

Reproductive development and classification of the red algal genus *Ceratodictyon* (Rhodymeniales, Rhodophyta)

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Ceratodictyon spongiosum Zanardini (Rhodymeniales, Rhodophyta) is a widely distributed tropical Indo-Pacific species, the thalli consisting of a reticulate network of algal axes surrounded and covered by a sponge symbiont. Several important reproductive features of the algal partner are described in detail for the first time. Procarp organization, early gonimoblast and fusion cell development, mature cystocarp structure, and cruciately divided tetrasporangia, as well as the occasional presence of vesicular ('gland') cells on medullary filaments, relate the alga to the family Rhodymeniaceae of the order Rhodymeniales, rather than to the Gracilariaceae or the Gigartinales as has been previously considered. It is argued that *Ceratodictyon* and the non-sponge-associated *Gelidiopsis* are closely related genera that should be maintained as distinct taxa, rather than combined into the single genus *Ceratodictyon* as has been advocated recently.

INTRODUCTION

The marine macroalga *Ceratodictyon spongiosum* Zanardini (1878) was originally described from the Aru Islands off the south-west coast of New Guinea. A short time later, it was redescribed as the synonymous *Marchesettia spongioides* Hauck (1882, 1884) from Singapore, Madagascar and New Caledonia, and is now known to be widespread in the tropical Indo-Pacific from east Africa (Jaasund 1976) to Shark Bay, Western Australia (Kendrick *et al.* 1990), Hong Kong (Tseng 1983), the Philippines (Silva *et al.* 1987) and southern Japan (Yoshida *et al.* 1985). In eastern Australia it occurs from the Capricorn Group at the southern end of the Great Barrier Reef (Cribb 1983) northwards to Torres Strait. The alga typically grows on intertidal coral reef flats and subtidal reef slopes (to c. 3 m depth), although subtidal collections from 8 m (Hauck 1884) and even unconfirmed depths of 100–140 m (Hauck 1889) have been reported.

Without exception, plants in the field grow symbiotically with the sponge *Sigmadocia symbiotica*, although sponge-free algal growth has been achieved in culture (Price *et al.* 1984). The nature of the symbiotic association and general features of the vegetative morphology of the alga have been variously illustrated (Askenasy 1888;

Okamura 1909; see also Price *et al.* 1984). Although Hauck (1882, 1884), Schmitz (1889) and Okamura (1909) have reported cystocarps, no information on procarp organization or cystocarp development has been published.

Schmitz (1889, p. 443) proposed (as a *nomen nudum*) a new tribe, the Ceratodictyeae, in the family Sphaerococcaceae, to include the single genus *Ceratodictyon*. More recent workers (Okamura 1942; Fritsch 1945; Kylin 1956; Norris 1987) have ignored this tribal designation and placed the genus in the family Gracilariaceae, order Gigartinales, on the basis of vegetative or supposed reproductive characteristics. This is despite Hauck's (1884, pl. 3, fig. 3) and Okamura's (1909, pl. 52, fig. 9) drawings of mature cystocarp sections which depict a large fusion cell very unlike anything found in the Gracilariaceae. A genus of similar vegetative structure to *Ceratodictyon*, *Gelidiopsis* Schmitz (1896), was later also placed in the tribe Ceratodictyeae by Schmitz & Hauptfleisch (1897). *Gelidiopsis* contains six species widely distributed in the Indian and central to western Pacific Oceans (Norris 1987), and is also generally included among the Gracilariaceae. Like *Ceratodictyon*, reports of cystocarps in *Gelidiopsis* provide few details. Norris (1987) has recently argued for the incorporation of *Gelidiopsis* into *Ceratodictyon* on the grounds that the

latter differs from the former only by its reticulate thallus. Norris argues that the work of Price *et al.* (1984), reporting the growth of non-reticulate, sponge-free plants of *Ceratodictyon* in culture, shows that the supposed distinction between the two genera is untenable.

Collections of cystocarpic *Ceratodictyon spongiosum* by the first author and *Gelidiopsis scoparia* (Montagne et Millardet) De Toni supplied by the second author have allowed us to investigate the correct family and ordinal placement of the two genera. This paper primarily reports the result of our observations on *Ceratodictyon*. Studies on *Gelidiopsis* will be presented in more detail elsewhere as we attempt to clarify species concepts in that genus.

MATERIALS AND METHODS

Fertile specimens of *Ceratodictyon spongiosum* occur sporadically during all seasons except for winter (June to August) among large populations of the species growing intertidally on the fringing coral reef at Geoffrey Bay (19°09' S; 146°52' E), Magnetic Island, off Townsville, Queensland. Material was fixed and stored in 5% formalin/seawater. Sections 10–40 μm thick were cut by hand or on a freezing microtome, then stained and mounted in an analine blue : corn syrup : water mixture (3 : 25 : 72).

