robe, S.A., on Posidonia, drift (Womersley, 10.ii.1973; ADU, A46416).

C. puberulum is a common epiphyte on Posidonia throughout its geographical range, and is less frequently found on Amphibolis; it is rare on other hosts. It is well characterized by the presence of several spines per segment near the apices and by the virtual covering of small spines on the cortical cells on older parts, though in occasional plants the latter may be rare or scarcely apparent (probably through loss with age). Kuetzing's figures (1862, pl. 95b, d) of the rounded tetrasporangial groups were incorrectly interpreted by Dixon (1960a, p. 347) as galls.

The proportions of nodal cortication to internodal space, and the relative size of the axial cells, may differ markedly in young branches, depending in part on whether older upper parts are present or new, often proliferous, young branches have developed from older parts. Young plants (less than 5 mm high) on *Posidonia* in northern Spencer Gulf, between February and July, have elongate segments (Fig. 6E) with long internodal spaces and only 1 to a few spines per node; later in the year the older parts enlarge and the cortex extends.

Kuetzing (1841, p. 739; 1849, p. 682) described *Echinoceras puberulum* from the Adriatic, but this species has apparently not been placed in *Ceramium*; it is listed by De Toni (1903, p. 1473) as a synonym of *C. ciliatum* (Ellis) Ducluz.

*Ceramium rubrum* (Hudson) C. Agardh 1811: 17. J. Agardh 1851: 127; 1876: 100; 1894: 37. De Toni 1903: 1476. Harvey 1844: 449; 1855: 557; 1859: 330; 1863, synop.: 47. Hooker and Harvey 1847: 409. Kylin 1944: 69, pl. 20, fig. 60. Newton 1931: 400, fig. 239. Reinbold 1897: 61. Sonder 1848: 167. Tate 1882: 17. Tisdall 1898: 503. Wilson 1892: 185.

Conferva rubra Hudson 1762: 486.

Ceramium rubrum var. proliferum J. Agardh. Sonder 1855: 514.

Ceramium rubrum var. pygmaeum Sonder 1848: 167.

Ceramium flagelliferum Kuetzing 1849: 686; 1863: 4, pl. 8e-g. Sonder 1853: 676.

- C. nobile J. Agardh 1894: 41. De Toni 1903: 1480. De Toni and Forti 1922: 56. Guiler 1952: 98. Laing 1927: 176. Lucas 1909: 53; 1929a: 26; 1929b: 53. Lucas and Perrin 1947: 369. Naylor 1954: 659. Reinbold 1898: 51.
- C. subcartilagineum J. Agardh 1894: 24. De Toni 1903: 1463. Ewart 1907: 91. Guiler 1952: 99. Levring 1946: 224. Lucas 1909: 53; 1929a: 26; 1929b: 53. Lucas and Perrin 1947: 367.

# Figs 2A, 7

*Thallus* (Fig. 7A) red to dark red, usually 5-15(-25) cm high, epilithic or epiphytic on seagrasses or larger algae, base usually single, erect, attached by a tuft of rhizoids originating from periaxial cells. *Branching* frequent to relatively sparse, pseudo-

dichotomous (especially near apices) or irregularly lateral, often with numerous small proliferous branchlets below; main branches sometimes slightly moniliform due to denser cell formation at the nodes and slightly swollen axial cells.



Fig. 2. C. rubrum. A, Part of branch 19–21 segments from apex, showing 'dovetailing' of cortical cell filaments giving complete cortication (A47024).

C. pusillum. B, Part of branch 21-24 segments from apex, showing slight internodal spaces between nodal cortication (A33116).

C. lenticulare. C, Segments of branch showing cortical cell lineages and lenticular internodal spaces (A45063).

C. excellens. D, Nodal cortication showing cortical cell lineages and narrow, annular, internodal space (A38371).

C. tasmanicum. E, Young nodal cortication showing cell lineages (A42758).

Branches  $\frac{1}{2}-1$  mm thick below, 250-500  $\mu$ m in diameter above, tapering only slightly until near the apices which are slightly involute to straight. Axial cells usually about as long as broad, becoming completely corticated (Figs 2A, 7B) close

to the apices, with the terminal cells of both the acropetal and basipetal corticating filaments becoming angular and dovetailing together to obscure the join. *Periaxial cells* 7(-8), each cutting off usually two cells acropetally and basipetally, continuing as corticating filaments often with two divisions if space permits; these inner cortical cells enlarge and elongate to L/B 3–5 (Fig. 7*C*). *Outer cortex* present, varying from a fairly complete cover to small cells lying largely over the margins of the inner cells (as seen in face view) but not usually forming rosettes except over the rounded periaxial cells (Fig. 7*C*). Hairs from the outer cortical cells often present in young parts.

*Carposporophytes* (Fig. 7D) 200-400  $\mu$ m across, closely surrounded by 2-5(-8) short, curved, involucral branchlets.

Spermatangia covering the surface of branches, arising first on the adaxial side.

*Tetrasporangia* (Fig. 7*E*) cut off at first from the periaxial cells or the immediate cortical derivatives and thus in rings of 10–15 sporangia along the branches, later from any inner cortical cell and thus scattered, variable in size (30–60  $\mu$ m long), spherical to ovoid, more or less cruciately divided, protruding slightly to moderately within the cortex and surrounded (in face view) by a rosette of outer cortical cells.

*Type locality.*– Britain.

Type.- Probably lost.

*Distribution.*- From Elliston, S.A. (probably from Fremantle, W.A.-MEL 45384) along southern Australia to Wilson's Promontory, Vic., and around Tasmania. This species is usually confined to areas of calm to moderate water movement, and is probably more widespread around the Australian coast.

A widely distributed species in temperate regions, especially in the northern Atlantic; probably present in most oceans though often referred to under other names.

Selected specimens studied.- Point Avoid, Eyre Pen., S.A., drift (*Womersley*, 2.xii.1975; ADU, A46912). Port Noarlunga, S.A., drift (*Womersley*, 30.xii.1975; ADU, A47024). Swan Bay, Port Phillip, Vic., 1 m deep (*Watson*, 6.x.1973; ADU, A44147).

Australian plants were referred to *C. rubrum* by early authors (see above) and by Harvey on herbarium sheets as *C. rubrum australe*, but were separated as a distinct species, *C. flagelliferum*, by Kuetzing (1849), based on plants from Tasmania (V.D.L., *Hooker*, type in L, 938, 303...214). J. Agardh (1894) later described this species as both *C. nobile* and *C. subcartilagineum*.

The type of C. flagelliferum is a relatively large plant typical in form of C. rubrum. C. nobile J. Agardh is based on specimens of Harvey's distributed as C. rubrum. In Herb. Agardh, Harvey's Alg. Aust. Exsicc. 467E from Port Phillip Heads (LD, 21457) has both tetrasporangial and cystocarpic plants, whilst 467H from Western Port (LD, 21456) consists of a large (25 cm high) tetrasporangial plant. The latter is chosen as lectotype of C. nobile, and isotypes are in the BM, MEL and probably in many other herbaria housing Harvey's Australian algae. Harvey's Trav. Set 258 from Phillip I. (entrance of Western Port), Vic., is represented by two cystocarpic plants in MEL (45368, 45370) which are similar in form to his 467H. The specimens are typical of the Australian C. rubrum as described above. Some of Harvey's 467E (though not so markedly in LD 21457) show strong development of proliferous, torulose, 'stichidiose' branchlets, as well as slight annular internodal spaces, and these plants are referred to C. excellens J. Agardh (see below).

The type of *C. subcartilagineum* J. Agardh is from Tasmania (*Gunn*) and is represented by two sheets in Herb. Agardh, LD (21036, 21037), of which the latter is chosen as lectotype. It is a slenderer plant than the type of C. *nobile*, but similar to that of C. *flagelliferum*.

Australian material here referred to *C. rubrum* appears to be not distinguishable from this variable species on British coasts. Extensive comparisons have been made of Australian specimens with field-collected material in Britain (during May–July 1976), and no consistent points of difference were found. The Australian material is rather less variable than the British in that complete cortication occurs in all specimens, apart from a very slight separation of the cortical bands near the branch apices (more clearly seen in slide preparations). *C. rubrum* has for a long time been considered a very variable species and numerous segregates have been described as varieties, forms, or separate species, especially where lower salinities occur as in the Baltic (see Rosenvinge 1923–1924, p. 387). Garbary (1974) has also shown that western Atlantic specimens referred to *C. rubrum* can vary considerably in the separation of the nodal cortical bands, depending on both day length and temperature.

While the Australian specimens referred to *C. rubrum* are relatively uniform, it is closely related to *C. pusillum* Harvey. As expressed in the key, southern Australian material of *C. rubrum* differs from *C. pusillum* in being generally larger with dichotomous or irregular and often proliferous branching, by the nodal cortical bands uniting relatively close to the apices with the cells usually dovetailing together, by the inner cortical cells becoming elongate in older parts with the outer cortical cells varying from a largely complete cover to rows along the larger inner cells but not forming distinct rosettes (except often around the periaxial cells), by the tetrasporangia usually developing from any inner cortical cell as well as the periaxial cells and thus on older parts appearing scattered, and by being generally a species of calm to moderate (often deeper) water movement.

While no one of the above features clearly distinguishes C. rubrum from C. pusillum, overall assessment of them permits ready separation of nearly all specimens of these taxa.

Ceramium divergens J. Agardh (1894, p. 27) was described from New Zealand (Invercargill) and Tasmania. The Tasmanian record was repeated by Lucas (1909, p. 53; 1929a, p. 26) and Guiler (1952, p. 98). J. Agardh's description was based largely on the New Zealand specimens, of which LD 21108 is a suitable lectotype. The Tasmanian specimens are almost certainly not C. divergens, which is completely corticated but with the older branches showing smaller cortical cells when the nodal cortication joins and with numerous short proliferous branchlets with divergent apices. Pending re-examination of the Tasmanian specimens of J. Agardh, they are provisionally referred to C. rubrum.

Ceramium pusillum Harvey 1863, synop.: 47. J. Agardh 1876: 104; 1894: 21. De Toni 1903: 1458. Laing 1927: 176(?). Lucas 1909: 53. Lucas and Perrin 1947: 367. Tisdall 1898: 503.

C. nobile sensu Womersley 1948: 160; 1950: 180 (NON J. Agardh 1894, = C. rubrum).

Figs 2B, 8

Thallus (Fig. 8A, B) light to dark red, 1-5(-10) cm high, epiphytic on various algae, with a single erect base attached by a tuft of multicellular, branched rhizoids, some descending between the cortex and lower axial cells. *Branching* of one to a few linear, straight to slightly flexuous branches usually with alternate, flabellate groups of

laterals (Fig. 8A, B), sometimes more irregularly branched, or with a few lower proliferous branchlets.

