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Recent developments in the systematics of the Gigartinaceae (Gigartinales, Rhodophyta) based on *rbc*L sequence analysis and morphological evidence

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SUMMARY

The phylogenetic systematics of the Gigartinaceae is discussed for seven genera and three undescribed generic lineages and 65 taxa representing 62 species based on an analysis of *rbc*L sequences and morphological evidence. An examination of *rbc*L trees resulting from analyses of these taxa identifies seven lineages: (i) *'Gigartina' alveata*; (ii) *Rhodoglossum/Gigartina*; (iii) *Chondracanthus*; (iv) *Ostiophyllum*; (v) *Sarcothalia*; (vi) *'Gigartina' skottsbergii*; and (vii) a large clade containing *Iridaea/'Sarcothalia', Mazzaella* and *Chondrus*. These lineages and *Chondrus* are strongly supported; however, two groups, *Iridaea/'Sarcothalia'* and *Mazzaella*, receive no bootstrap support. The morphology of the female reproductive system is investigated with the aid of computer-generated, color-coded tracings of photographs of cystocarps seen in cross section at different developmental stages. Seven basic cystocarp types were found which corresponded to species groups seen in *rbc*L trees. These were: (i) a *'Gigartina' alveata* group in which the carposporangia-bearing filaments develop apomictically from gametophytic cells; (ii) a *Rhodoglossum/Gigartina* group in which gonimoblast filaments penetrate the surrounding envelope fusing progessively with envelope cells; (iii) a *Chondracanthus* group in which gonimoblast filaments penetrate the envelope but fuse with envelope cells only at late developmental stages; (iv) a *Sarcothalia* group in which the gonimoblast filaments displace an envelope composed mainly of secondary gametophytic filaments and link to envelope cells by terminal tubular gonimoblast cells; (v) an *Iridaea* group similar to the *Sarcothalia* group, but with an envelope composed of a mixture of medullary cells and secondary gametophytic filaments; (vi) a *Mazzaella* group that lacks a true envelope and in which gonimoblast filaments connect to modified gametophytic cells by means of terminal tubular cells; (vii) a *Chondrus* group in which gonimoblast filaments penetrate the medulla and link to modified medullary cells by means of conjunctor cells forming secondary pit connections. The further separation of these groups into genera is based largely on tetrasporangial characters.

Key words: biogeography, cystocarp, Gigartinaceae, Gigartinales, molecular systematics, red algae, Rhodophyta, seaweeds.

INTRODUCTION

In 1993, Hommersand, Guiry, Fredericq and Leister proposed a revised classification of the marine red algal family Gigartinaceae in which 69 species were classified into four extant (*Chondrus* Stackhouse, *Gigartina* Stackhouse, *Iridaea* Bory nom. cons. and *Rhodoglossum* J. Agardh) and three reinstated (*Chondracanthus* Kützing, *Sarcothalia* Kützing and *Mazzaella* G. de Toni, f.) genera based on developmental and morphological criteria. This treatment included formal descriptions, keys and photographs of diagnostic characters. The seven genera received support in a subsequent phylogenetic study based on sequence analysis of plastid-encoded *rbc*L (Hommersand *et al.* 1994). Five species were added to the Gigartinaceae, either as new combinations or reinstated taxa, and two of the four species placed in *Species incertae sedis* in Hommersand *et al.* (1993), *'Gigartina' alveata* and *'Gigartina' skottsbergii* were identified as belonging to undescribed genera (Hommersand *et al.* 1994). The status of *Sarcothalia* remained confused with two species, *S. decipiens* and *S. scutellata*, falling into a separate group clustering with *Iridaea* in the *rbc*L tree, rather than with *S. stiriata*, the type species of *Sarcothalia*.

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In the present paper, we investigate the phylogenetic systematics of the Gigartinaceae based on an analysis of *rbc*L sequences from 65 collections representing 62 species and re-examine the morphological basis for separating genera by means of computer-aided color tracings of photographs of stages of cystocarp development. Genera that appear in quotation marks (e.g. *'Gigartina'*) are thought by us not to belong under their present generic name. Species names that have been incorrectly applied in the literature are also placed in quotes. The complete scientific name (genus, species and authority) is given for each species in Appendix I. Herbarium abbreviations follow Holmgren *et al.* (1990).

MATERIALS AND METHODS

Methods of DNA extraction, amplification and sequencing of *rbc*L were as previously described (Freshwater and Rueness 1994; Hommersand *et al.* 1994; Fredericq *et al.* 1999). Parsimony and distance analyses of *rbc*L sequence data were performed using the PAUP computer program (v. 4.0, Swofford 1998). Parsimony trees were inferred using a three-part heuristic search scheme designed to increase the likelihood of swapping within the 'island' of trees containing the most parsimonious solution (Maddison 1991). Initial searches consisted of 500 random sequence additions, using STEEPEST DESCENT, MULPARS (but permitting only 20 trees to be held at each step) and the NNI (nearest neighbor interchange) swapping algorithms. Trees found in these initial searches were then swapped to completion using STEEPEST DESCENT, MULPARS and TBR (tree bisection reconnection) swapping algorithms. In an effort to search for additional islands of shorter trees, TBR was used to swap on all trees up two steps less parsimonious than minimal. Reported tree lengths were calculated, including all characters. Consistency (CI) and retention (RI) indices (Kluge and Farris 1969; Farris 1989) were calculated by excluding uninformative characters. Support for nodes of parsimony trees was assessed by calculating bootstrap proportion (BP) values (Felsenstein 1985) based on 500 resamplings of heuristic searches with 10 random additions and the MULPARS and TBR swapping algorithms. A neighbor-joining tree (Saitou and Nei 1987) was inferred based on Kimura two-parameter distances (Kimura 1980). Bootstrap support for nodes in the neighbor-joining tree were based on 1000 resampling replications.

Morphological observations were made on plants fixed in 8–10% formalin/seawater and preserved in 5% formalin/seawater. Hand sections were stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) mounted in 1:1 Hoyers mounting medium and photographed with a Zeiss photomicroscope III, as described in Hommersand *et al.* (1992). Photographic prints were scanned into a Macintosh G3 computer using Photoshop 5.0 (Adobe Systems Inc., CA, USA). Each cell was traced in color, the images assembled with MacDraw Pro, and photoprints made with a Fujix Pictrography 3000 digital image printer (Fugi Photo Film Co. Ltd, Tokyo, Japan).