OBSERVATIONS

Vegetative structure

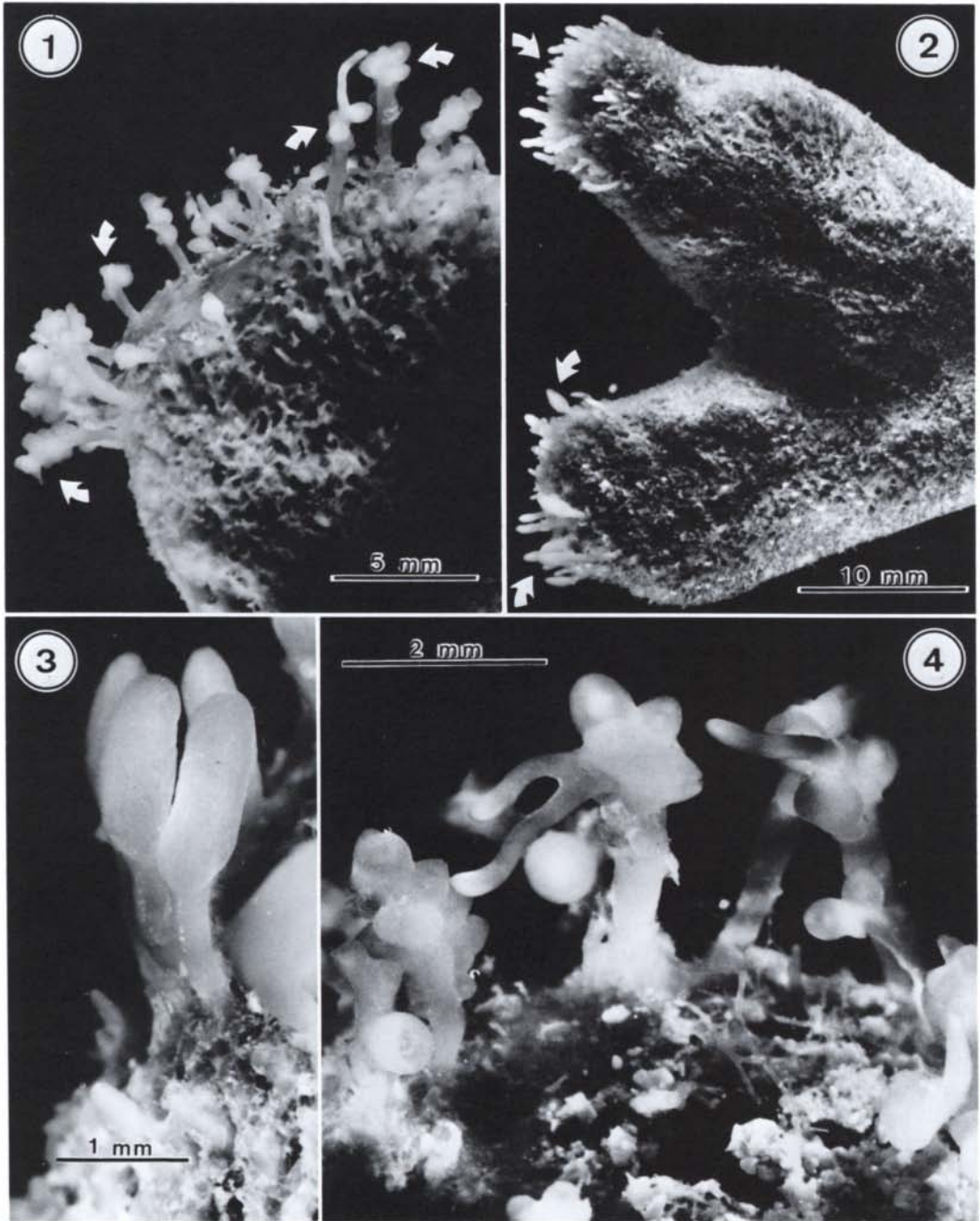
The symbiotic association forms irregular cushions or hummocks of recumbent, often imbricate, axes. Individuals commonly reach 15–30 cm in diameter and 5–15 cm in height (Hauck 1884), although exceptionally large specimens up to 70 cm in diameter have been collected in the Townsville region. On the coarsest scale, the organism consists of subcylindrical to compressed, subdichotomous to irregularly branched, occasionally anastomosing axes 5–10(–20) mm in diameter (Figs 1, 2; see Price *et al.* 1984: fig. 1). Each symbiont axis is itself a composite of numerous terete algal axes 100–250(–350) μm in diameter that intertwine and anastomose to form a dense reticulum (Price *et al.* 1984: fig. 2). Interstices of varying widths (Fig. 5) occur between the exclusively vegetative algal filaments of the

reticula, and are filled to a greater or lesser extent with epiphytic sponge tissue. The surfaces of most symbionts are punctuated by scattered, prominent holes (called 'oscula') that are the exit pores for water currents set up by the sponge choanocytes (Price *et al.* 1984: fig. 1). The specimens are anchored at numerous points to solid substrata (such as dead coral and reef rock) by slightly splayed but otherwise unmodified bases or lateral extensions of major axes, there being no expanded discs or thickened holdfast pads formed. Algal reproductive structures occur on short, exserted, non-anastomosing axes that are generally aggregated distally on forks or lobes of the reticulate axes (Figs 1–4).