Branches 400-600  $\mu$ m thick below, 100-200  $\mu$ m in younger branches, tapering gradually until near the apices which are usually fairly straight (Fig. 8C). Axial cells about as long as broad (shorter near apices), becoming completely corticated close to the apices apart from a narrow separation marked by smaller cells terminating the acropetal growth compared to slightly larger cells terminating the basipetal growth of the younger segment (Figs 2B, 8C); this separation often visible for many segments from the apices, though the acropetal and basipetal cortical cells abut each other. Periaxial cells (7-)8-9(-10), each cutting off two cells acropetally and basipetally (Fig. 2B), these continuing as corticating filaments often with two divisions if space permits, the cells usually angular and isodiametric at first. These inner cortical cells enlarge but remain subspherical to ovoid (L/B rarely more than 2) (Fig. 8D). Outer cortex of small cells present, commonly forming rosettes around many of the larger inner cortical cells as well as the periaxial cells (Fig. 8D).

*Carposporophytes* (Fig. 8*E*) usually near branch apices, globular, 200–300  $\mu$ m across, with 2–4(-6) short involucral branches.

Spermatangia (Fig. 8F) covering several segments, especially in axils of upper branches, later spreading around the branch.

*Tetrasporangia* (Fig. 8G) derived from the periaxial cells, forming prominent whorls of 10–15 (often including immature ones), often with some cut off later from inner cortical cells, mostly cruciately divided, ovoid,  $35-50 \ \mu m$  long by 20–40  $\mu m$  broad.

*Paraspores* not infrequently occur on *C. pusillum*.

Lectotype locality.- Port Fairy, Vic. (Harvey).

Lectotype.- Herb. Harvey, TCD (Alg. Aust. Exsicc. 474D).

*Distribution.*– Epiphytic on larger algae from Cottesloe and Garden I., W.A., around southern Australia to Gabo I., Vic., and around Tasmania. Laing's (1927, p. 176) doubtful record from New Zealand needs checking.

Selected specimens studied.- Point Peron, W.A., reef pools (Mitchell, 22.ix.1966; ADU, A30746). Robe, S.A., reef pool, on Mychodea (Womersley, 18.xii.1971; ADU, A41147). Carpenter's Rocks, S.A., 3-4 m deep on Plocamium (Shepherd, 4.xii.1968; ADU, A33116). Bridgewater Bay, Vic., on Laurencia elata, low eulittoral (Beauglehole, 26.xii.1950; ADU, A15615). Gabo I., Vic., 18 m deep on Plocamium (Shepherd, 17.ii.1973; ADU, A43507).

C. pusillum appears to be always epiphytic, on various algae (rarely on Posidonia) under conditions of strong water movement, especially at the outer edge of rock platforms in the sublittoral fringe or uppermost sublittoral. Deeper growing plants—to 34 m in Investigator Strait—have more irregular branching but otherwise agree with C. pusillum. In contrast, C. rubrum in Australia is characteristic of calmer waters and may be epiphytic or epilithic.

In his original description, Harvey gave three localities "Western Australia, G. Clifton. Port Fairy, W.H.H. Warrnambool, H. Watts", but following the description he cited "Harv. Alg. Exsicc. n. 474". Accordingly Harvey's 474D in TCD from Port Fairy, Vic., is selected as lectotype of C. pusillum. A specimen from Harvey's "Travelling Set", from Port Fairy and numbered 528, is in MEL (45330), labelled by Harvey "Ceramium (Microcladia) pusillum ms". This can be regarded as an isotype. Harvey's 467A in BM is probably C. pusillum, though Harvey referred this number to C. rubrum. Liquid-preserved material of *C. pusillum* and *C. rubrum* can usually be readily identified, but dried material is often not so easily distinguished. The habit of *C. pusillum*, with the alternate flabellate branch systems, and the habitat in strong water movement, permit field recognition. Microscopically, *C. pusillum* generally shows smaller, terminal acropetal cells abutting larger terminal basipetal ones of the cortical filaments, even after the slight gap between the nodal cortication near the apices has closed up. The subspherical to ovoid inner cortical cells with rosettes of outer cortical cells are also normally characteristic, in contrast to the more elongate inner cortical cells with rosettes around the periaxial cells only, in *C. rubrum*. Prominent rings of tetrasporangia, with sporangia much less frequently formed from the inner cortical cells, are also more characteristic of *C. pusillum* than of *C. rubrum*, though both species are variable in this respect.

The name *Ceramium pusillum* Schousboe was used in Algae Schousbianae No. 215, but according to Bornet (1892, p. 321) this unpublished name is a synonym of *Spermothamnion turneri* var. *variabile* J. Agardh.

# Ceramium lenticulare, sp. nov.

# Figs 2*C*, 9

*Thallus* (Fig. 9A, B) light to dark red,  $\frac{1}{2}$ -7 cm high, epilithic or on solid substrates, with a single erect (or slight prostrate) base attached by a tuft of uniseriate rhizoids. *Branching* (Fig. 9A, B) complanate, regularly alternate (usually at intervals of 4-5 cells) with one to several narrowly to broadly pyramidal branches from near the base, and small, proliferous branchlets on the lower parts of robust specimens (Fig. 9A).

Branches 300-500(-700)  $\mu$ m in diameter below, terete to slightly compressed, tapering to 75–150  $\mu$ m in diameter near the apices which are usually more or less straight and taper abruptly (Fig. 9D, E) to the apical cell. Axial cells subspherical throughout (often slightly broader than long), becoming largely corticated near the apices apart from the usual presence of a lenticular internodal space (Figs 2C, 9C) on the surface (in the complanate view) of the branches, resulting from the cortication closing up on the sides but not the central part of each segment; the lenticular space is usually visible throughout the thallus except in oldest parts where it may close, but may be less clear in dried specimens. The terminal acropetal cortical cells are usually smaller than the basipetal ones (Figs 2C, 9C) and tend to lie outside the adjacent basipetal cells when the cortication has largely or completely closed. Periaxial cells 6-7, each cutting off normally two cells (Fig. 2C) acropetally and basipetally, which continue to produce 1 or 2 derivatives (the number of successive divisions depending on the robustness of the thallus and the size and age of the axial cells), to form nodes 5-7 cells long (Fig. 9C) in upper parts, 8-9 (or more) cells long in older parts; a slight outer cortex of small cells is cut off and this may become extensive in robust plants with some rosettes around the periaxial cells; inner cortical cells remain isodiametric to ovoid, sometimes elongating in old robust specimens.

Carposporophytes (Fig. 9D) 150–300  $\mu$ m across, subspherical, with 2–4 moderately stout branchlets forming an involucre.

Spermatangia forming patches, especially on the sides of the branches, later becoming largely confluent.

Tetrasporangia (Fig. 9E, F) in several successive segments near the ends of branches or in short 'stichidiose' proliferous laterals (Fig. 9F), formed first in the plane of

branching but soon becoming whorled, situated largely within the cortex or covered by involucral filaments of cells, subspherical to ovoid and 20–25  $\mu$ m across, cruciately or tetrahedrally divided.

*Diagnosis.*- Thallus  $\frac{1}{2}$ -7 cm altus, fronde erecto e base singulo ramos complanatos alternos (4-5 cellulis separatos) saepe copiose inferne ferente. Rami 300-500(-700)  $\mu$ m diam. inferne, 75-150  $\mu$ m diam. ad apices, cellulae axiales subglobosae vel ovoideae, plerumque corticatae sed a fronte ramorum visu spatiis lenticularibus inter nodos evolutis. Cellulae periaxiales 6-7 plerumque duas cellulas acropete et basipete efferentes, deinde divisae in nodos longitudine 5-7 cellularum superne, veteribus autem ramis ad 8-9 cellulas longitudine, cortice externo saepe parvo. Tetrasporangia ad apices vel in copiosis ramis lateralibus portantur, primo opposita deinde verticillata plerumque involucrata, cruciatim vel tetraedrice divisa.

*Type locality.*- Vivonne Bay, Kangaroo I., S.A. 1-5 m deep on jetty pile (*Kraft*, 19.i.1974).

#### Holotype.- ADU, A45063.

Distribution.- Apart from the type and a specimen from the same situation, 0-7 m deep (*Kraft*, 15.vii.1972; ADU, A42544), also known from the shaded end (under cliffs) of a large, high-level, rock pool on the southern side of Ellen Point, Vivonne Bay, S.A. (*Womersley*, several specimens in ADU collected in January, May, August and October (e.g. A30855); hence probably present throughout the year); from Apollo Bay, Vic.,  $0-\frac{1}{2}$  m deep on a pipeline in the dock (*Owen* and *Kraft*, 1.ix.1971; ADU, A39505); and probable specimens from King I., Bass Strait (*Spong*; NSW 138903) and the River Derwent Estuary, Tas. (*Lucas*, Nov. 1923; NSW 138901).

C. lenticulare is characterized by its complanate habit with regularly alternate branching, by the cortication and resultant lenticular internodal space (from which the name is derived), and by the 'stichidiose' tetrasporangial branches, both on normal branches and especially on short proliferous laterals. While identical in basic morphology, cell details and reproduction, the Vivonne Bay pool specimens are slenderer than the type, while the Apollo Bay specimens are considerably more robust.

C. lenticulare is closely related to both C. planum Kuetzing (1849, p. 687) from South Africa and to C. apiculatum J. Agardh (1876, p. 105; 1894, p. 20) from New Zealand; the latter requires detailed re-description from verified liquid-preserved material. C. planum (see Simons 1966, p. 157) appears to be a more robust species (though not more so than the Apollo Bay specimens) with more complete cortication and lacking any lenticular internodal space; the tetrasporangia may be more emergent than in C. lenticulare. C. cancellatum C. Ag. (a synonym of C. planum) was recorded from Sealer's Cove, Vic., by Harvey (1863, synop.: 47), followed by Tisdall (1898, p. 503) and Garnet (1971, p. 96), but it has not been possible to check this record. C. apiculatum, which was based on New Zealand specimens previously referred to C. cancellatum, appears to be a more robust species with more complete cortication, separated by a narrow continuous space only near the apices. These comparisons with C. apiculatum are based on CHR 36421 from Tauranga (Hodgkins No. 7), an Algae Muellerianae specimen from "W. coast of New Zealand", Herb. Holmes in BM, and "East coast, N.Z. Lat. S. 43°. April 1949 D.L.", also in BM. C. apiculatum was recorded from Western Port, Vic., by Wilson (1892, p. 184), followed by Tisdall (1898, p. 503), but Wilson's specimens in MEL (45398, 45399) are C. excellens J. Ag.