RESULTS

Nucleotide sequence data for *rbc*L were generated from 65 taxa within the red algal family Gigartinaceae (Appendix I). The data set contained sequences from 31 newly sequenced Gigartinaceae and more complete *rbc*L sequences for many of the species included in an earlier study (Hommersand *et al.* 1994). Sequences for *Phyllophora crispa* and *Mastocarpus stellatus* (Phyllophoraceae) were included as outgroup taxa based on the sister relationship of this family to the Gigartinaceae (Freshwater *et al.* 1994; Fredericq *et al.* 1996; Saunders and Bailey 1997). Tree lengths of 100 000 randomly generated trees had a skewed distribution ($g_1 = -0.288$, $P < 0.01$) indicating the presence of non-random structure in these data (Hillis and Huelsenbeck 1992; Hillis *et al.* 1993). The sequence data set contained 421 parsimony informative characters.

Parsimony and neighbor joining analyses results were in agreement and only parsimony results are included here. Parsimony analyses of the data set resulted in 30 minimal length trees of 2164 steps, CI = 0.341 and RI = 0.693 (Fig. 1). Six species groups received strong bootstrap proportion (BP) support in these analyses: *Chondracanthus* (BP = 100); *Sarcothalia* (BP = 100); a cluster of southern hemisphere *Mazzaella* species including *M. convoluta, M. laminarioides, M. membranacea* and *M. 'affinis'* (BP = 93); *Mazzaella californica, M. leptorhynchos, M. affinis* (BP = 99); *Mazzaella sanguinea, M. flaccida, M. splendens and M. linearis* (BP = 100), and *Chondrus* (BP = 94). Additionally, three species groups were moderately to well supported: a *Gigartina/Rhodoglossum* clade (BP = 84); *Gigartina*-sensu stricto (BP = 76) and a group containing the two strongly supported clades of north-east Pacific *Mazzaella* species previously mentioned (BP = 79). Larger groupings of taxa supported in these analyses included clades containing *Chondrus* and *Mazzaella* (BP = 76); *'Sarcothalia', Iridaea, Mazzaella* and *Chondrus* (BP = 100); *'Gigartina' skottsbergii, Iridaea/'Sarcothalia', Mazzaella* and *Chondrus* (BP = 80); *Sarcothalia, 'Gigartina' skottsbergii, Iridaea/'Sarcothalia', Mazzaella* and *Chondrus* (BP = 99), and a clade containing the previous taxa and *Ostiophyllum* (BP = 81).

Stages of cystocarp development that had been illustrated previously for the type species of each of the seven currently recognized genera in the Gigartinaceae (Fredericq *et al.* 1992; Hommersand *et al.* 1992, 1993) were examined and those that contained critical diagnostic characters were selected for further analysis in this study. As gametophytic and carposporophytic

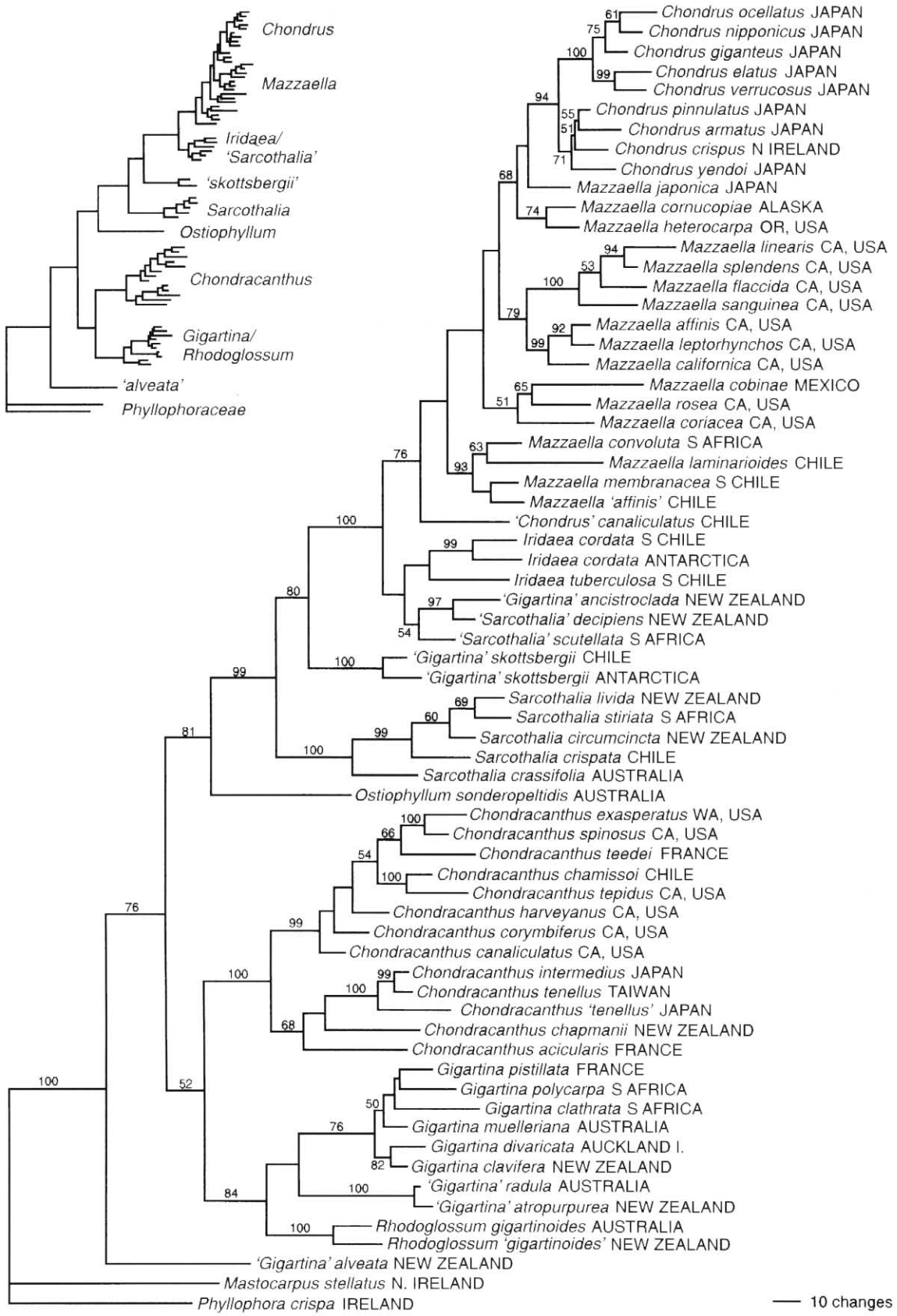


Fig. 1. One of 30 minimal trees (L = 2164, CI = 0.341, RI = 0.693) resulting from parsimony searches of *rbc*L sequence data for 65 Gigartinaceae and two outgroup taxa. Branch lengths are proportional to the number of mutational changes and bootstrap proportion values are shown for branches with support ≥ 50%. The major groups of taxa discussed in this paper are outlined in the condensed tree.