Each algal axis of the reticulum grows from a dome-shaped, multiaxial apex that gives rise proximally to a pseudoparenchymatous outer cortex and a central medulla of aggregated narrow filaments (Figs 6, 7). In completely vegetative axes (Fig. 7) the outer cortex is a single layer of cuboidal to rectilinear cells [2.5–5.0(–7.5) μm in diameter by 6–15 μm in length in transverse section] subtended by progressively larger, increasingly elongate cells [5–15(–20) μm in diameter by (25–)30–60 μm in length] linked by numerous secondary pit connections, which in turn surround a compact medullary core of filamentous cells 12–30 μm in diameter by 85–140(–175) μm in length. In the fertile axes (Fig. 6), however, the cortex may consist of many layers of small-celled, anticlinal cortical cells and the medullary filaments may be separated by conspicuous gaps. Particularly in regions of relatively lax medulla, vesicular ('gland') cells occur singly and laterally on isolated medullary cells (Fig. 8).

Reproduction

The algal and sponge partners reproduce completely independently of one another, the sponge forming gametes and brooding the larvae (J. Fromont, personal communication). It is not known when or by what means the symbiosis is established. Algal reproductive structures occur on modified terminal branches that project from the tips of the reticulate matrix of the symbiotic association or laterally at sites of apparent wounding or abrasion (Figs 1–4). The presence of sponge spicules embedded in the tissue of fertile branches suggests that the sponge coating may withdraw or be sloughed off from the exserted axes as they develop.



Figs 1–4. Gross morphology of *Ceratodictyon spongiosum*.

Fig. 1. Fertile algal axes (arrows) with clusters of cystocarps arising from the reticulate thallus of the algal/sponge symbiont.

Fig. 2. Almost parallel aggregates of tetrasporangial axes (arrows) exerted from the algal/sponge reticulum.

Fig. 3. Detail of tetrasporangial nemathecia.

Fig. 4. Detail of cystocarp-bearing axes.

Cylindrical, terminal nemathecium containing the tetrasporangia completely encircle the terete, unbranched bearing axes (Figs 2, 3). The sporangia are laterally attached to subsurface cells and the spores are usually decussately cruciately arranged, although many sporangia are very irregularly divided (Fig. 14). Occasionally, cells borne in positions homologous to tetrasporangia remain undivided but elongate considerably, protruding beyond the surface cuticle somewhat like hairs (Fig. 14). The function of such structures is unknown.

Gametophytes are dioecious. Spermatangial plants are apparently rare, only a few specimens having been collected, in contrast to the relative frequency with which tetrasporophytes and female gametophytes are encountered. The spermatangia occur in swollen, exerted axes that superficially resemble tetrasporangial nemathecium, although they are much more mucilaginous in texture. Spermatangial mother cells form a continuous layer over the outer cortex, and each cuts off one or two spermatangia distally, sometimes in chains of two (Fig. 15). Medullae of the spermatangial branches are characterized by particularly prominent gaps and cavities.

Female gametophytes produce dense clusters of terete to slightly flattened protruding axes that may be either simple or sparingly branched (Figs 1, 4). Cystocarps occur in large numbers on all radii of the fertile axes, often in aggregates with partly confluent pericarps (Fig. 4). Mature cystocarps are protuberant, bluntly conical, and pierced by a single apical ostiole.

Procars are not generally recognizable in our material, despite the abundance of carposporophyte stages ranging from early gonimoblasts to mature cystocarps. Carpogonial branches appear to be 3-celled and borne singly on a slightly enlarged and more deeply staining supporting cell, which also bears a 2-celled auxiliary-cell branch (Fig. 16). The auxiliary mother cell is initially connected only to the auxiliary and supporting cells, but later becomes secondarily pit-connected to cells of adjacent vegetative filaments. No proteinaceous body is apparent in the auxiliary mother cell or gonimoblast initial, as is often reported in members of the Rhodymeniaceae (Sparling 1957; Lee 1978).