Another related species, C. stichidiosum J. Agardh (1876, p. 105; 1894, p. 21) was described from the Chatham Is and Tasmania, but it appears that a Chatham Is

specimen in LD (20859) should be taken as the lectotype; the Tasmanian specimen is almost certainly not the same, but may be a form of C. *excellens*. C. *stichidiosum* differs from C. *lenticulare* in being completely corticated with fairly regular cells (see Levring 1945, p. 19, fig. 6) and is markedly different in habit with tufted and not complanate and alternate lesser branching.

C. lenticulare is closely related to C. excellens, as discussed under the latter species.

# Ceramium excellens J. Agardh 1894: 48. De Toni 1903: 1491. Guiler 1952: 98. Lucas 1909: 53; 1929a: 26. Lucas and Perrin 1947: 369.

C. torulosum J. Agardh 1876: 99; 1894: 47. De Toni 1903: 1490. Guiler 1952: 99. Lucas 1909: 53; 1929a: 26.

NON C. torulosum Roth 1806: 125, = Lomentaria articulata (Huds.) Lyngbye.

C. nodiferum sensu J. Agardh 1894: 31. Lucas 1909: 53. Lucas and Perrin 1947: 369. Tisdall 1898: 503. Wilson 1892: 185. (NON J. Agardh 1876: 99, from the Chatham Is).

C. apiculatum sensu Wilson 1892: 184. Tisdall 1898: 503 (NON J. Agardh 1876: 105).

# Figs 2*D*, 10

*Thallus* (Fig. 10*A*, *B*) red to dark red, usually 5-20(-30) cm high, epilithic, with a single or several erect axes (or occasionally a slight prostrate base) producing several long lateral branches and attached by a tuft of uniseriate-celled rhizoids. *Branching* alternate, usually complanate (Fig. 10*B*) and regularly alternate in younger parts but below often more irregularly branched, commonly with small, proliferous, often fertile branchlets along the lower main branches.

Branches  $\frac{1}{2}-1\frac{1}{2}$  mm in diameter below, decreasing gradually to 150-250  $\mu$ m in diameter just below the relatively straight, markedly tapering apices; proliferous branchlets on older branches 120–180  $\mu$ m in diameter, often basally constricted. Axial cells about as long as broad above, extending to twice as long as broad in older branches, becoming largely corticated except for a narrow, annular, internodal space (normally  $< \frac{1}{5}$  the length of the nodal cortication but occasionally almost as long in upper parts) present throughout the upper thallus (Figs 2D, 10C), but with the cortication usually closing completely on older branches and extending as the axial cells enlarge. Periaxial cells usually 8, each cutting off a regular pattern of 2 cells acropetally and 2 (rarely 3) basipetally (Fig. 2D), these continuing as corticating filaments usually each with two divisions, occasionally one; divisions normally synchronous, producing a straight edge to the cortication (except where axial cells have elongated relative to cortical development), with smaller terminal cells on the acropetal filaments than on the basipetal ones (Fig. 2D), ultimately often with further production of small cells closing the internodal space completely. Outer cortex produced from the periaxial cells (Figs 2D, 10C) and some of the larger inner cortical cells (which elongate to L/B up to 5), often with well developed rosettes over these cells, and on older parts a further cortical layer of small cells may be cut off, forming a distinctly thicker cortex over the central part of the nodal cortication; in some specimens, scattered small outer cortical cells become gland-like.

Carposporophytes (Fig. 10D) near the ends of short lateral branchlets, globular, 205-400  $\mu$ m across, with 2-4(-5) short, relatively stout, involucral branches.

Spermatangial patches covering several segments, largely in the axils of upper branches, sometimes surrounding small lateral branches.

*Tetrasporangia* (Fig. 10*E*) formed mainly in stichidiose branch ends or proliferous laterals which are basally constricted, derived from periaxial cells and forming a ring

of 8-12 lying within and bulging the acropetal cortical filaments (Fig. 10*E*), thus producing a torulose appearance to the branch; tetrasporangia subspherical to slightly ovoid,  $30-50 \ \mu m$  in diameter, cruciately divided.

Lectotype locality.- Tamar R. mouth, Tas. (Oakden).

Type.- Herb. Agardh, LD (21757, lectotype).

*Distribution.*- From the head of the Great Australian Bight, S.A., to Western Port, Vic., and around Tasmania. This appears to be usually a deep water species.

Selected specimens studied.- Investigator Strait, S.A., 31 m deep (Watson, 24.i.1971; ADU, A38371). Low Head, Tas. (Perrin, Sept. 1948; ADU, A9020).

C. torulosum J. Agardh is based on a Gunn specimen from "East coast, Tas." (Herb. Agardh, LD, 21752), which is identical with the later described C. excellens J. Agardh. C. torulosum J. Agardh is invalidated by C. torulosum Roth, a synonym of Lomentaria articulata. Some specimens in Herb. Agardh, LD, from Orford, Tas., and Port Phillip, Vic. (Wilson), placed under C. torulosum J. Agardh, are not this species.

Wilson (1892, p. 185) and J. Agardh (1894, p. 31), followed by Tisdall (1898, p. 503), Lucas (1909, p. 53) and Lucas and Perrin (1947, p. 369), referred some Port Phillip specimens to *C. nodiferum* J. Agardh; these specimens in Lund appear to belong to *C. excellens*. The relationships of the Chatham Is *C. nodiferum* need further study. Wilson (1892, p. 184) and Tisdall (1898, p. 503) also referred some specimens (MEL 45398, 45399) of *C. excellens* to the New Zealand *C. apiculatum* J. Agardh.

C. excellens is usually well characterized by its normally complanate form and the presence throughout much of the thallus of the clearly defined, narrow and straight edged, annular internodal space; this is usually relatively longest nearer the apices, but is rarely more than  $\frac{1}{5}$  as long as the nodal cortication (except in specimens with enlarged axial cells), and in the old branches the cortex often closes completely.

In a few specimens referred to *C. excellens* (e.g. Robe, S.A., *Womersley*, 9.x.1972; ADU, A42762; and others in NSW from Port Phillip, Vic., and northern Tasmania), the nodal cortication has a somewhat irregular margin and the internodal spaces are relatively long; these features show similarity with *C. tasmanicum*, but in the branching pattern and other details of the cortication they are similar to *C. excellens*.

The torulose and stichidiose tetrasporangial branchlets are also usually characteristic of *C. excellens*. Older plants may have cortication complete except in the upper branches, and the adventitious tetrasporangial branchlets may be profuse. This form (e.g. Alg. Aust. Exsicc. 467E) was confused by Harvey with his *C. rubrum* (of which 467H is a typical Australian example). It is likely that the Tasmanian specimens referred by J. Agardh (1876, p. 106) to his *C. stichidiosum* (type from the Chatham Is) are also *C. excellens* J. Ag. This reference was followed by Lucas (1909, p. 53; 1929*a*, p. 26) and Guiler (1952, p. 98). No Tasmanian specimens under *C. stichidiosum* exist in LD.

C. excellens is closely related to C. lenticulare, but differs in its habit, greater dimensions, and in details of the nodal cortication, especially in the uniform presence of the narrow, annular internodal space compared to the lenticular internodal space in C. lenticulare. Whereas the axial cells of C. lenticulare remain isodiametric throughout, in larger branches of C. excellens they elongate to L/B about 2 and the cortex extends to maintain complete cover of these cells; the latter also develops a considerably greater outer cortex.

C. excellens is also closely related to C. tasmanicum, but differs in having complanate branching (at least of younger parts) and in the more regular nodal cortication with the narrow, annular internodal space; C. excellens usually also has a thicker cortex and well defined rosettes in the central part of the nodal cortication. Some apparent intermediates between these two species do occur.

# Ceramium tasmanicum (Kuetzing) comb. nov.

- Trichoceras tasmanicum Kuetzing 1849: 680; 1862: 26, pl. 85a-c. J. Agardh 1851: 141. De Toni 1903: 1497.
- Ceramium aequabile J. Agardh 1894: 44. De Toni 1903: 1486. Guiler 1952: 98. Lucas 1909: 53; 1929a: 26.
- C. diaphanum sensu Harvey 1844: 449; 1859: 330; 1863, synop.: 48. Tate 1882: 17(?). Tisdall 1898: 503. Wilson 1892: 184.
- C. strictum sensu Levring 1946: 224.

# Figs 2*E*, 11

*Thallus* (Fig. 11*A*) dark red, 1–10 cm high, epilithic or epiphytic (mainly on *Codium fragile*), usually bushy and tufted with several erect axes from the base which is attached by a tuft of branched, uniseriate-celled, rhizoids with occasional multicellular pads, originating from the periaxial and larger cortical cells of the lower 1–5 axial cells. *Branching* usually dense and irregular on all sides, the upper parts sub-dichotomous in varying planes, usually (especially in plants from rough-water coasts) with frequent small proliferous branchlets from the lower nodes; older branches often torulose due to the swollen nodes.

Branches (300-)400-800  $\mu$ m in diameter below (most robust in rough-water forms),  $60-100 \ \mu m$  in diameter shortly below apices, tapering gradually (apart from the slender proliferous branchlets on broader older branches) to relatively slender, involute to moderately straight apices. Axial cells L/B  $1-1\frac{1}{2}(-2)$  above with internodal spaces  $\frac{1}{2}-1(-2)$  times as long as the nodal cortication (Fig. 11*E*, *F*); cortication on older branches extending irregularly (Fig. 11B) but usually not closing completely. Periaxial cells (5-)7-8, each cutting off 2-3 cells acropetally and basipetally (Fig. 2E), which each cut off a further 1-3 cells which continue to divide to form nodes 6-7 cells long near to the apices, usually slightly more developed acropetally than basipetally; cortex extending gradually (Fig. 11B) until in larger branches where extension is more rapid and irregular (usually more so acropetally), with elongate cells, the nodal margins varying from relatively straight to most irregular, but usually maintaining an internodal space. Outer cortex of small cells formed in relatively young nodes (Fig. 11B, C), later covering the whole nodal cortex (except at the margins) as an irregular, loose (especially in prepared mounts and older nodes) layer of small, rounded, widely separated cells, without distinct rosettes except sometimes over the periaxial cells; long, slender hairs are usually formed profusely from the terminal acropetal and outer cortical cells of young branches.

Carposporophytes (Fig. 11D) on upper branches, globular, 100–200  $\mu$ m across, with 3–6 straight to slightly curved branchlets arising just below them.