filament types that characterize stages of cystocarp development appear as shades of gray that are difficult to distinguish, color diagrams were prepared by tracing the cells from the black and white prints directly on to the computer screen where they were analyzed. Where published photographs were inadequate, unpublished photographs were used. Species illustrated in Fig. 2 are as follows: Fig. 2a *Rhodoglossum gigartinoides*, original figure; 2b, *Chondracanthus chapmanii*, original figure; 2c, *Chondracanthus teedei* (Hommersand & Fredericq 1990, fig. 168); 2d,e *Gigartina pistillata* (Hommersand *et al.* 1992, figs 48,53); 2f *Gigartina pistillata*, original figure; 2g,h, *Sarcothalia stiriata* (Hommersand *et al.* 1993, figs 14,15); 2i, *Iridaea cordata* (Hommersand *et al.* 1993, fig. 9); 2j, *I. cordata*, original figure; 2k, *Mazzaella californica* (Hommersand *et al.* 1993, fig. 6); 2l, *Chondrus crispus* (Fredericq *et al.* 1992, fig. 28). Stages were selected to show important diagnostic relationships between unmodified primary gametophytic filaments (blue); primary gametophytic filaments modified as a result of nuclear replication and protein synthesis (purple); secondary gametophytic filaments produced after diploidization of a functional auxiliary cell (green); modified secondary gametophytic filaments formed as a result of the replication of haploid nuclei and protein synthesis (black dots); gonimoblast (carposporophytic) filaments and their nuclei (orange); heterokaryotic filaments formed by the uniting of gonimoblastic with gametophytic cells (brown); mature carposporangia with diploid nuclei (magenta). The tetrasporangial stages referred to in the discussion are from Hommersand *et al.* (1993, figs 28–40) and other sources.

DISCUSSION

Molecular phylogeny

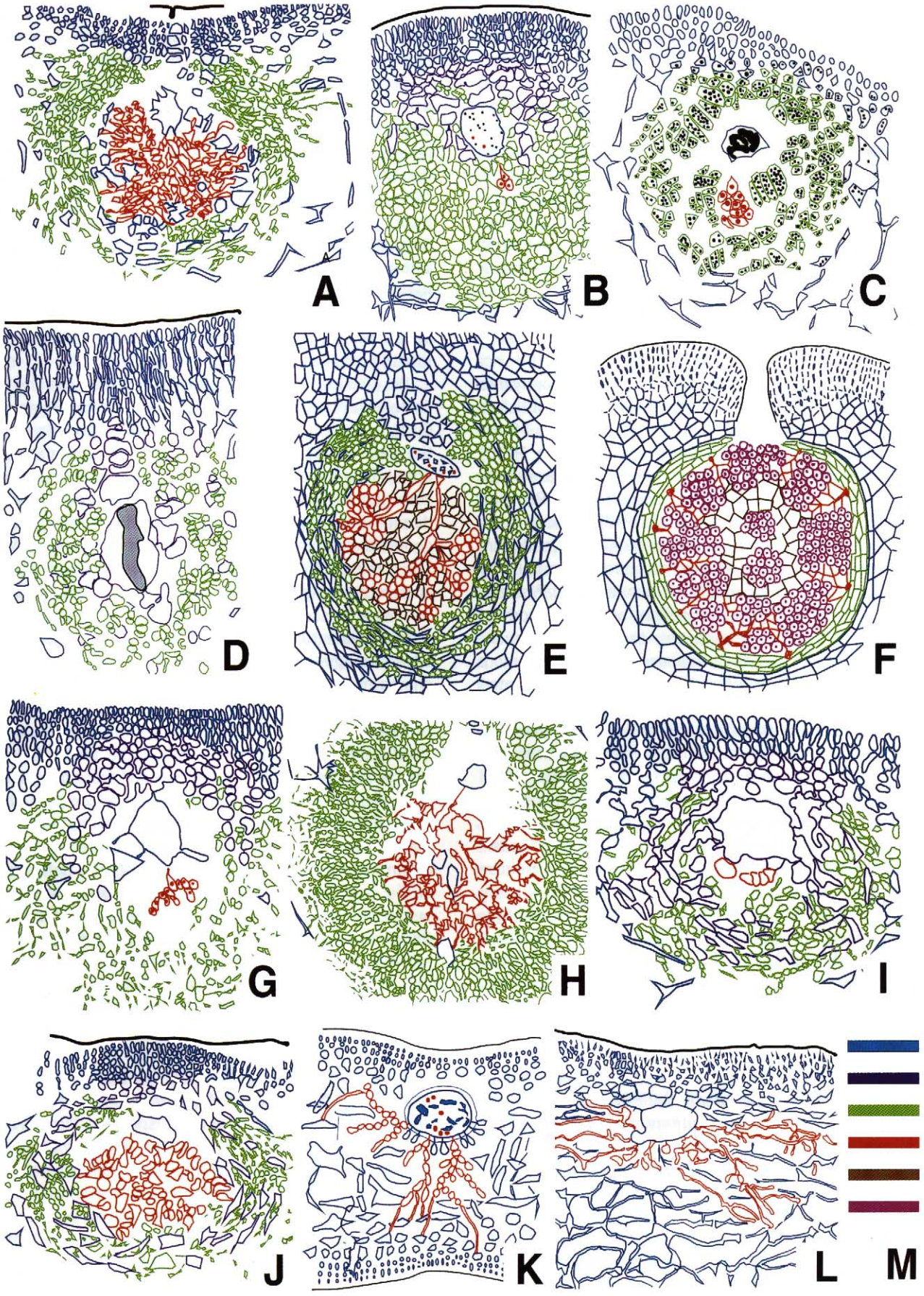
An examination of *rbc*L trees resulting from analyses of the Gigartinaceae taxa included here identifies seven lineages: (i) *'Gigartina' alveata*; (ii) *Rhodoglossum/Gigartina*; (iii) *Chondracanthus*; (iv) *Ostiophyllum*; (v) *Sarcothalia*; (vi) *'Gigartina' skottsbergii*; and (vii) a large clade containing *Iridaea/'Sarcothalia', Mazzaella* and *Chondrus*. These lineages and *Chondrus* are strongly supported; however, two groups, *Iridaea/'Sarcothalia'* and *Mazzaella* receive no bootstrap support in the current analyses. *'Gigartina' alveata* is resolved as a basal lineage in the Gigartinaceae. Its basal position has been a consistent feature of *rbc*L trees (Hommersand *et al.* 1994; Hommersand and Fredericq, unpubl. data, 1999). The *Gigartina/Rhodoglossum* and *Chondracanthus* clades form a monophyletic group in all 30 minimal trees, but there is no bootstrap support for this relationship. Within the *Gigartina/Rhodoglossum* clade there are distinct groups of species. Two of these, *Rhodoglossum* and *'Gigartina' radula/'G.' atropurpurea*, are strongly supported (BP = 100), while *Gigartina*-sensu stricto receives moderate support (BP = 76). There is little resolution of species relationships within the *Gigartina* clade. Within *Chondracanthus*, a split between eastern and western Pacific species is resolved in all minimal trees. The group containing the eastern Pacific cluster is strongly supported (BP = 99), whereas the western Pacific group receives only weak support (BP = 68). Two Atlantic species, *C. teedei* and *C. acicularis* are resolved in the eastern and western Pacific groups, respectively.