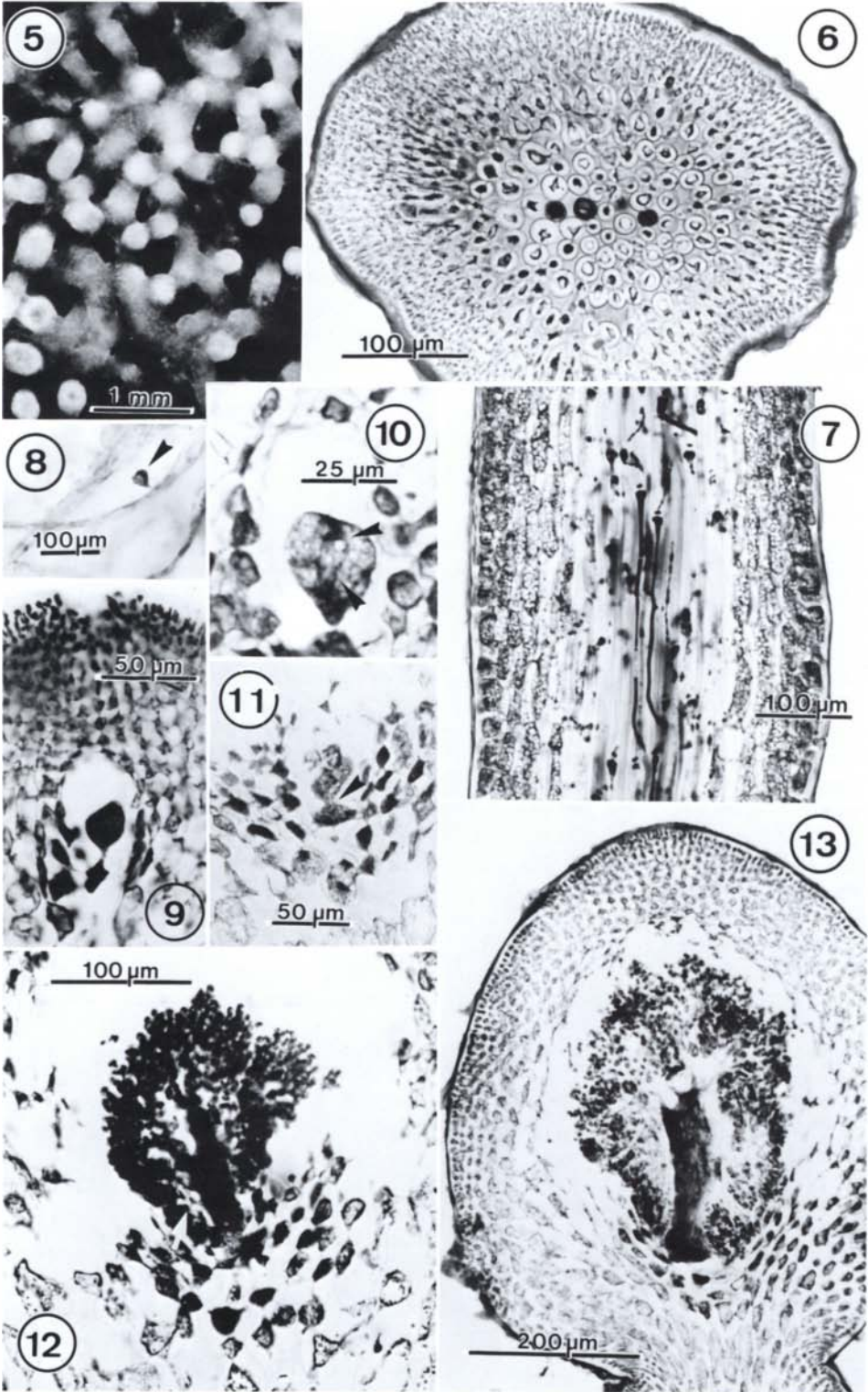
Diploidization of the auxiliary cell, presumably by a connecting cell cut from the fertilized carpogonium, was not observed in our material. Carpogonial branch cells could not be unambiguously recognized in any of the post-fertilization

preparations. Following presumed fertilization and diploidization, the auxiliary cell and auxiliary mother cell enlarge considerably (Figs 9–11), become deeply stained, and subsequently fuse together (Fig. 11) to form the early stage of a conspicuous fusion cell that will ultimately incorporate the supporting cell and the bulk of the earliest-formed gonimoblast cells (Fig. 12). The gonimoblast initial apparently arises by an oblique to nearly longitudinal division of the auxiliary cell (Fig. 10), and continues to develop into an apical cluster of cells by repeated divisions of its derivatives (Fig. 11). Cells surrounding the base of the fusion cell become deeply staining (Figs 11, 12), and presumably play a nutritive role. The mature carposporophyte (Fig. 13) forms an almost spherical mass of carposporangia surrounding all but the anchoring 'foot' of the fusion cell. Carposporangia are spherical to ovoid and range from 5–13 μm in diameter. Although individual clusters of carposporangia develop on the ramifications of the fusion cell, the clusters merge into a synchronously maturing whole rather than developing at different rates and producing the distinct gonimolobes characteristic of many Rhodymeniales (cf. Sparling 1957; Lee 1978; Moe 1979). Inner cells of the gonimoblast arms progressively fuse back on to the fusion cell, resulting in a dense carposporangial mass borne on few if any unincorporated sterile cells (Fig. 12). Normally, a single carposporophyte occupies the centre of each pericarp, but a single instance of two separate carposporophytes within one pericarp was observed.