Spermatangia (Fig. 11E) covering the nodal cortex of young branchlets, commencing adaxially but soon spreading around the node.

*Tetrasporangia* (Fig. 11*F*) in whorls of 2–6 (mature), arising from the periaxial cells (or immediate cortical derivatives), largely involucrate within the cortex, cruciately divided, subspherical to ovoid,  $30-40 \ \mu m$  broad by  $35-60 \ \mu m$  long.

Type locality.- Tasmania (Gunn 1310, ex Hooker).

*Type.*- L, 938, 303...216.

*Distribution.*- Western Australia (Harvey); from Robe, S.A., to Western Port, Vic., and around Tasmania, on coasts of strong water movement.

Selected specimens studied.- Vivonne Bay, Kangaroo I., S.A., reef surface (uppermost sublittoral) (*Womersley*, 6.iv.1972; ADU, A42420). Robe, S.A., in pools and on *Codium fragile (Womersley*, 9.x.1972; ADU, A42758, A42763). Crawfish Rock, Western Port, Vic., 0-3 m deep (*Watson*, 15.ix.1968; ADU, A32769).

J. Agardh, in describing *C. aequabile* based on Harvey's Alg. Aust. Exsicc. 468F (as *C. diaphanum*) from Brighton, Port Phillip, Vic. (type in LD, 21678), apparently overlooked Kuetzing's *Trichoceras tasmanicum*. Harvey's Port Phillip specimens are identical with the latter. However, Harvey's specimens from "W. Aust." (in TCD) referred to *C. diaphanum* are slenderer and have longer internodes without an extending cortex, and this Western Australian plant needs further study in relation to *C. diaphanum* and *C. tasmanicum*.

The branching, nodal cortication, and especially the extending cortex often with an irregular growing margin are characteristic of C. tasmanicum. Slender and more loosely branched forms, usually from relatively calm water localities, may be superficially similar to C. cliftonianum, but are usually recognizable by the extending cortex on older axes and by the whorls of tetrasporangia if present.

One specimen from Crawfish Rock, Western Port, Vic. (ADU, A32769), also shows gland-like cells and little if any extending cortex; its habit however is typical of *C. tasmanicum* and it is provisionally referred to this species.

C. tasmanicum is certainly closely related to the European C. diaphanum (Lightfoot) Roth [including C. strictum Harvey, to which Levring (1946, p. 224) referred the Australian taxon], and may well have to be brought within this variable species. Feldmann-Mazoyer (1940, pp. 302-19) discussed the C. diaphanum complex in the Mediterranean and Lucas (1953) discussed the varieties and forms in the Netherlands. The dimensions Lucas gave for var. diaphanum are generally similar to those of C. tasmanicum, and some forms also show an acropetal extending cortex.

However, *C. tasmanicum* is maintained as a separate species pending further study of the cortical cell lineages in *C. diaphanum* and also since in the former (but apparently not in the latter) the cortex in older branches extends basipetally as well as acropetally. Typical *C. tasmanicum* is somewhat more robust than most forms of *C. diaphanum*.

*C. tasmanicum* is also closely related to *C. excellens*, but most specimens are specifically distinct. Liquid-preserved material usually shows clearly the irregular branching on all sides of the former compared to the complanate branching of the latter, and the nature of the cortication and width of the internodes is also characteristic (see key). Some specimens, however, do intergrade in the nodal characteristics and length of the internodal space (see under *C. excellens*).

*Ceramium isogonum* Harvey 1855: 557; 1862: pl. 206*B*; 1863: synop.: 48. J. Agardh 1876: 96; 1894: 30. De Toni 1903: 1469; 1924: 510. Guiler 1952: 98. Lucas 1909: 53; 1929*a*: 26. Lucas and Perrin 1947: 369, fig. 186. Mazza 1912: 594. Tisdall 1898: 503. Wilson 1892: 184. Womersley 1950: 180.

# Figs 3A, 12

Thallus (Fig. 12A, B) grey-red to red-brown,  $\frac{1}{2}$ -3(-6) cm high in rough-water

forms, to 12 cm high under slight to moderate water movement, epilithic or epiphytic on various algae or *Posidonia*, with one to several axes arising from prostrate basal parts attached by numerous rhizoids which arise from the periaxial and inner cortical cells and consist of one to a few uniseriate cells and a digitate pad which becomes



Fig. 3. C. isogonum. A, Nodal cortication and tetrasporangia (A37504).

*C. australe. B*, Two nodes showing periaxial and pseudoperiaxial cells, and cortical cell lineages. *C*, Cross section of node showing periaxial and pseudoperiaxial cells (both A39252).

C. cupulatum. D, Cupulate nodes with acropetal (only) development of cortical cells, the terminal cell often bearing a hair (A15430).

C. macilentum. E, Nodes with involucrate tetrasporangia, periaxial and pseudoperiaxial cells, and acropetal (only) development of cortical cells (A41286).

multicellular. *Branching* regularly pseudodichotomous, rarely with a few proliferous laterals.

*Branches* in rough-water forms 400–600  $\mu$ m in diameter below, tapering gradually to about 200  $\mu$ m near the apices, in slight water movement 200–400  $\mu$ m below tapering

to about 100  $\mu$ m near the apices; apices usually involute. Axial cells L/B about  $1(-1\frac{1}{2})$  in rough-water forms, extending in lower parts of plants in slight water movement to L/B 2-3(-4), with distinct internodal spaces throughout and regular, welldefined nodal cortical bands (Fig. 12D). Periaxial cells 7-8(-9), each cutting off two cells acropetally and basipetally, these cutting off (1-)2 further cells, which divide further in older parts, to form nodal bands 5-7 cells long and usually broader than long (Fig. 3A); ultimate acropetal cortical cells generally smaller than basipetal ones, developed more or less synchronously, leaving a very short (especially in rough-water forms) and well-defined internodal space (Fig. 12D, E) in the younger branches, this space in older parts becoming as long as the nodal band in rough-water forms and up to 4 times as long in forms in slight water movement. Outer cortex (Figs 3A, 12C) developed from the larger inner cortical cells and periaxial cells, with small cells which may appear as rosettes. Darkly staining gland cells (Fig. 12C, D) occur occasionally to profusely, sometimes absent, derived from the smaller outer cortical cells, scattered over the nodes.

Carposporophytes 150–350  $\mu$ m across, with 2–4 short involucral branchlets.

Spermatangia (Fig. 12D) cut off from outer cortical cells, covering the node on all sides.

*Tetrasporangia* (Figs 3A, 12E) prominent, external and completely naked, derived initially from the first acropetal cortical derivatives of the periaxial cells and thus forming an irregular ring around the upper edge of the nodal cortication, later from other cortical cells, cruciately or tetrahedrally divided, spherical, 50–70  $\mu$ m in diameter.

Type locality.- Garden I., W.A.

Type.-- Herb. Harvey, TCD (Trav. set 286).

Distribution.- From Garden I., W.A. along southern Australia to Wilson's Promontory, Vic., on rough-water rock platforms just below low tide level (stouter forms) and also 2-4(-8) m deep in conditions of slight to moderate water movement, e.g. at American R. inlet on Kangaroo I. and at Port Lincoln, S.A. (slender, larger forms). Also probable records from Gunnamatta Bay, Port Hacking, N.S.W. (*Womersley*, 23.viii.1945; ADU, A2076), Botany Bay, N.S.W. (NSW 138539) and Moreton Bay, Qld (*Watson*, 22.viii.1975; ADU, A46542). Lucas (1929*a*, p. 26) records it from Tasmania.

Selected specimens studied.- Elliston, S.A., 4 m deep (Shepherd, 22.x.1970; ADU, A37504, A37518). Billy Light's Point, Port Lincoln, S.A., 4 m deep (Shepherd, 23.viii.1975; ADU, A46534). Muston, American R. inlet, Kangaroo I., S.A., 2-3 m deep (Kraft, 17.vii.1972; ADU, A42539 and Kraft et al., 16.iv.1973; ADU, A43756).

*C. isogonum* is usually distinctive, being recognizable as a relatively stout species (especially on rough-water coasts) with regular subdichotomous branching. The usual presence of gland cells and prominent, naked tetrasporangia, together with the well-defined nodal cortical bands (both superficially and in cell detail) further characterize the species. Harvey's original description and illustrations apply to the form from rock platforms under strong water movement; in conditions of slight to moderate water movement, a form with longer axial cells and internodal spaces occurs, but the nodal cortication and reproductive features are identical with the rougher water forms.

Weber van Bosse (1923, p. 329) recorded *C. isogonum* from Indonesia, but detailed study is needed to verify this record from well outside its Australian distribution.

# *Ceramium australe* Sonder 1845: 52; 1848: 167. J. Agardh 1851: 124; 1876: 93; 1894: 16. De Toni 1903: 1449. Harvey 1855: 557; 1863, synop.: 48. Lucas 1909: 53. Tisdall 1898: 503?

Gongroceras australe (Sonder) Kuetzing 1849: 679.

# Figs 3B, C, 13A-D

*Thallus* (Fig. 13*A*) brown-red to deep red, 1-4(-6) cm high, epiphytic on seagrasses or red algae, with several erect branches arising from slight, prostrate, basal filaments attached by uniseriate-celled rhizoids which may develop multicellular pads, and which arise from the periaxial (occasionally pseudoperiaxial) cells. *Branching* regularly subdichotomous in varied planes, without proliferous branchlets.

Branches (160–)200–300  $\mu$ m in diameter below, decreasing gradually to 100–150  $\mu$ m in diameter near the apices, then tapering more abruptly to the strongly involute apices. Axial cells isodiametric near apices, L/B (1–)2–2½(-3) below, with regular, straight-margined bands of nodal cortication (Fig. 13B) mostly 80–120  $\mu$ m long, separated by an internodal space  $\frac{1}{4}$ –1 times the nodal length above and 2–3 times in the lower parts. Periaxial cells 6–7, each cutting off laterally (so that they lie in the periaxial cell ring) two slightly smaller pseudoperiaxial cells (Figs 3B, C, 13B, C), each of which cuts off one cell acropetally and basipetally, these then dividing to form one or two cells which usually divide again, forming nodal cortication (5–)7 cells long (Figs 3B, 13B, C); the true periaxial cells cut off one cell acropetally and this cuts off one or two more, but no cells are cut off basipetally (Fig. 3B); first acropetal derivative of the periaxial cells commonly cutting off a large gland-like cell (Fig. 13C); no outer cortex is formed.

Carposporophytes unknown.

Spermatangia unknown.