The undescribed species *Ostiophyllum sonderopeltidis* Kraft mscr. terminates a long branch at the base of a large clade of gigartinacean taxa. The length of the branch leading to this taxon, as well as the bootstrap support for its topological position (BP = 81, 99) upholds its uniqueness within the Gigartinaceae. A large clade beginning with *Sarcothalia* and including the remaining genera in the family is identified in *rbc*L trees and has strong bootstrap support (BP = 99). Within this assemblage, a *Sarcothalia* clade containing the type species, *S. stiriata*, is strongly supported (BP = 100) and resolved in a basal position. The species from southern South America and the Antarctic Peninsula known as *'Gigartina' skottsbergii* is also resolved as a distinct lineage within this large clade. It is separated from other species by a long branch length and its topological position has moderate to strong support (BP = 80, 100).

A clade containing species of *Iridaea/'Sarcothalia', Mazzaella* and *Chondrus* is strongly supported (BP = 100). A complex of *Mazzaella* and *Chondrus* species receives moderate support (BP = 76) within this larger clade. In the minimal tree shown in Fig. 1, the type species of *Iridaea, I. cordata* and *I. tuberculosa, 'Sarcothalia' scutellata, 'S.' decipiens* and *'Gigartina' ancistroclada* are resolved as a monophyletic clade, but this is not the case in all minimal trees and there is no bootstrap support for this relationship.

The *Mazzaella/Chondrus* complex contains some monophyletic groups that are well supported, but the

Fig. 2(a–m). Color-coded diagrams of stages in cystocarp development as described in the Results. (a) *Rhodoglossum gigartinoides*; (b) *Chondracanthus chapmanii*; (c) *Chondracanthus teedei*; (d–f) *Gigartina pistillata*; (g,h) *Sarcothalia stiriata*; (i,j) *Iridaea cordata*; (k) *Mazzaella californica*; (l) *Chondrus crispus*. (m) Color-coded bars: blue, unmodified primary gametophytic filaments; purple, primary gametophytic filaments modified as a result of nuclear replication and protein synthesis; green, secondary gametophytic filaments produced after diploidization of a functional auxiliary cell; black dots, modified secondary gametophytic filaments formed as a result of the replication of haploid nuclei and protein synthesis; orange, gonimoblast (carposporophytic) filaments and their nuclei; (magenta) heterokaryotic filaments formed by the uniting of gonimoblastic with gametophytic cells (brown); mature carposporangia with diploid nuclei.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arrangement of these groups has no bootstrap support and is not consistent in minimal trees. Among them is a cluster of South American and South African *Mazzaella* species (BP = 93), a *Mazzaella californica* group (BP = 99), a *Mazzaella splendens* group (BP = 100) and *Chondrus* (BP = 94). A clade consisting of the *Mazzaella californica* and *Mazzaella splendens* groups receives moderate support (BP = 79) and an association between *M. cornucopiae* and *M. heterocarpa* is weakly supported (BP = 74). Within *Chondrus*, a split between a weakly supported *'crispus'* clade with four species (BP = 71) and a strongly supported *'ocellatus'* clade with five species (BP = 100) is present in all minimal trees.

Morphology and systematics

The status of the Gigartinaceae as a monophyletic family sister to the Phyllophoraceae was established based on morphological evidence (Kylin 1956; Guiry and Garbary 1990; Hommersand and Fredericq 1990) and phylogenetic analyses of *rbc*L sequence data (Freshwater *et al.* 1994; Fredericq *et al.* 1996) and 18S rRNA (Saunders and Bailey 1997). In both families, the vegetative thallus is multiaxial with medullary and inner cortical cells linked to surrounding cells by both primary and secondary pit connections. Whereas in the Phyllophoraceae, medullary and inner cortical cells are typically compacted to form a pseudoparenchyma, in the Gigartinaceae the cells are more loosely arranged and often stellate in shape, separated by copious matrix material. The supporting cell bears a three-celled carpogonial branch and serves as the auxiliary cell from which numerous gonimoblasts arise in both families; however, the first cell of the carpogonial branch bears a sterile filament in the Phyllophoraceae (Masuda 1987; Guiry and Garbary 1990) but is naked in the Gigartinaceae (Hommersand *et al.* 1992; Fredericq *et al.* 1992). Members of the Phyllophoraceae have either an isomorphic or a heteromorphic life history with erect gametophyte and crustose tetrasporophyte generations, or the tetrasporophyte develops as a pustule directly on the female gametophyte. In contrast, members of the Gigartinaceae have only isomorphic life histories with erect gametophytic and tetrasporophytic generations. Cystocarps are reported to have a similar internal structure in most species of Phyllophoraceae, whereas cystocarp anatomy varies widely in the Gigartinaceae. In the Phyllophoraceae, the tetrasporangia are either solitary, as in *Mastocarpus* (formerly in the Petrocelidaceae), borne in seriate rows in nemathecia on erect or crustose thalli, or are formed in tetrasporangial pustules borne on the gametophyte. Tetrasporangia are, for the most part, formed in nonnemathecial sori in Gigartinaceae. The ancestral condition appears to be one in which the tetrasporangia are borne in branched chains in ordinary primary cortical filaments. In some species, both primary and secondary filaments bear tetrasporangia, whereas in others the tetrasporangia are borne only in secondary filaments formed in the inner cortical and/or medullary regions.

Each of the nine groups identified in Fig. 1 is characterized by a particular cystocarp type. These groups also correspond to six of the seven genera presently recognized in the Gigartinaceae plus three groups that warrant recognition at the generic rank, namely, *'Gigartina' alveata*, *Ostiophyllum sonderipeltidis* Kraft mscr. and *'Gigartina' skottsbergii*. *Rhodoglossum*, *'Gigartina' radula*/*'G.' atropurpurea* and *Gigartina* fall within the same lineage but are separated by a combination of cystocarpic and tetrasporangial characters. Tetrasporangial characters, while not of primary importance, often reinforce generic boundaries or serve to identify infrageneric groups.