The cavity into which the carposporophyte develops apparently begins to form in conjunction with the increase in size of the auxiliary cell that presumably accompanies fertilization (Fig. 9). Differentiation of the ostiole and vigorous anticlinal growth of the cortex above the auxiliary cell also occur concomitantly with presumed fertilization and result in a protuberant pericarp (Fig. 9). The inner layers of the pericarp in mature cystocarps (Figs 12, 13) consist of longitudinally elongated cells, but do not form the elaborately reticulate tissue which in several genera of the Rhodymeniaceae is termed a *tela arachnoidea* (Sparling 1957).

DISCUSSION

Reproductive features of *Ceratodictyon* clearly link it with the Rhodymeniales rather than with



Gracilaria or any of the families of the Gigartinales. The form of the procarp, composition of the fusion cell, disposition of the carposporangia, and structure of the pericarp are typical of the Rhodymeniales. The presence of vesicular cells and production of spermatangia across the whole surface of fertile axes are other features not observed in members of the Gracilariaceae.

Within the Rhodymeniales, however, the position of *Ceratodictyon* is not altogether clear. Three families are presently recognized in the order (Lee 1978): the Champiaceae, Lomentariaceae and Rhodymeniaceae. The one uniformly distinguishing feature of the Champiaceae (Sparling 1957) appears to be the possession of at least some hollow axes (hollow in the sense of being largely cell-free, since cavities in all members of the Rhodymeniales are generally mucilage-filled), the cavities being bordered by distinct and widely separated longitudinally running filaments that appear like ribs or struts in interior-surface views. Such axes are regularly segmented by single cell-layered diaphragms. Nevertheless, solid portions of genera such as *Chylocladia* (Bliding 1928, fig. 15) appear to be closer to the axial structure of *Ceratodictyon* than those of any other members of the order. However, tetrasporangia in the Champiaceae are intercalary and tetrahedrally divided, and carposporophytes include either several inner layers of sterile gonimoblast cells on which a surface layer of terminal carposporangia is borne, or a relatively massive fusion cell bearing a single layer of carposporangia directly (Bliding 1928; Lee 1978).

Members of the Lomentariaceae are also largely hollow but, according to Lee (1978), may lack

longitudinally aligned medullary filaments at the periphery of the cavities. Definitive characters of the family are the terminal, tetrahedrally divided tetrasporangia, which form in distinctively sunken sori, and the regularly or irregularly positioned, multilayered septa that occlude the hollow axes. The one major feature of *Lomentaria* that appears to be shared with *Ceratodictyon* is the shape of the fusion cell, which tends in both genera to be stalk-like but fairly massive, the original outlines of the component cells being completely obscured at maturity (Lee 1978: figs 51A, 52A, C, 59D, F; Ms Helen Foard, personal communication), in contrast to *Champia* (Bliding 1928: fig. 10A; Lee 1978: fig. 68D) and members of the Rhodymeniaceae. Carposporophytes of *Lomentaria* differ, however, from those of *Ceratodictyon* in having distinct gonimolobes, as is generally true of the order.

The Rhodymeniaceae contains the largest number of genera and species of any of the families of the Rhodymeniales, and is also the most anatomically diverse. Its members exhibit medullary structures ranging from pseudoparenchymatous throughout to almost completely hollow, with some species having hollow laterals borne on solid stipes or lateral axes. When hollow, plants of the Rhodymeniaceae lack such features of the Champiaceae or Lomentariaceae as 'distinct free longitudinal filaments' in the medulla (Guiry & Irvine 1981), tetrahedrally divided tetrasporangia, and indented tetrasporangial sori. All but the single genus *Hymenocladia* produce cruciately divided tetrasporangia, the sporangia in *Hymenocladia* being intercalary, tetrahedrally divided, and borne in solidly constructed axes. Sparling

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Figs 5–13. Vegetative and reproductive morphology of *Ceratodictyon spongiosum*.

Fig. 5. Section through the sponge/algal reticulum showing the irregular interstices and the various alignments of the algal axes.

Fig. 6. Cross-section through a cystocarpic axis showing the deep, anticlinal cortex and relatively loosely aggregated medullary filaments.

Fig. 7. Longitudinal section through a vegetative algal axis showing the single-layered outer cortex and densely aggregated medullary filaments.

Fig. 8. Vesicular cell (arrowhead) attached laterally to a medullary cell.