Tetrasporangia (Fig. 13D) produced in irregular abaxial series, with up to three per node formed successively, spreading more around the node; sporangia cut off acropetally from periaxial cells, slightly basally involucrate by cortical filaments with slightly longer cells (but few, if any, more cells) than in sterile nodes; tetrasporangia subspherical to pyriform, irregularly horizontally divided into bispores (in plants observed), 50–65  $\mu$ m across plus a prominent sheath which remains after spore discharge.

Type locality.- Western Australia (Preiss). Probably from near Perth.

*Type.*– Isotypes in LD (20679, on *Corallina*, selected as lectotype), TCD (on *Laurencia*), and S (on *Corallina*). None located in MEL.

*Distribution.*- Known from the type locality and Fremantle vicinity (*Harvey*, Alg. Aust. Exsice. 471A), W.A., and from Tipara reef, Spencer Gulf, S.A., 5 and 11 m deep, on *Amphibolis* (*Shepherd*, 13.vii.1971, 13.xii.1971; ADU, A39252, A41217 respectively); Baudin Rocks, Guichen Bay, S.A., on *Posidonia australis*, 2–3 m deep (*Shepherd*, 15.ii.1975; ADU, A46123); from North Walkerville (Waratah Bay), Vic., drift on *Hymenocladia?* (*Sinkora* A1572, 23.ii.1972; ADU, A43146 and MEL 45447), and from Leven, Tas. (*Lodder*; MEL 45454).

Both the Lund isotype and Harvey's Alg. Aust. Exsicc. 471A (in LD) agree well with the above description. However, Harvey's Friendly Islands Algae No. 59, distributed as *Ceramium australe* Sonder, is not this species since it does not have the periaxial and nodal cell arrangement of this species and has whorled, largely involucrate tetrasporangia.

The epithet *australe* was also used by Cramer (1864, p. 104) for a species referred to his *Herpoceras*; this species is described below as *C. filiculum*.

While superficially similar to C. isogonum, C. australe is very distinctive in the pattern of nodal cortication. The lateral formation of pseudoperiaxial cells, which lie largely in the periaxial ring as seen in thallus section, thus giving a ring of 18 or 21 cells with the larger periaxial cells separated by two smaller pseudoperiaxial cells, is a pattern not seen in any other southern Australian species of Ceramium. Since each periaxial cell cuts off only a single cell acropetally, they have pit-connections with only 3 cells compared to most other species with 4 cells derived from each periaxial cell [C. flaccidum (see below) also cuts off 3 cells but in a different pattern]. In the Lund and TCD isotypes and commonly but not always in other specimens, many of the first acropetal derivatives of the periaxial cells cut off a comparatively large and densely protoplasmic gland-like cell (Fig. 13C).

The tetrasporangia as observed in the Tipara specimens all appear to have only an irregularly horizontal division, though the sporangia appear mature; further observations on the sporangial division and release of the spores are needed.

#### Ceramium cupulatum, sp. nov.

C. repens Harvey 1863, synop.: 48. J. Agardh 1876: 92. De Toni 1903: 1446. Lucas 1909: 52. Lucas and Perrin 1947: 365.

NON C. repens (Dillw.) C. Agardh 1817: 63, = Spermothamnion turneri, or C. repens Zanardini 1847: 41, = C. rubrum?

# Figs 3D, 13E–1

Thallus (Fig. 13E) red, to 1 cm high, forming a dense cover on *Corallina*, with extensive prostrate filaments attached by one to several (clumped) rhizoids arising from the periaxial cells on the underside of the filaments; rhizoids single or often densely grouped, usually unicellular plus the multicellular pad of one or a group of rhizoids. *Erect filaments* numerous, arising from most nodes of the prostrate filaments; nodes, especially in erect filaments, cupulate in form due to acropetal development only of cortical cells.

Branches 75–200  $\mu$ m in diameter (at nodes), fairly uniform in diameter to just below the erect or involute, usually tapering, apices (Fig. 13*F*, *I*). Axial cells isodiametric near apices, elongating to L/B 2–4 below, with prominent nodal bands 35–80  $\mu$ m long and internodal spaces about as long as the nodes near apices (Fig. 13*F*), elongating to 2–4 times as long below. Periaxial cells 6–8, each cutting off two cells acropetally (Fig. 3*D*) with continued divisions into one or two cells (progressively smaller) to give a node 4–5 cells long in upper parts, 6–7 cells long below; usually no basipetal cells are cut off by the periaxial cells (Figs 3*D*, 13*F*), and no outer cortical cells are formed, but in A19591 some of the periaxial cells in older nodes cut off single cells laterally (partly in the periaxial ring) or just basipetally; slender hairs are produced by many of the terminal cortical cells of each node.

Carposporophytes (Fig. 13G) borne part way up the erect branches, surrounded by 3–7 slightly curved to straight laterals (often relatively long) which arise from periaxial cells of the axial cell bearing the carposporophyte; carposporophytes globular, 200–300  $\mu$ m across.

Spermatangia (Fig. 13H) covering the nodes of erect branches, produced from all cortical cells of a node.

*Tetrasporangia* (Fig. 13*I*) at first unilateral but becoming verticillate on upper parts of erect branches, prominent, with several produced successively from each node from the periaxial cells, with the lower  $\frac{1}{3}-\frac{1}{2}$  of the tetrasporangia involucrate by cortical filaments; these filaments usually showing 2–3 more divisions than the other nodal cortical filaments, which are often only 3–4 cells long; tetrasporangia with prominent persistent sheaths, 35–60  $\mu$ m in diameter, subspherical, cruciately divided.

Diagnosis.– Thallus caespitosa ad 1 cm altus, epiphyticus in Corallina, pronis filis ramos multos erectos nunc simplices nunc subdichotomos vel laterales producentibus; nodi cupulati. Rami 75–200  $\mu$ m diam., cellulae axiales in parte basali 2–4 plo longiores latitudine, ad apicem isodiametricae, nodi 35–80  $\mu$ m longi, spatiis inter nodos in parte basali 2–4 longioribus quam nodis et ad apicem eiusdem longitudinis. Cellulae periaxiales 6–8 quaeque cellulas duas acropete efferentes, deinde denuo divisae nodos ad 4–5 cellulas longitudine superne, ad 6–7 cellulas longitudine inferne producere; cellulae basipetae et cellulae externae corticales plerumque absunt. Tetrasporangia inferne involucrata sursum verticillata cruciatum divisa.

Type locality.- D'Estrees Bay, Kangaroo I., S.A., on Corallina cuvieri in pools at reef edge (Womersley, 24.viii.1950).

Holotype.- ADU, A15430; isotypes also under this number.

*Distribution.*- Only known from the type locality; from Point Sinclair, S.A., lower eulittoral on *Corallina (Womersley*, 7.ii.1954; ADU, A19591); and from Port Phillip, Vic., on *Corallina (F. v. Mueller)*.

C. repens Harvey was recorded from Diego Garcia, Mahé, by Reinbold (1907, p. 576), but it seems unlikely that this record applies to the southern Australian species.

*C. cupulatum* is a distinctive species, characterized by its small size, epiphytic habit on *Corallina*, and especially by the cupulate nodes produced by the spreading, acropetal development from the periaxial cells. The commonly clumped rhizoids are similar to those of *C. filiculum*.

C. avalonae Dawson (1949, p. 17, figs 31, 56; 1950, p. 133, figs 25, 26) appears most closely related to C. cupulatum, having the nodal cortical cells derived only acropetally from the periaxial cells. However, C. avalonae is apparently a slenderer plant, growing entangled with other algae rather than in tufts, and has less well defined cupulate nodes, and the tetrasporangia are less involucrate; it thus seems preferable to recognize them as distinct species. Dawson (1962, p. 52) was clearly incorrect in placing his C. avalonae as a synonym of C. caudatum Setchell and Gardner; their nodal cortical structure is quite different.

Ceramium macilentum J. Agardh 1894: 15. De Toni 1903: 1445. Lucas 1909: 52. Lucas and Perrin 1947: 365.

# Figs 3E, 14A-D

*Thallus* (Fig. 14*A*) light red, from a few millimetres to 6 cm high, erect or often in tangled masses, on solid substrates, ascidians or epiphytic on various algae, attached by rhizoids of 1–3 uniseriate cells with a multicellular pad and which arise usually singly from a periaxial cell of each (or many) node of prostrate filaments. *Branching* subdichotomous to 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.

Branches 70–130(–150)  $\mu$ m in diameter below, tapering often very slightly to 50–70  $\mu$ m several cells below the (normally) involute apices. Axial cells L/B (1–)1 $\frac{1}{2}$ –2(–3) above, elongating in larger specimens to 6–8 times, with a narrow cortical nodal band 35–50  $\mu$ m long (Fig. 14B). Periaxial cells usually 6, most of which divide obliquely to form a wedge-shaped pseudoperiaxial cell (Figs 3E, 14B, D) 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 (Figs 3E, 14B); very occasional basipetal cells (Fig. 3E) may be cut off from the periaxial cell 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.

*Carposporophytes* (Fig. 14*C*) with 1–2 irregularly globular lobes, 100–200  $\mu$ m across, subtended by 2–4 curved branchlets.

Spermatangia forming patches on the adaxial sides of nodes, later tending to spread around the node.

Tetrasporangia (Figs 3E, 14D) in prominent, abaxial, unilateral 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 cruciately to tetrahedrally divided, 40–75  $\mu$ m in diameter, with a persistent sheath.

Type locality.- Port Phillip, Vic. (Wilson).

Type.- Herb. Agardh, LD, 20616.

Distribution.- From Port Denison, W.A., around southern Australia to Western Port, Vic., and probably on the New South Wales coast (e.g. Botany Bay, N.S.W., Lucas Jan. 1914; NSW 138625).

Selected specimens studied.- Douglas Bank, northern Spencer Gulf, S.A., 20 m deep (Johnson, 19.xi.1975; ADU, A46700). Muston, American R. inlet, Kangaroo I., S.A., 2-3 m deep (Kraft et al., 16.iv.1973; ADU, A43755). Port Stanvac, S.A., 5-6 m deep on jetty piles (Lewis, 3.ii.1972; ADU, A41286). Crawfish Rock, Western Port, Vic., 6 m deep (Watson, 28.v.1974; ADU, A45418).

*C. 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, thus giving a very narrow nodal ring of cells; the unilateral rows of partly involucrate sporangia are also characteristic. There is considerable variation, however, in branching, diameter of the filaments, and degree of extension of the axial cells.