We consider *'Gigartina' alveata* from New Zealand to be representative of an undescribed monotypic genus. Cystocarpic plants of *'G.' alveata* are abundant in the field, whereas tetrasporangial plants are rare. Our unpublished morphological observations reveal that the carposporangia are typically borne in chains derived directly from vegetative cells, rather than arising from gonimoblasts produced from diploidized auxiliary cells. Thus, the most common life history would appear to be apomictic. Long thought to be absent, tetrasporangial sori were described by Lindauer (1939) from a few random collections and we have also observed a few tetrasporangial plants. Tetrasporangia are produced in chains in primary cortical filaments, as described for *Iridaea cordata* (Hommersand *et al.* 1993, figs 32, 33).

Two lineages, *Rhodoglossum/Gigartina* and *Chondracanthus*, have cystocarps in which the gonimoblasts tend to penetrate the surrounding envelope, rather than to displace it as in *Sarcothalia* or *Iridaea* (compare Fig. 2a–f with 2g–j). *Rhodoglossum gigartinoides* (Fig. 2a) represents either an archetypal or intermediate condition in which the developing gonimoblasts both penetrate and displace gametophytic filaments. They penetrate some of the primary medullary filaments (blue) and displace the secondary enveloping filaments (green). At a later stage, the gonimoblast filaments link to both types of vegetative cells by means of cell fusions and small tubular gonimoblast cells and produce masses of carposporangia in short, branched chains (Hommersand *et al.* 1993, figs 19,20; Edyvane and Womersley 1993, figs 13,19–21). *'Gigartina' radula* from Australia and *'G.' atropurpurea* from New Zealand, two virtually identical species, form their cystocarps in the same manner as in *Rhodoglossum* (Womersley 1994, fig. 92b,93b, as *Sarcothalia radula*), the chief distinction being that the procarps are borne in papillae in the *'Gigartina'* forms and in superficial sori on smooth blades in *Rhodoglossum*.

An envelope composed of small-celled secondary filaments develops early in members of the *Chon-*

dracanthus and *Rhodoglossum/Gigartina* lineages (Hommersand *et al.* 1993, figs 18,22,25), well before the first appearance of gonimoblasts. In *Chondracanthus*, the secondary filaments arise largely from inner cortical cells and form a compact envelope that is subsequently penetrated by young gonimoblast filaments (Fig. 2b,c). The auxiliary cell contains small haploid (black) and larger diploid (red) nuclei and the nuclei of envelope cells are unmodified in *Chondracanthus chapmanii* from New Zealand (Fig. 2b). In contrast, *Chondracanthus teedei* from Europe possesses an auxiliary cell containing large nuclei with amplified levels of DNA and enlarged envelope cells containing numerous haploid nuclei (Fig. 2c). The cystocarp in *C. chapmanii* is assumed to be primitive and that of *C. teedei* to be advanced, with *C. chamissoi* (Hommersand *et al.* 1993, figs 22–24) intermediate. *Chondracanthus chapmanii* falls in an *'acicularis'* group in the *rbc*L tree (Fig. 1) in which cystocarp formation does not cause cessation of tip growth, with the result that the cystocarps occur along bends in the branches. In contrast, species belonging to the *'teedei'* group have subterminal cystocarps in short branchlets or papillae. In *Chondracanthus*, the gonimoblast filaments appear to link to inner envelope cells only at late stages of cystocarp development (Hommersand and Fredericq 1990, figs 170, 171) and all the carposporangial filaments derive directly from gonimoblast filaments.

In members of the *Rhodoglossum/Gigartina* clade, the secondary filaments that comprise the envelope develop partly from inner cortical cells, but also from medullary cells. This is especially true for species of *Gigartina*. Numerous short, highly branched filaments arise directly from such cells as the auxiliary cell enlarges and initiates gonimoblast filaments (Fig. 2d; Hommersand *et al.* 1992, figs 48–50). Later, as gonimoblast filaments penetrate the envelope and link to envelope cells, successive envelope layers are produced from the compacted primary medullary filaments (Fig. 2e; Hommersand *et al.* 1992, figs 51,53,56). Unlike the behavior seen in *Chondracanthus*, the gonimoblast filaments link to envelope cells progressively as they grow, depositing diploid nuclei into the gametophytic cells and the resulting heterokaryotic cells (Fig. 2e, brown), as well as the gonimoblast cells (Fig. 2e, orange), produce short, branched filaments that mature into carposporangia (Fig. 2f, magenta). The resulting cystocarp is compartmentalized into clusters of carposporangia suspended in a network of sterile envelope filaments (Fig. 2f; Hommersand *et al.* 1993, fig. 27).

Tetrasporangial sori provide accessible characters for identifying members of the *Chondracanthus* and *Rhodoglossum/Gigartina* lineages. Tetrasporangia differentiate entirely from primary cortical filaments in *Chondracanthus* and form compact sori composed of branched chains (West and Guiry 1982, figs 10,11; Guiry 1984, fig. 20a–d; Hommersand *et al.* 1993, fig. 38). In *Rhodoglossum*, the tetrasporangial sori are small, with the tetrasporangia in rows derived from divisions of surface cortical cells and radiating inwardly from the subsurface (Edyvane and Womersley 1993, figs 22–27; Hommersand *et al.* 1993, figs 36,37). In *'Gigartina' radula/'G.' atropurpurea*, the tetrasporangial sori are immersed within the medulla and bear tetrasporangia in short chains produced in secondary medullary filaments, much as in *Sarcothalia* (Womersley 1994, fig. 92c). In fact, it is this similarity in soral development that prompted Womersley to transfer *'Gigartina' radula* to *Sarcothalia*. The tetrasporangial sori of *Gigartina* sensu stricto are distinctive in that they are formed from a mixture of primary and secondary inner cortical filaments in linear or irregular sori, differentiate a separation layer between the inner cortex and outer medulla and are released by excision and gelatinous extrusion (Hommersand *et al.* 1992, figs 74–88).

The undescribed genus and species *'Ostiophyllum sonderopeltidis'* Kraft mscr. is a small, orbicular subtidal plant no more than a centimeter in diameter that has only been found attached to *Sonderopelta coriacea* Womersley et Sinkora. The cystocarps are marginal with a prominent ostiole, as in *Gigartina*, but without an evident sterile envelope, at least at maturity. Tetrasporangial sori are scattered across the blade in pits provided with conspicuous ostioles, with the tetrasporangia occuring in chains at the base of a pit formed through the inward growth of dividing apical cells (G. T. Kraft, pers. comm., 1993). Such tetrasporangial filaments, although unique, appear to be primary rather than secondary filaments.