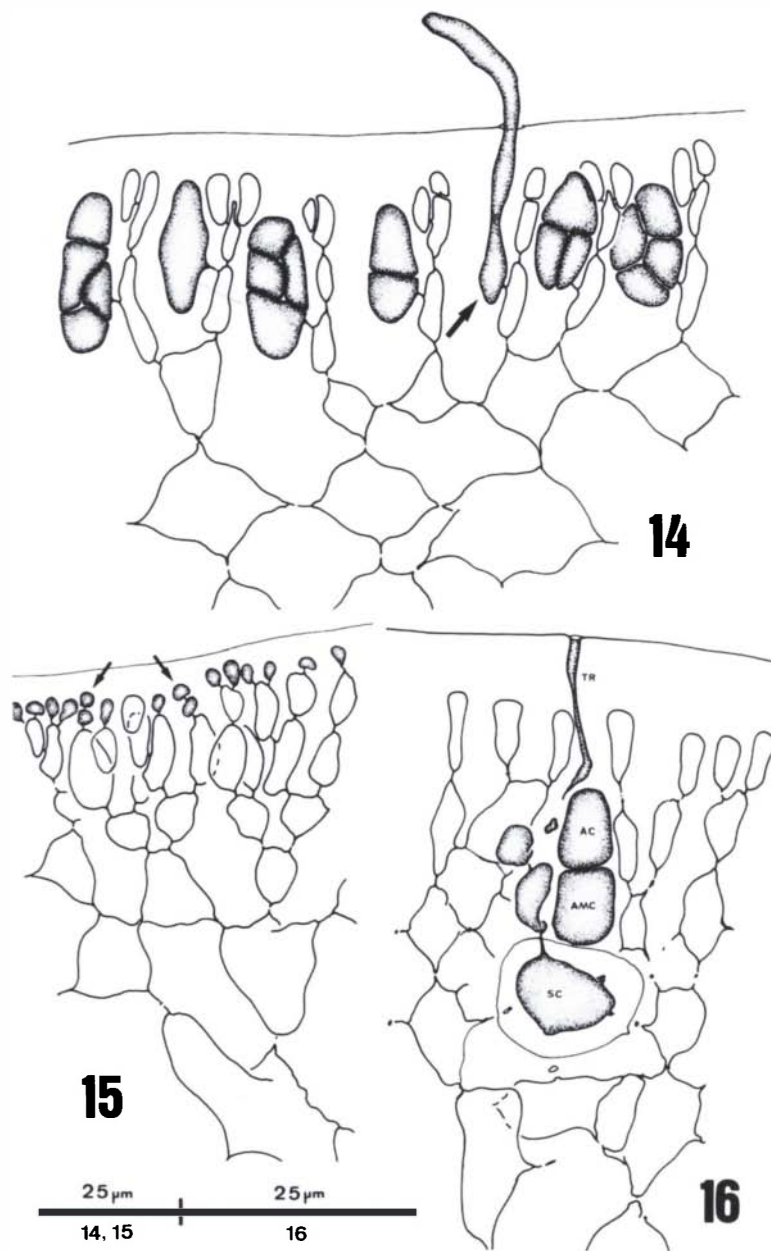
Fig. 9. Appearance of auxiliary cell prior to gonimoblast initiation. Auxiliary mother cell has formed secondary connections to contiguous vegetative cells, and development of ostiole and pericarp is well advanced.

Fig. 10. Oblique division (arrowheads) of the auxiliary cell to form the gonimoblast initial.

Fig. 11. Early stage of gonimoblast development. Auxiliary and auxiliary mother cells are in the process of fusing (arrowhead).

Fig. 12. Mid-development of the carposporophyte. Fusion cell is surrounded by nutritive cells at its base, and cells comprising the inner layers of the gonimolobes have completely fused on to the fusion cell. Some branches (arrow) occur very near the base of the fusion cell.

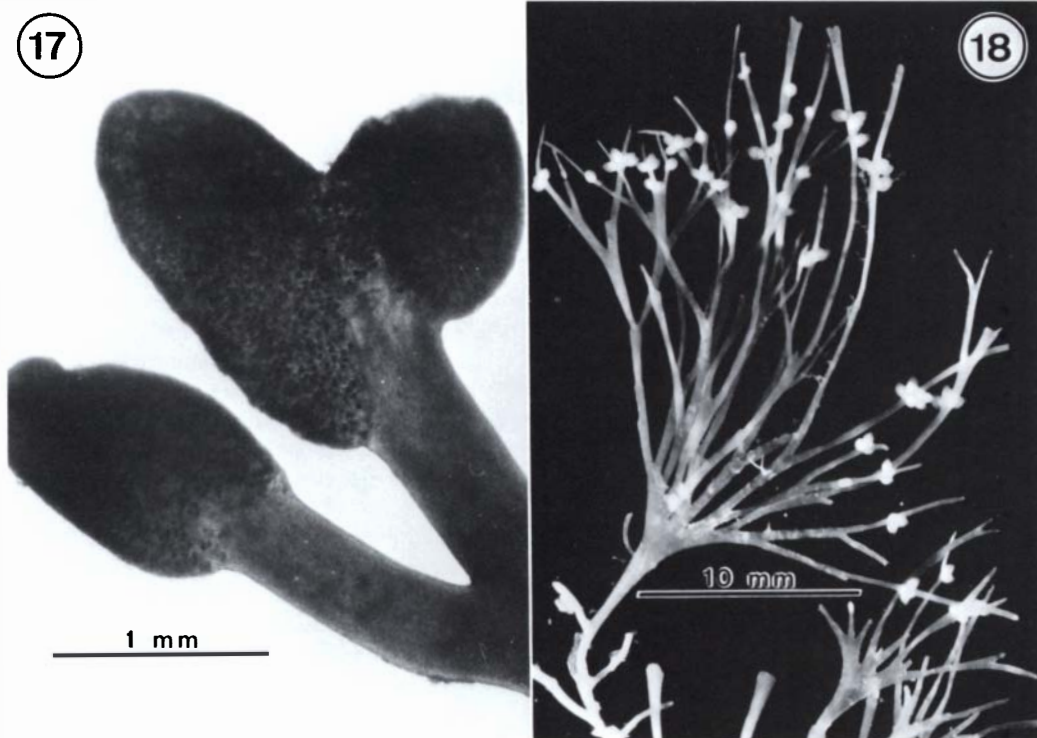
Fig. 13. Longitudinal section of mature cystocarp (not in plane of the ostiole) showing massive fusion cell and uniform development of carposporangia in the consolidated gonimolobes.