C. macilentum appears to be moderately common in regions of slight water movement. The closest species in southern Australia is the slightly more robust C. cliftonianum, which differs in its much greater cortical development, without pseudoperiaxial cells; occasionally, however, specimens apparently intermediate between them may be found. In the presence of pseudoperiaxial cells, C. australe shows relationship with C. macilentum but differs significantly in the more regular and twinned arrangement of the pseudoperiaxial cells and a more developed cortex, as well as in dimensions and sporangial arrangement.

Whether C. macilentum is distinct from all other slender species of Ceramium cannot be determined until the cortical development of extra-Australian species is studied in detail. The illustrations of Feldmann-Mazoyer (1940, fig. 107) for C. tenerrimum (Martens) Okamura suggest that pseudoperiaxial cells may be present and

that there is slight if any basipetal development in Mediterranean material referred to this species. However, it appears uncertain that the Mediterranean species is identical with the Japanese C. tenerrimum which Nakamura (1965, p. 133) and Itono (1977, pp. 111, 199, figs 13K, 15C, D, 38B, C) describe as having basipetal cortical cells and whorled tetrasporangia. The taxon described by Itono (1972, p. 78, figs 6, 7; 1977, pp. 32, 100, 196, figs 13C, 37B) as C. fastigiatum var. flaccida Petersen is also closely related to C. macilentum.

#### Ceramium flaccidum (Kuetzing) Ardissone 1871: 40.

Hormoceras flaccidum Kuetzing 1862: 21, pl. 69a-d.

- Ceramium gracillimum Griffiths and Harvey ex Harvey 1848: pl. 206. J. Agardh 1851: 118; 1876: 95; 1894: 43. Guiler 1952: 98. Harvey 1855: 557; 1859: 330; 1863, synop.: 48. Lucas 1909: 53; 1929a: 26; 1929b: 53. Lucas and Perrin 1947: 369. Nakamura 1965: 136, fig. 6, pl. 1 figs 5,6. Reinbold 1898: 51. Tisdall 1898: 503. Wilson 1892: 184.
  - NON C. gracillimum C. Agardh 1824: 140 (= Compsothamnion).
- NON Hormoceras gracillimum Kuetzing 1841: 733 (= C. diaphanum?). C. gracillimum var. byssoideum (Harvey) Mazoyer 1938: 323. Dawson 1962: 57, pl. 20 figs 2, 3, pl. 21 figs 2, 3. Feldmann-Mazoyer 1940: 293, fig. 109. Itono 1972; 76. figs 2, 3: 1977; 32.
- 105, 197, 265, figs 13*H*, 14*A*-*D*, 37*C*.
- Ceramium byssoideum Harvey 1853: 218.
  - NON C. byssoides Ducluzeau 1805: 66 [placed by De Toni (1903: 1329) as a synonym of Callithamnion corymbosum (Sm.) Lyngbye.]
- C. byssoideum var. alternatum Ballantine and Humm 1975: 158, fig. 2.
- C. transversale Collins and Hervey 1917: 145, pl. 5 figs 29-31.
- C. fimbriatum Setchell and Gardner 1924: 777, pl. 26 figs 43, 44. Dawson 1962: 56, pl. 19 fig. 3, pl. 20 figs 6, 7. Itono 1977: 33, 106, 197, figs 13*I*, 14*E*-*G*, 37*D*. Nakamura 1965: 143, fig. 8.
- C. taylorii Dawson 1950: 127, pl. 2 fig. 13, pl. 4 figs 31-33; 1962: 65, pl. 26 figs 1-3. Itono 1972: 76; 1977: 33, 108, 198, figs 13K, 14H.
- C. masonii Dawson 1950: 126, pl. 2 figs 11, 12.
- C. miniatum sensu Womersley 1950: 180 (NON Suhr ex J. Agardh 1851: 135).

# Figs 4*A*–*D*, 14*E*–*H*

Thallus (Fig. 14E) light red to dark red-brown, slender, variable in height  $[\frac{1}{2}-5(-10)$  cm], usually as epiphytic tufts (on Corallina and a variety of algae), occasionally as a tuft on rock or on other firm substrates, with prostrate basal filaments producing several to numerous erect axes, attached by unicellular rhizoids (including the digitate pads) arising from the periaxial cells of prostrate filaments. Branching (Fig. 14G) alternate or occasionally subdichotomous, irregular to almost complanate above, usually with moderately short laterals near the apices and becoming denuded in lower parts where the red-brown nodes contrast with the colourless internodal regions of the elongate cells; proliferous branchlets, slenderer than parent branches, often present.

Branches with nodes usually broader than internodes, variable in thickness depending partly on degree of water movement; in strong water movement, 150–250  $\mu$ m in nodal diameter below, tapering gradually to 75–100  $\mu$ m near the apices; in slight water movement, 100–150  $\mu$ m in nodal diameter below, decreasing to 60–80  $\mu$ m near the apices; apices slightly to strongly involute. Axial cells isodiametric near apices, extending to L/B 4(-6) below, with nodes 5–9(–11) cells long and usually slightly broader acropetally than basipetally; internodal space shorter than nodes near apices, soon elongating to 3–6(–8) times as long as node. Periaxial cells 6–7, each cutting off 2 cells acropetally which further cut off 1 or 2 cells to produce acropetal chains 3–4 cells long, successively smaller; basipetally, only a single, elongate derivative



(Figs 4A-D, 14F) is cut off from each periaxial cell, and this derivative may then divide in various ways (often in the one plant)—(a) to form a further (and sometimes

**Fig. 4.** *C. flaccidum. A*, Nodes of a young branch with single basipetal periaxial derivatives. *B*, Older nodes with most basipetal derivatives divided; a single clavate hair present (both A43757). *C*, Node of more robust form showing cortical lineages and one acropetal gland cell. *D*, Node on older branch with slight outer cortex and several gland cells (*C*, *D*, A42759).

C. filiculum. E, Node of young branch. F, Node on older mature branch (both A32635).

C. cliftonianum. G, Cortex of node of robust plant, with regular basipetal cells (A30860). H, Nodal cortex of slender plant, with two basipetal cells (A34110).

again) elongate cell which remains intact (Fig. 4A); (b) to cut off two smaller cells (Fig. 14F), often from the corners, which may then each cut off one or two cells and

this may be repeated; (c) the elongate first (or later) derivative may divide transversely (Figs 4B, C, 14F) into 2-4 small isodiametric cells, one only of which remains in pit-connection with the periaxial cell. Thus a node 6-8 cells long is formed. A few outer cortical cells (Fig. 4D) may be cut off from the first periaxial cell derivatives in older plants, but they usually lie almost within the cortical layer. In some plants, the terminal cortical cells (especially acropetal) and sometimes other cortical cells become gland-like (Fig. 4D), but this is a variable feature. Slender hairs are commonly produced from the cortical cells near apices, and in some plants few to many abaxial, elongate-clavate hairs (Fig. 4B) are also produced ('fimbriate' forms).

Slide mounts commonly show a narrow annular space (Fig. 14F) between the periaxial cells and the basipetal derivatives, probably because of the single pit-connection to the latter; this space is occasionally visible in living material.

Carposporophytes globular, 200–300  $\mu$ m across, with 3–6 slightly curved involucral branchlets.

Spermatangia (Fig. 14G) covering the nodal cells of young branches.

*Tetrasporangia* (Fig. 14*H*) usually in whorls of (2–)4–7, produced acropetally from the periaxial cells, with a prominent cupulate involucre largely covering the sporangia, formed by cell enlargement rather than further divisions of the acropetal cortical filaments; sporangia subspherical, 35–50  $\mu$ m in diameter, tetrahedrally to sub-cruciately divided.

Type locality.- Kilkee, Co. Clare, Ireland (Harvey).

*Type.*- L, 940,265...55 (lectotype and isotype). Isotypes in BM, TCD and probably elsewhere.

*Distribution.*– Probably cosmopolitan in cold temperate to tropical seas. Along the whole southern Australian and Tasmanian coasts, extending north along eastern Australia. Common near low tide level and in wave-washed pools, on rock or epiphytic (especially on *Corallina*).

Selected specimens studied.- Wanna, S.A., low eulittoral (Gordon, 15.v.1968; ADU, A32633). Aldinga, S.A., reef pools (Womersley, 28.v.1972; ADU, A42255). Muston, American R. inlet, Kangaroo I., S.A., 2-3 m deep on Heterozostera (Kraft et al., 16.iv.1973; ADU, A43757). Cape Lannes, S.A., low eulittoral (Womersley, 15.v.1972; ADU, A42392). Little Dip (S. of Robe), S.A., mid eulittoral pools (Womersley, 8.x.1972; ADU, A42759).

This species has commonly been known as C. gracillimum Griffiths and Harvey, based on Harvey's specimens and his description in Phycologia Britannica. However, Harvey was using Kuetzing's (1841) name gracillimum and states that Kuetzing considered Harvey's Kilkee material the same as his from the Adriatic. Kuetzing (1862, p. 21) later apparently realized he was in error in considering Harvey's material the same as his, for he described and figured both his own gracillimum and Harvey's Kilkee plant, the latter as Hormoceras flaccidum using Harvey's earlier provisional manuscript species epithet. Thus flaccidum appears to be the earliest valid epithet for this species, first referred to Ceramium by Ardissone (1871). The type of H. gracillimum Kuetzing in L also does not agree with the usual concept of this species, but is probably related to C. diaphanum (Lightfoot) Roth. (Comment based on slide and information from P. S. Dixon.)

In any case, *Ceramium gracillimum* (Kuetz.) Zanardini (1847, p. 223) (the first author making this combination) is invalidated by *C. gracillimum* C. Agardh (1824, p. 140), a name which probably applies to a *Compsothamnion*.

Harvey (1849, pl. 206) depicted well the habit of *C. flaccidum*, and described its most common occurrence on *Corallina* at about extreme low water. He did not give any details of the nodal cortex, but the type (and isotype under the same number) in L, and isotypes in BM, show the typical structure as described above, as does liquid preserved material from Duggerna Rocks, Kilkee, growing on *Corallina* about low tide level (*O. Morton*, 1.ix.1977; ADU A48144). Since then, this taxon has been described under a variety of names. The next earliest name, *C. byssoideum* Harvey (predated by *C. byssoides* Ducluzeau), was based on Florida, U.S.A., material. This name has usually been reduced to varietal status as *C. gracillimum* var. *byssoideum* (Harvey) Mazoyer (see Feldmann-Mazoyer 1940, p. 293), the variety being distinguished by its smaller size. As described above, however, the species is variable in its height and robustness, and such a variety is not worth distinguishing. Similarly, var. *alternatum* Ballantine and Humm is typical of the species in branching pattern, although the nodal cortication is not described.