The three basal lineages in the large clade that includes the remaining genera in the Gigartinaceae: *Sarcothalia*, *'Gigartina' skottsbergii* and *Iridaea/'Sarcothalia'* possess cystocarps in which the developing gonimoblast filaments displace the envelope and penetrate and connect to medullary and secondarily produced envelope cells by means of long tubular cells, rather than by growing between and linking to interspersed gametophytic cells. Historically, species belonging to this assemblage have been placed in *Gigartina* if the cystocaps are emergent or borne on papillae, or in *Iridaea* if they are immersed within the thallus. Our observations show that this is not a reliable character. Instead, the three lineages identified in *rbc*L trees can be separated morphologically only by subtle differences in cystocarp development.

The *Sarcothalia* lineage, containing the type species *S. stiriata*, possesses cystocarps in which the envelope is made up almost entirely of secondary filaments. During cystocarp development, cells of the inner cortex adjacent to the auxiliary cell become densely filled with cytoplasm and neighboring cells may fuse (Fig. 2g, purple). Secondary filaments originating from inner cor-

tical cells surround the young gonimoblast filaments (Fig. 2g, green) and radiate outwardly, forming a thick envelope composed almost entirely of secondary filaments (Fig. 2h). At maturity, cells at the center of the cystocarp expand, becoming vacuolate, and the carposporangia around the periphery form prominent radiating rows terminated by elongated tubular cells that penetrate deeply into the envelope (Hommersand *et al.* 1993, figs 16,17). Tetrasporangial sori originate in the outer medulla from a small cluster of medullary cells and consist entirely of radiating secondary filaments, with most of the cells transformed into tetrasporangia (Hommersand *et al.* 1993, figs 34,35; Womersley 1994, fig. 94a,b,e,f).

The species from southern South America and the Antarctic Peninsula known as *'Gigartina' skottsbergii* belongs to an undescribed monotypic genus. It is superficially similar to *Gigartina* in that procarps are borne on secondary papillae and form prominent emergent cystocarps. The envelope formed around the diploidized auxiliary cell develops entirely from medullary cells and, while broad in dimensions, is so thinly traversed with secondary filaments that the whole structure appears to be composed entirely of medullary cells (G. L. Leister, pers. comm., 1990). To the casual observer it would appear as though an envelope were absent. The contents of the medullary cells and secondary filaments are consumed continuously through the tubular gonimoblast filaments as the cystocarp expands, so that a typical envelope composed of compressed filaments is never formed. As in *Sarcothalia*, the tetrasporangia are formed entirely in secondary filaments, which, however, originate from medullary cells in the center of the thallus in much the same manner as in some species of *Chondrus*.

In the *Iridaea/'Sarcothalia'* lineage, a prominent envelope forms around the diploidized auxiliary cell and is displaced by the expanding gonimoblast filaments, as in true *Sarcothalia*; however, the secondary filaments that comprise the envelope develop from medullary as well as inner cortical cells and are interspersed among them (Fig. 2i,j, purple, green). Inner cortical cells become densely filled with cytoplasm and often fuse with one another (Fig. 2i). The terminal tubular gonimoblast cells are not as long as in true *Sarcothalia*, but they function in the same way. At maturity, chains of carposporangia form around elongated sterile gonimoblast filaments and there is no central area of vacuolate gonimoblast cells (Hommersand *et al.* 1993, figs 12,13). Cystocarps in *'Sarcothalia' decipiens*, *'S.' scutellata* and *'Gigartina' ancistroclada* develop initially as in *Iridaea*, in that secondary filaments that form the envelope arise primarily from medullary cells; however, they also contain some vacuolate inner gonimoblast cells like those seen in typical *Sarcothalia* and the envelope is a much looser structure than in either *Sarcothalia* or *Iridaea* and approaches that seen in *'Gigartina' skottsbergii* (M. H. Hommersand, unpubl. data, 1999). Tetrasporangia are produced in branched chains derived from the transformation of inner primary cortical cells in *Iridaea* (Hommersand *et al.* 1993, figs 32,33) and in secondary filaments forming linear sori in the inner cortex and outer medulla in *'Sarcothalia'* (G. L. Leister and M. H. Hommersand, unpubl. data, 1999).

'Chondrus' canaliculatus from Chile has been shown by Arakaki *et al.* (1997) not to belong in *Chondrus*. Morphologically, it is intermediate between *'Sarcothalia'* in the *Iridaea/'Sarcothalia'* group and *Mazzaella*. An envelope is present around the cystocarp; however, the enveloping filaments develop gradually and are more diffuse than in *Iridaea* or *'Sarcothalia'* and the tetrasporangia form in secondary filaments in linear sori in the outer medulla, much as in *'Sarcothalia'*.

The *Mazzaella/Chondrus* clade appears to have evolved from an *Iridaea*-like ancestor through the loss of the primary envelope. In the absence of an envelope, primary medullary cells, sometimes supplemented by secondary filaments, become modified for a nutritive function in both *Mazzaella* and *Chondrus*. The general pathway of cystocarp development in *Mazzaella* species is similar to that described by Hommersand *et al.* (1993) for *M. californica*. Numerous gonimoblast initials issue from a diploidized auxiliary cell and initially penetrate the surrounding inner medullary and cortical filaments, attaching to them by means of terminal tubular gonimoblast cells (Fig. 2k; Hommersand *et al.* 1993, figs 5–7). Gametophytic cells contacted by terminal gonimoblast cells undergo nuclear divisions and become densely filled with cytoplasm when compared with untransformed vegetative cells. The contents of the contacted cells are consumed and the developing gonimoblast filaments soon generate a defining margin that looks like a weak envelope, but does not correspond to the preformed envelope found in *Sarcothalia* or *Iridaea*. The modified filaments are contacted by terminal tubular gonimoblast cells in *Mazzaella* and by small conjunctor cells in *Chondrus*, as described below. The five *Mazzaella* and two *Chondrus* lineages identified in the *rbc*L tree differ in the details of cystocarp development and these differences are currently under investigation. The type and arrangement of the tetrasporangia are variable throughout the *Mazzaella* group, sometimes developing entirely in primary cortical filaments, as in *Mazzaella affinis* (Kylin 1928, fig. 29a–c, as *Rhodoglossum affine*), sometimes in both primary and secondary filaments, as in *Mazzaella californica* (Hommersand *et al.* 1993, figs 30,31) and sometimes entirely in secondary filaments, as in *Mazzaella splendens* (Kylin 1928, fig. 27a,b, as *Iridaea cordata*). For a survey of tetrasporangial types, see Kim (1976, figs 53–69).