Figs 14–16. Reproduction of *Ceratodictyon spongiosum*.

Fig. 14. Various stages in the initiation and differentiation of tetrasporangia, including regularly and irregularly divided types. A hair-like extrusion (arrow) of unknown function occurs in the position of a tetrasporangium.
Fig. 15. Outer cortex of a spermatangial axis. Spermatangia occur singly and in chains of two (arrows) on surface mother cells.

Fig. 16. Procarp configuration indicative of 3-celled carpogonial branch and 2-celled auxiliary cell branch, the auxiliary mother cell not yet linked to adjacent cells by secondary pit connections. AC = auxiliary cell; AMC = auxiliary mother cell; SC = supporting cell; TR = trichogyne.



Figs 17, 18. *Gelidiopsis* species.

Fig. 17. *Gelidiopsis variabilis* (Oahu, Hawaii, 10.xii.1977. Leg. G. Kraft & M.S. Doty; MELU, K6476). Simple and compound tetrasporangial nemathecia.

Fig. 18. *Gelidiopsis scoparia* (North Barnard Island, Great Barrier Reef, 5.xii.1977. Leg. John Lewis; MELU, L1341). Habit of plant with clustered cystocarps.

(1957) accepted division of the family into the two subfamilies Rhodymenioidae and Hymenocladoidae (as the Rhodymeniae and Hymenocladiae), based solely on the difference in tetrasporangial division pattern, although Lee (1978) considers this feature to be insufficiently important by itself to support subfamily recognition.

The strongest link between *Ceratodictyon* and the Rhodymeniaceae is its cruciately divided tetrasporangia. Features that would appear to be inconsistent with the family, however, such as the more-or-less solid construction of the axes in conjunction with occasionally produced vesicular cells, appear to be unique in the order. Like *Ceratodictyon*, the subantarctic genus *Cenacrum* of the Rhodymeniaceae produces scattered vesicular cells on inner medullary cells, but plants of the latter are initially mostly hollow and progressively fill the medullary cavities with rhizoidal filaments (Ricker & Kraft 1979). Rhizoids are completely absent in *Ceratodictyon*. The initial division of the zygote in *Ceratodictyon* ap-

pears to be oblique or nearly longitudinal, as opposed to being transverse and separating the auxiliary cell into more or less equal halves, as is generally reported for the order (Bliding 1928; Sparling 1957; Lee 1978; Moe 1979; Ricker & Kraft 1979). In addition, the fusion cell characteristics of *Ceratodictyon* mentioned above, in which the shapes of the component cells are totally obscured during development, and gonimoblast filaments are capable of arising from proximal positions (Fig. 12), do not appear to be typical of the Rhodymeniaceae. Distinct gonimolobes are another feature absent in *Ceratodictyon*, as are protein bodies in the auxiliary cells.

Only within genera of the Champiaceae are there cystocarpic features that differ substantially from those of the remainder of the Rhodymeniales, the carposporophyte of *Champia* consisting of a terminal layer of carposporangia borne on inner layers of sterile gonimoblasts, and those of *Chylocladia* and *Gastroclonium* consisting of a

single layer of large carposporangia borne directly on a prominent fusion cell that develops from a procarp with two fusion cells (Bliding 1928). Like the Rhodymeniaceae and Lomentariaceae, mature carposporophytes of *Ceratodictyon* contain little if any unconsolidated sterile tissue, the earliest-formed gonimoblast cells progressively fusing back on to the ramified fusion cell.

The present major determinants of family placement in the Rhodymeniales appear to be overall thallus structure and tetrasporangial division pattern, with no or only minor emphasis placed on the genesis and anatomy of the carposporophyte (Sparling 1957; Lee 1978). Whether these considerations will remain pre-eminent as more genera of the order are critically studied is uncertain, but the available criteria indicate that the affinities of *Ceratodictyon* appear to lie most strongly, if not entirely comfortably, with the Rhodymeniaceae.