More recent names applied to *C. flaccidum*, all of which show the habit, dimensions, nodal development and reproduction of this species, and should therefore be regarded as synonyms, are:

- C. transversale Collins and Hervey (1917) from Bermuda [P.B.A. 2049 from Harrington Sound, 1.v.1912, Collins (UC, 693099) examined].
- C. fimbriatum Setchell and Gardner (1924) from Baha California [type slide of Marchant 87a (in UC, no sheet found) examined, containing a few fragments of C. fimbriatum]. The hairs supposedly characteristic of this species are of variable occurrence in specimens of C. flaccidum.
- C. taylorii Dawson (1950) from Baha California [isotype slide of Dawson 3393 (UC, 925470) examined].
- C. masonii Dawson (1950) from Baha California [slide of Dawson 6730 (ADU, A14772) examined].

C. recticorticum Dawson (1950, p. 124, pl. 3 figs 23, 24) has the same basipetal cortical development as C. flaccidum, but in addition single cells are often (not always) cut off acropetally according to type material and Dawson's figures; this may characterize recticorticum as a distinct species, but it is closely related to C. flaccidum and its variation needs study. Probably several other names will prove to be synonyms of C. flaccidum when their nodal cortication is analysed.

A further old epithet which probably applies to *C. flaccidum* is *Ceramium pulchellum* (Kuetzing) Grunow 1870, p. 62 (see also Kylin 1938, p. 14, fig. 7*C–E*), which is based on *Hormoceras pulchellum* Kuetzing (1849, p. 676; 1862, p. 23, pl. 75*d–i*), from Table Bay, South Africa. De Toni (1903, p. 1481) placed *H. pulchellum* Kuetzing doubtfully under *C. diaphanum*, and Simons (1966, p. 162, fig. 3-1, pl. 2-2) placed it as var. *pulchellum* (Kuetz.) Simons of *C. diaphanum*. Simons gave the same Kylin (1938) reference for both var. *pulchellum* and his newly described *C. papenfussianum* Simons (1966, p. 159, fig. 2, pl. 2-1). The latter is almost certainly a synonym of *C. flaccidum*. Three specimens in ADU (A40680, 40681, 40683) from Olifantsbosch, S. Africa (*Isaac*), and annotated by Simons in 1961 as *C. pulchellum* has not been located in the Rijksherbarium, Leiden (see Lucas 1953, p. 323). Lucas places *C. pulchellum*, on the basis of another specimen identified by Kuetzing, under *C. diaphanum* var. *zostericola* (Thuret) Feldmann-Mazoyer, and comments "In rare cases the corticated zones are

divided into two parts by a horizontal hyaline space"—i.e. as in *C. flaccidum*. Until Kuetzing's type of *C. pulchellum* is located, the application of this name must remain uncertain.

The name C. pulchellum (Kuetz.) Grunow is however invalidated by C. pulchellum C. Agardh (1811, p. 19) which applies to a freshwater alga from Sweden.

Another, even earlier, name which must be accounted for is *C. loureiri* C. Agardh (1824, p. 137) from Cochin China, which Dawson (1954, p. 446) suggests may be similar to *C. taylorii*. This type of *C. loureiri* (a Loureiro specimen) has not been located in either LD or LINN (by J. H. Price).

C. flaccidum is a variable species in size and to some degree in robustness, as well as in the presence of 'fimbriate' hairs and gland cells. It is characterized by being relatively slender with alternate, lateral branching, with the cells and internodal spaces relatively short above but elongating markedly below where few lateral branches remain; in living plants the short, pigmented nodes contrast with the long colourless internodes.

The most striking features however are the uniform formation of only one cell basipetally from each periaxial cell, compared to two cells acropetally, and the unicellular rhizoids and pads in contrast to the uniseriate-celled and multicellular pads of other southern Australian species. Further divisions of this single basipetal derivative do, however, vary considerably, even in the one plant. In slender species (of calm habitats), the single first derivative may cut off a second single elongate cell, and this even a third, remaining in this state. It is common however for the first single derivative to cut off (often from its corners) two cells, which then divide into one or commonly two more cells. Also, the first single elongate derivative commonly divides transversely, so that it appears that 2, 3 or even 4 cells correspond basipetally to one periaxial cell; the pit-connections, however, show the origin of these cells. A consequence of continuing production of pairs of cells acropetally in the node, and a single basipetal cell at least initially, is that the acropetal part of the node commonly broadens compared to the slightly narrower basipetal part, and (especially in stained and mounted specimens where the cells contract slightly) the basipetal cortication becomes separated by a narrow 'line' or space from the periaxial cells and acropetal cortication; this is only occasionally visible in living specimens.

# Ceramium filiculum, sp. nov.

C. miniatum sensu Harvey 1855: 557; 1862: pl. 206A; 1863, synop.: 48. J. Agardh 1876: 104; 1894: 18 (both in part). De Toni 1903: 1454; 1924: 508 (both in part). Lucas 1909: 53. Lucas and Perrin 1947: 367, fig. 185. Mazza 1912: 591. Tisdall 1898: 503. Wilson 1892: 185. NON Suhr ex J. Agardh 1851: 135.

Herpoceras australe Cramer 1864: 104, pl. xi fig. 14, pl. xii figs 1-7.

# Figs 4E, F, 15A-E

*Thallus* (Fig. 15*A*) red to dark red, to  $1(-1\frac{1}{2})$  cm high, epiphytic on cartilaginous brown (and occasionally red) algae, at first with a single erect base attached by rhizoids descending from the lower segments, and later with prostrate filaments attached by relatively massive holdfasts (Fig. 15*B*) formed of numerous, usually tightly clumped, rhizoids originating from all the cortical cells on the underside of a node, and with the ends of the peripheral rhizoids splayed out and becoming multicellular. *Branching* essentially complanate (Fig. 15*A*), alternate and usually 3 cells

apart (occasionally 4, rarely 5), forming flabellate groups of laterals, usually without proliferations.

Branches terete,  $100-200(-280) \ \mu m$  in diameter below, with the laterals  $80-150 \ \mu m$  in diameter near their bases, tapering to  $50-70 \ \mu m$  shortly below the straight to slightly involute apices (Fig. 15*C*, *D*). Axial cells L/B about  $1(-1\frac{1}{2})$  throughout the thallus, with internodal spaces  $\frac{1}{2}-1(-2)$  times as long as nodal bands in mature parts, shorter near the apices. Periaxial cells 6, each cutting off usually 2 cells acropetally and 2(-3) cells basipetally (Fig. 4*E*, *F*); the basipetal cells usually cut off only 1 (rarely 2) more cell so that basipetal chains in older parts are only 2 cells long except in the oldest parts where they may be 3 cells long; acropetally, the derivatives cut off (1-)2(-3) cells which divide similarly twice in mid parts of the thallus and up to 4 times in older parts, with some cells being cut off in the reverse direction; the node is thus 5-6 cells long (30-70  $\mu$ m) in mid parts of the thallus, and may be up to 9 cells long (80-150  $\mu$ m) in older parts (Fig. 4*F*); the nodes have relatively straight margins and the acropetal development is always greater than the basipetal. No real outer cortex is formed. Fine, slender hairs occur in actively growing plants.

Carposporophytes (Fig. 15C) occur on upper branches, globular, 150–250  $\mu$ m across, with 3–6 relatively robust, usually slightly curved, involucral branchlets.

Spermatangia (Fig. 15D) covering the nodal cortex of upper branches and often reaching the apices, surrounding the branchlet or sometimes mainly adaxial.

*Tetrasporangia* (Fig. 15*E*) in lateral branch groups, opposite in the plane of branching with the fertile branchlet ovoid in section, arising acropetally from the opposite periaxial cells (often with a later formed sporangium), largely involucrate within the cortical filaments (which may be 1–2 cells longer than in vegetative parts), cruciately divided, subspherical to ovoid,  $30-40(-50) \mu m$  across.

Diagnosis.- Thallus ad  $1(-l\frac{1}{2})$  cm altus, epiphyticus, filis pronis per haptera crassa rhizoideorum multorum fasciculatorum affixis; rami filorum erectorum, complanati alterni, plerumque 3 cellulis separati, lateralibus filis flabelliformibus. Rami in parte basali 100-200(-280)  $\mu$ m diam., ad apices 50-70  $\mu$ m, cellulae axiales subglobosae  $1-l\frac{1}{2}$  plo longiores latitudine, spatia inter nodos  $\frac{1}{2}-1(-2)$  plo longiora quam nodi basaliter, ad apicem breviora. Cellulae periaxiales sex, quaeque cellulas duas acropete et basipete efferentes, deinde denuo divisae in nodos longitudine ad 5-6 cellulas superne, ad 9 cellulas longitudine inferne; cortex externus abest. Tetrasporangia quoad planum ramificationis opposita, plerumque involucrata, cruciatim divisa.

Type locality.- Port Noarlunga, S.A., in low eulittoral pools on offshore reef, on basal leaves of Sargassum lacerifolium (Womersley, 13.iii.1977).

Holotype.- ADU, A47978. Isotypes also under this number.

Distribution.- From Fremantle, W.A., to Port Noarlunga, S.A., Port Phillip Heads, Vic. (Tisdall), and from Kiama to Terrigal, N.S.W. (on *Ecklonia*). Usually growing under moderate to strong water movement, epiphytic on large brown algae. Laing's (1927, p. 176) doubtful record from New Zealand needs checking.

Selected specimens studied.- Elliston, S.A., on Sargassum, reef pools (Gordon, 16.v.1968; ADU, A32635). Cape Carnot, S.A., on Myriodesma harveyanum, sublittoral fringe (Womersley, 8.i.1951; ADU, A15104). Wanna, S.A., on M. harveyanum, drift (Womersley, 19.ii.1959; ADU, A22391). Port Noarlunga, S.A., on Sargassum lacerifolium in pools on offshore reef (Womersley, 13.iii.1977; ADU, A47978).

This Australian species was first placed in C. miniatum Suhr by Harvey (1855,

p. 557; 1862, pl. 206*A*). *C. miniatum* Suhr ex J. Agardh was described from Callao, Peru, but doubts about the locality were expressed by J. Agardh (1894, p. 18). Howe (1914, p. 157) and Taylor (1939, p. 152) believed the Peru locality correct. However the Australian taxon, though related, is almost certainly different from the South American, and in any case *C. miniatum* Suhr ex J. Agardh (1851) is invalidated by *Ceramium miniatum* C. Agardh (1824, p. 141) from the Mediterranean (a *Callithamnion*?).