The South American and South African cluster of *Mazzaella* species have cystocarps that lack secondary

filaments and the tetrasporangia are formed entirely in secondary filaments. The *'rosea'* group contains three species including one new combination:

Mazzaella coriacea (Dawson) Hughey comb. nov. (Monterey Co., California to Punta Maria, Baja California, Mexico)
Basionym: ***Rhodoglossum coriaceum*** Dawson, *Bull. So. Calif. Acad. Sci.* **44**: 75–6, pl. 25, fig. 10, 1945. [Lectotype: UC 696949! Isotypes: UC 696950! 696951!]

Species belonging to the *'rosea'* group have large cystocarps of indefinite size in which new carposporangia differentiate at the periphery of the cystocarp cavity after some of the mature carposporangia have been released. Species in the *'californica'* group have smaller cystocarps of definite size that lack secondary gametophytic filaments; those in the *'splendens'* group also have cystocarps of definite size, but they produce secondary gametophytic filaments early in cystocarp development that do not, however, form a well-defined envelope. The '*heterocarpa*' group, with two species, *Mazzaella heterocarpa* and *M. cornucopiae* (North American representatives), have conspicuous cystocarps of indefinite size which, however, develop differently from those found in the '*rosea*' group. Finally, *Mazzaella japonica* has small, spherical cystocarps that develop in much the same way as in *M. californica*.

The genus *Mazzaella* is paraphyletic to *Chondrus* in both molecular and morphological analyses and the two are separated at the present time by a single diagnostic character. In *Mazzaella,* the gonimoblast filaments link to medullary and inner cortical cells by means of terminal tubular cells and a boundary forms between carposporophytic and gametophytic regions as nutriment is consumed. In *Chondrus*, the gonimoblast filaments extend for some distance through the medulla and contact the medullary filaments directly by means of small conjunctor cells forming secondary pit connections. This stage was illustrated by Mikami (1965) for *Chondrus pinnulatus, C. ocellatus, C. nipponicus* (as *C. crispus*), and *C. giganteus*. As Mikami pointed out, such medullary filaments become thick and rich in cytoplasm before contact and collapse afterwards. Fredericq *et al.* (1992, figs 33–35) showed that in *Chondrus crispus* the medullary cells that are contacted undergo synchronous nuclear divisions and protein synthesis prior to linkage with gonimoblast cells and that both gonimoblast cells and heterokaryotic medullary cells form carposporangial chains. No clear morphological distinction separates the two *Chondrus* clades identified in *rbc*L trees. Some species in the *'ocellatus'* group produce an enveloping region in young cystocarps that presumably contain secondary filaments, but others do not. Some members have ocellate cystocarps in which the carposporangial chains mature at a distance from the auxiliary cell and the central region remains clear at maturity; others do not (Mikami 1965). Crossability studies by Brodie *et al.* (1993) showed that forms of *C. ocellatus* were weakly crossable with *C. nipponicus*, a species that is morphologically similar to *C. crispus,* but which falls within the *'ocellatus'* clade in *rbc*L trees. Instead, *Chondrus crispus* from the North Atlantic is most closely associated with *C. pinnulatus/C. armatus* in *rbc*L trees.

The classification of the Gigartinaceae proposed earlier by Hommersand *et al.* (1993, 1994) based on the comparative development of carposporophyte and gametophyte generations in relation to cystocarp morphology is confirmed and extended here. The inclusion of new taxa and more complete sequences for existing taxa have increased bootstrap support for the seven more basal lineages. The distinction between *'Sarcothalia'*, including *'Gigartina' ancistroclada*, and true *Sarcothalia* and its weakly supported association with *Iridaea* is confirmed and remains a problem for future study. The existence of a large clade containing seven to nine lineages of *Mazzaella* and *Chondrus* species is also confirmed and strengthened, as is the paraphyletic status of *Mazzaella* relative to *Chondrus*.

The conclusion that the Gigartinaceae originated and evolved many of its basal lineages in the Pacific Ocean along the eastern and southern edge of Gondwanaland and later spread along the Pacific coast of South and North America, ultimately reaching the Atlantic Ocean and Europe (Hommersand 1986; Hommersand *et al.* 1994, fig. 2, map) is supported. Some disjunct species, such as *Rhodoglossum gigartinoides, 'Gigartina' skottsbergii* and *Iridaea cordata*, are separated by relatively long branch lengths in the *rbc*L trees, reflecting vicariant distribution patterns. The vicariant event in the case of *Rhodoglossum gigartinoides* could be associated with the opening of the Tasman Sea from 80 to 60 Ma, and for *'Gigartina' skottsbergii* and *Iridaea cordata*, the separation of South America from the Antarctic Peninsula with the formation of Drake Passage and establishment of the circum-Antarctic current from 30 to 21 Ma (Kennett 1982).

The present study confirms that the primary morphological characters separating genera and genetic lineages in *rbc*L trees are subtle details in cystocarp development that reflect strategies for the provision of nutriment by the gametophyte for carposporophyte development. While important as diagnostic characters, the organization and placement of tetrasporangial sori are less reliable. Plesiomorphous types in which the tetrasporangia are formed in primary cortical filaments have evidently given rise numerous times to advanced types in which the tetrasporangia are formed partly or entirely in secondary cortical or medullary filaments. In some cases, tetrasporangial characters reinforce the established circumscription of genera; in others they tend to break down taxonomic boundaries. Future progress toward an understanding of the phylogenetic

systematics of the Gigartinaceae will require monographic studies of each of the genera and species clusters including detailed observations of their developmental morphology, as well as molecular studies incorporating more taxa and additional genes.