For the present, we advocate recognition of Schmitz's (1889) tribe Ceratodictyeae, containing both *Ceratodictyon* and the genus *Gelidiopsis*, as a subdivision of the Rhodymeniaceae. Although the name 'Ceratodictyeae' is introduced without diagnosis by Schmitz (1889), it appears to be properly validated by characteristics specified in a key to the subdivisions of the Rhodymeniales given by Schmitz & Hauptfleisch (1897, p. 384). In contrast to the Ceratodictyeae, members of the Rhodymeniaceae have carposporophytes in which the fusion cell is columnar and consists of elements identifiable as the precursor cells, has auxiliary or gonimoblast-initial cells containing a protein body, and produces two or three morphologically distinct lobes of synchronously developing carposporangia.

Schmitz (1896) described the vegetative and reproductive anatomy of *Gelidiopsis* as being very similar to that of *Ceratodictyon*, a fact that we have confirmed from cystocarpic material of *Gelidiopsis scoparia* collected on the Great Barrier Reef. Schmitz defined *Ceratodictyon* as having reticulate, sponge-associated fronds of a kind not seen in *Gelidiopsis*. Several authors, such as Price *et al.* (1984), have described and illustrated these features of *Ceratodictyon* as it invariably appears to occur in nature. Numerous anastomoses between the algal axes that compose the thalli lead to a complex 3-dimensional network throughout. The anastomoses develop close to the growing apices of the major axes and not, as stated by Norris (1987), only between 'secondarily formed'

branches. In contrast to the thallus construction of naturally occurring *C. spongiosum*, branch anastomoses were not recorded in laboratory cultures of the species (Price *et al.* 1984), although the anatomy of the free-living and cultured axes was otherwise broadly similar. Occasional anastomoses occur in certain species of *Gelidiopsis*, generally between elements of the prostrate systems or lower branches, but in none of the species is the thallus in the form of a regular 3-dimensional meshwork, or invariably encountered only in intimate association with sponges.

Norris (1987) uses the culture results of Price *et al.* (1984) to justify the sinking of *Gelidiopsis* into *Ceratodictyon*, emphasizing that branches 'remain free from one another' in both free-living plants of most *Gelidiopsis* species and cultured *Ceratodictyon spongiosum*. This may be true, but from our experiences of both genera in the field we would be reluctant to merge such distinctive entities. *Ceratodictyon* has not been grown to reproductive maturity in culture, and it is arguably premature to dismiss the consistent reticulate structure and sponge association that always seem to occur under natural conditions as taxonomically insignificant. Although Fritsch (1945, p. 583) reports that the sponge symbiont can lead an independent existence, this claim is apparently based on a misidentification (Bergquist & Tizard 1967; Price *et al.* 1984). The sponge partner has never been found free-living in the Townsville area, and attempts to maintain it separately in culture have failed (R. Fricker, personal communication). The relationship may therefore be an obligate one for both partners. Norris's claim (1987, p. 239), that a contingent sponge association may be the cause of the elaborate reticulation of the algal axes compared to the rest of the *Gelidiopsis* species, has not been experimentally tested, although it is conceivable that the mere juxtaposition of the axes through the binding action of the sponge could induce or facilitate their fusion. In this admittedly uncertain context, we feel that *Ceratodictyon* should be defined in a restrictive way that distinguishes it from *Gelidiopsis* by emphasizing its unusual habit and probably unique biology.

We support Schmitz (1896) in considering the reproductive and vegetative anatomies of *Ceratodictyon spongiosum* and the various *Gelidiopsis* species to be similar, if not virtually identical. Confirmation of this hypothesis awaits a thorough study of the type species, *Gelidiopsis variabilis* (J. Agardh) Schmitz. But even if this should

prove to be the case, both *Ceratodictyon* and *Gelidiopsis* will remain well-defined and easily distinguishable as genera at several levels, and we support Schmitz's judgement rather than that of Norris in this regard. In addition to the striking habit differences and consistent sponge association, there is a marked contrast between the diameters, location, and morphology of reproductive as opposed to vegetative axes in *Ceratodictyon spongiosum*, that is not exhibited by the few species of *Gelidiopsis* in which these features have been documented. Tetrasporangial nemathecia in *Gelidiopsis* (Fig. 17) are sometimes compound and appear to be more highly differentiated from the supporting vegetative axes than are those of *Ceratodictyon* (Fig. 3), and cystocarps of *Gelidiopsis scoparia* (Fig. 18) occur along unmodified major axes, although these features admittedly might be considered matters more of degree than kind.

Norris's depiction of carpogonial branches in *Gelidiopsis variabilis* (Norris 1987: fig. 5), on which his acceptance of *Ceratodictyon* (including *Gelidiopsis*) as a member of the Gracilariaceae is partly based, appears to represent some vegetative anomaly, perhaps associated with the culture-induced 'coralloid' terminal growths in which he found them. Norris's illustration does not depict carpogonial branches typical of either the Rhodymeniaceae or Gracilariaceae (cf. Fredericq & Hommersand 1989).

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