C. filiculum was later described by Cramer (1864, p. 103) as a new genus and species, *Herpoceras australe*, based largely on the striking rhizoidal holdfasts. Cramer's excellent illustrations are unmistakable. However, similar holdfasts are found to a lesser extent in C. cupulatum and do not provide a satisfactory generic separation in view of the full agreement of all other features with Ceramium. H. australe Cramer is pre-dated by C. australe Sonder (1845), and the original manuscript name of Harvey (1855, p. 557) is here used for the Australian species.

C. miniatum was also recorded with doubt from New Zealand by Laing (1927, p. 176) and Naylor (1954, p. 659), but these records need verification.

C. filiculum appears to be a distinctive species, characterized by the striking holdfast of usually densely clumped rhizoids, the regular, alternate and complanate branching usually 3 cells apart, with short axial cells throughout, by the rather regular nodal cortex with short internodal spaces, and by the opposite, involucrate tetrasporangia.

It is apparently always epiphytic on larger, usually cartilaginous, brown and occasionally red algae.

Ceramium cliftonianum J. Agardh 1876: 93; 1894: 16. De Toni 1903: 1449. Lucas 1909: 53.

 C. ramulosum Hooker and Harvey 1847: 410. J. Agardh 1851: 121; 1876: 95; 1894: 15. De Toni 1903: 1446. Guiler 1952: 98. Harvey 1859: 330; 1863, synop.: 48. Lucas 1909: 52; 1929a: 26.

Lucas and Perrin 1947: 365. Sonder 1853: 676. Tisdall 1898: 503. Wilson 1892: 185. NON C. ramulosum Meneghini 1844: 185 (from the Adriatic), = C. ciliatum (Ellis) Ducluz. Gongroceras ramulosum (Hook. and Harv.) Kuetzing 1849: 678; 1862: 25, pl. 81*a*-d.

- C. deslongchampsii sensu Hooker and Harvey 1847: 410. Lucas 1909: 53; 1929a: 26. Guiler 1952: 98 (see Harvey 1859: 330).
- C. nodosum sensu Hooker and Harvey 1847: 410 (see Harvey 1859: 330).
- C. tenuissimum sensu Lucas 1909: 53. Guiler 1952: 99.
- C. fastigiatum sensu Harvey 1855: 557; 1863, synop.: 48. Guiler 1952: 98. Lucas 1909: 53. Lucas and Perrin 1947: 366 (as record only). Tisdall 1898: 503. Wilson 1892: 184.

#### Figs 4G, H, 15F-J

Thallus (Fig. 15F) light to dark red, forming erect often much branched or entangled tufts from a few millimetres to 10(-15) cm high, on rock or other firm substrates' (e.g. tunicates) or epiphytic, with prostrate branches attached by uniseriate-celled rhizoids with pads becoming multicellular; 1–3 rhizoids arise from the periaxial cells at each node. *Branching* in actively growing erect parts subcomplanate with fairly regular laterals usually 3–6 cells apart with broad axils, but often more irregular and sparse, commonly with older branches bearing proliferous laterals which are often markedly slenderer.

Branches 125–200(-300)  $\mu$ m in diameter below, tapering either gradually or in some plants more abruptly to (25–)50–75(–100)  $\mu$ m in diameter below the tapering apices, which are usually relatively straight, occasionally slightly involute or in some plants divergent. Axial cells L/B about 1 near the apices (Fig. 151), elongating to 2–3(–4) below, with clear internodal spaces throughout. *Periaxial cells* usually 6, each first cutting off 2 cells acropetally and usually soon after 2 cells basipetally (Figs 4G, 15 I); these latter cells only arise in the lower parts in some plants (e.g. ADU, A34110, Fig. 15G). Acropetal cortical cells usually each cutting off 1 or 2 smaller cells, thus giving a node 4 cells and 30-50  $\mu$ m long in the upper parts (Fig. 4G); on older, lower, branches further acropetal cells, and sometimes basipetal ones, may be cut off, giving a node 5-6(-9) cells and 75-125  $\mu$ m long, with the acropetal development always greater (and usually with smaller cells) than the basipetal; internodal space  $\frac{1}{2}$ -1 times the nodal length in upper parts, and 1-3(-4) times as long in lower parts of the thallus. On lower branches, occasional small cortical cells may be cut off in the reverse direction, and in some robust specimens a slight outer cortex may develop on the oldest parts; slender hairs commonly present on cortical cells near branch apices.

*Carposporophytes* (Fig. 15G) on upper branches, globular, 150–250(–300)  $\mu$ m across, with 1–4 slightly curved involucral branchlets.

Spermatangia (Fig. 15H) covering cortical cells of upper nodes, sometimes largely restricted to the adaxial sides.

*Tetrasporangia* (Fig. 15*I*, *J*) in unilateral, abaxial series, with 1–3 per node, cut off from one (or two) periaxial cells, involucrate over their lower half or less by branched acropetal cortical filaments 3–4 cells long from the periaxial cells, with the involucral cells lying in the outer part of the common gelatinous sheath with the tetrasporangia centrally situated; tetrasporangia tetrahedrally (rarely cruciately) divided, subspherical to ovoid, 35–50  $\mu$ m across.

Type locality.- Western Australia (Harvey).

Type.- Herb Agardh, LD (20690).

*Distribution.*- From Western Australia (Fremantle and Rottnest I.) along southern Australia to (probably) Botany Bay, N.S.W., and around Tasmania.

Selected specimens studied.– Pearson I., S.A., 35 m deep (Shepherd, 10.i.1969; ADU, A34110). Douglas Bank, Spencer Gulf, S.A., 10 m deep (Johnson, 16.vii.1975; ADU, A47992). Investigator Strait, S.A., 25 m deep (Watson Stn Y7, 15.i.1971; ADU, A39344). West I., S.A., 20–23 m deep (Shepherd, 8.x.1966; ADU, A30860).

C. cliftonianum is a moderately common species along southern Australia, from 1 to 35 m depth, occurring as tufts or often entangled masses of slender filaments, in moderate water movement. It is characterized by its dimensions, the nodal development, and the unilateral, half involucrate tetrasporangia. There is, however, considerable variation, especially in development of the basipetal cortical cells with occasional specimens having them only on the older branches. This is shown in small slender forms epiphytic on *Posidonia*, 2–10 m deep, in the northern part of Spencer Gulf, S.A. (e.g. ADU, A48104, A47991, A47992). While these plants usually have basipetal cortical cells at least on the older parts, younger parts (or most of small plants) often do not. Occasionally plants (ADU, A47992—Fig. 15J) have distinctly cruciately divided tetrasporangia, but the species normally has tetrahedrally divided sporangia. While it is desirable that this form from northern Spencer Gulf be investigated further, it seems best to refer it to *C. cliftonianum*. It is clear, however, that further studies on variation within this species are needed.

The type material of *C. cliftonianum* is smaller but otherwise identical in dimensions, nodal development and tetrasporangia with that of *C. ramulosum* Hooker and Harvey from Tasmania (*Gunn* in BM, ex K). The latter species was distributed by Harvey as Alg. Aust. Exsicc. 469 I from Georgetown, Tas.

Until extra-Australian species are more thoroughly investigated, comparisons of *C. cliftonianum* with other slender species are scarcely possible. *C. cliftonianum* appears closely related to *C. tenuissimum* (Roth) J. Agardh (c.f. Feldmann-Mazoyer 1940, p. 299, figs 113, 114) in cortical appearance and in having unilateral, abaxial and involucrate tetrasporangia, but the latter usually has gland cells and details of the cortical development are not available. Roth's type of *C. tenuissimum* is also apparently lost, but critical comparisons with 'authentic' European material of this species are clearly needed.

C. cliftonianum also appears to be closely related in dimensions, nodal cortication and tetrasporangial arrangement to C. fastigiatum Harvey from Britain, and the latter name was applied to Australian specimens by Harvey and others (see synonymy). However C. cliftonianum rarely has the strongly fastigiate habit Harvey (1849, pl. 255) illustrated for C. fastigiatum but is usually more irregular in its branching. Detailed study of authentic and liquid-preserved material of C. tenuissimum and C. fastigiatum may show that C. cliftonianum is inseparable from one of these older species, but for the present it seems best to keep the Australian taxon separate.

Some specimens of C. *cliftonianum* show similarity with slender specimens of C. *tasmanicum*, but the latter is normally readily separated in well grown plants by the extending cortex on older branches and by the whorled and not unilateral tetrasporangia.

C. macilentum often occurs together with C. cliftonianum but the latter differs clearly in not having pseudoperiaxial cells and normally greater basipetal and acropetal cell development.

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Fig. 6. C. puberulum. A, Habit of plants on Posidonia australis (A43754). B, Older axes covered with short secondary spines (A43888). C, Branches with spermatangia (A46416). D, Branch with abaxially swollen nodes with tetrasporangia (A46416). E, Branch of slender form with tetrasporangia (A47826).



Fig. 7. C. rubrum. A, Habit of female (left) and tetrasporangial (right) plants (A46912). B, cortication of young branch. C, Cortication of older branch showing rosettes around periaxial cells and elongate inner cortical cells. D, Carposporophyte with involucral branches. E, Tetrasporangial branch (B-E, A47024).



**Fig. 8.** *C. pusillum. A*, Habit of large plant (A41147). *B*, Habit of smaller more typical plants. *C*, Young branches showing internodal spaces near apices. *D*, Older branch showing smaller terminal acropetal cells abutting larger basipetal cells, ovoid to subspherical inner cortical cells, and rosettes of outer cortical cells (especially around periaxial cells). *E*, Carposporophyte. *F*, Spermatangial sori on male plant. *G*, Tetrasporangia in whorls on young branches (*B*-*G*, A33116).



**Fig. 9.** *C. lenticulare. A*, Habit of robust specimens (A39505). *B*, Habit of slender specimen (A30855). *C*, Branch showing lenticular internodal spaces. *D*, Upper branches with carposporophyte. *E*, Upper branches with abaxial or opposite tetrasporangia. *F*, Proliferous stichidiose tetrasporangial branches (*C*-*F*, A45063—type),



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**Fig. 11.** C. tasmanicum. A, Habit. B, Cortex of branch showing irregular growth starting to extend. C, Cortex of older branch. D, Carposporophyte with associated branchlets. E, Branches with spermatangia. F, Branches with whorled tetrasporangia (all A42758).



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C. cliftonianum. F, Habit (A34110). G, Carposporophyte on plant with few basipetal cortical cells (A34110). H, Branches with spermatangia (A34110). I, Branches with involucrate, abaxial tetrasporangia and normal formation of basipetal cortical cells (A30860). J, A slender form with tetrasporangia (A47992).