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Appendix I

Species	Authority	Collection information	% *rbc*L sequenced	GenBank accession no.[a]
Chondracanthus acicularis	(Roth) Fredericq in Hommersand *et al.* 1993	Île Verte, Roscoff, Brittany, France, Coll. J. Cabioch, 9.iii.92	98	U02938
Chondracanthus canaliculatus	(Harvey) Guiry in Hommersand *et al.* 1993	Pigeon Point, San Mateo Co., California, coll. M. H. Hommersand, 20.v.1992	95	U02939
Chondracanthus chamissoi	(C. Agardh) Kützing 1843.	Lechagua, near Ancud, Chiloé, Chile, coll. S. Fredericq & M. E. Ramírez, 23.ii.1993	98	AF146193
Chondracanthus chapmanii	(J.D. Hooker et Harvey in Harvey) Fredericq in Hommersand *et al.* 1994	Island Bay, Wellington, New Zealand, coll. W. A. Nelson, 23.v.1993	98	U02940
Chondracanthus corymbiferus	(Kützing) Guiry in Hommersand *et al.* 1993	Pigeon Point, San Mateo Co., California, coll. M. H. Hommersand, 21.xii.1992	98	U02941
Chondracanthus exasperatus	(Harvey et Bailey) Hughey in Hughey *et al.* 1996	Tacoma Narrows, Tacoma Co., Washington, coll. J. R. Hughey, 4.v.1997	90	AF146194
Chondracanthus harveyanus	(Kützing) Guiry in Hommersand *et al.* 1993.	Pacific Grove, Monterey Co., California, coll. J. R. Hughey, 11.vii.1995	93	AF146195
Chondracanthus intermedius	(Suringar) Hommersand in Hommersand *et al.* 1993	Tokawa, Choshi, Chiba Pref., Japan, coll M. Yoshizaki, 22.v.1993	98	U02942
Chondracanthus spinosus	(Kützing) Guiry in Hommersand *et al.* 1993	Pacific Grove, Monterey Co., California, coll. J. R. Hughey, 14.vii.1996	90	AF148519
Chondracanthus teedei	(Roth) Kützing 1843	Île Verte, Roscoff, Brittany, France, coll. J. Cabioch, 5.iii.1993	91	U03024
Chondracanthus tenellus	(Harvey) Hommersand in Hommersand *et al.* 1993	Wang Hai Xiang, Taiwan, Coll. S. Fredericq & S-M. Lin, 8.vii.1994	99	AF146196
Chondracanthus 'tenellus'	[non (Harvey) Hommersand in Hommersand *et al.* 1993)	Okinoshima, Tateyama Bay, Chiba Pref., Japan, coll. M. Yoshizaki, 18.vi.1993	95	AF146197
Chondracanthus tepidus	(Hollenberg) Guiry in Hommersand *et al.* 1993	S. Mission Bay, San Diego, Co., California, coll. P. A. & D. R. Hughey, 6.iii.1996	90	AF146198
Chondrus armatus	(Harvey) Okamura 1930	Oshoro, Hokkaido Japan, coll. S. Fredericq, 5.ix.1993	90	AF146201
'Chondrus' canaliculatus	(C. Agardh) Greville 1830	Punta Horcón, Valparaiso Prov., Chile, coll. S. Fredericq & M. E. Ramírez, 17.i.1994	94	AF146199
Chondrus crispus	Stackhouse 1797	Bally Castle, Co. Antrim, Northern Ireland, UK, coll. C. A. Maggs, 20.i.1992	98	U02984
Chondrus elatus	Holmes 1895	Tokawa, Choshi, Chiba Pref., Japan, coll. M. Yoshizaki, 22.v.1993	98	U02985
Chondrus giganteus	Yendo 1920	Tokawa, Chosi, Chiba Pref., Japan, coll. M. Yoshizaki, 7.vi.1993	98	U02986
Chondrus nipponicus	Yendo 1920	Oshoro, Hokkaido, Japan, coll.S. Fredericq, 5.ix.1993	98	AF146200
Chondrus ocellatus	Holmes 1895	Matsugahana, Amatsukominato, Awa-ken, Chiba Pref. Japan, coll. M. Yoshizaki, 21.v.1993	98	U02988
Chondrus pinnulatus	(Harvey) Okamura 1930	Oshoro, Hokkaido, Japan, coll. S. Fredericq, 5.ix.1993	98	AF146202
Chondrus verrucosus	Mikami 1965	Matsugahana, Amatsukominato, Awa-ken, Chiba Pref., Japan, coll. M. Yoshizaki, 21.v.1993	98	U02987
Chondrus yendoi	Yamada et Mikami in Mikami 1965	Muroran, Hokkaido, Japan, coll. S. Fredericq, 6.ix.1993	98	AF146203
'Gigartina' alveata	(Turner) J. Agardh 1851	Tauranga Bay, Northland, New Zealand, coll. W. A. Nelson, ii.1993	93	U03422
'Gigartina' ancistroclada	Montagne 1845	Horseshoe Bay, Stewart I., New Zealand, coll. W. A. Nelson, viii.1994	93	AF146217
'Gigartina' atropurpurea	(J. Agardh) J. Agardh 1885	Island Bay, Wellington, New Zealand, coll. W. A. Nelson, 23.v.1993	94	U03423
Gigartina clathrata	(Decaisne) Rabenhorst 1878	Oudekraal, Cape Peninsula, South Africa, Coll. J. Bolton, 28.ii.1993	56	U03426
Gigartina clavifera	J. Agardh 1876	Princess Bay, Wellington, New Zealand, coll. W. A. Nelson, 23.v.1993	92	U03424
Gigartina divaricata	J.D. Hooker et Harvey 1845	Adams Is., Survey Bay, Auckland Is., coll. T. Grant, 11.xii.1996	95	AF146204
Gigartina muelleriana	Setchell et Gardner 1933	Flinders Jetty, Victoria, Australia, coll. G. W. Saunders and G. T. Kraft, 10.ii.1993	92	U03427
Gigartina pistillata	(S.G. Gmelin) Stackhouse 1809	Santec, Brittany, France, coll. J. Cabioch, 6.iv.1993	90	U03429
Gigartina polycarpa	(Kützing) Setchell et Gardner 1933	Kommetjie, Cape Peninsula, South Africa, coll. J. Bolton, 24.ii.1993	90	U03431
'Gigartina' radula	(Esper) J. Agardh 1848	Evans Cave, Cape Lannes, S Australia, Australia, coll. M. H. Hommersand, 11.ix.1995	99	AF146205
'Gigartina' skottsbergii	Setchell et Gardner 1936	Playa de San Antonio, Bahía de Ancud, Chiloé, Chile, coll. M. E. Ramírez, 14.iv.1993	63	U03432
'Gigartina' skottsbergii	Setchell et Gardner 1936	Bahía Collins, King George I., S. Shetland Is. Antarctic Pen., coll. S. Fredericq & J. Rodriguez, 10.ii.1994	98	AF146206

Iridaea cordata	(Turner) Bory 1826	Punta Daniel Este, Magellanes, Chile, coll. S. Fredericq & M. E. Ramírez, 19.ii.1994	99	AF146207
Iridaea cordata	(Turner) Bory 1826	Hellerman Rocks near Laggard I., Arthur Harbor, Anvers I. Antarctica, coll. R. L. Moe, 20.i.1988	75	U02989
Iridaea tuberculosa	(J.D. Hooker et Harvey) Leister in Hommersand *et al.* 1993	Fuerte Bulnes, Magellanes, Chile, coll. S. Fredericq & M. E. Ramírez, 10.ii.1994	93	AF146208
Mastocarpus stellatus	(Stackhouse) Guiry in Guiry *et al.* 1994	Bally Castle, Co. Antrim, Northern Ireland, UK, coll. C. A. Maggs, 20.i.1992	100	U29920
Mazzaella affinis	(Harvey) Fredericq in Hommersand *et al.* 1993	Pacific Grove, Monterey Co., California, coll. M. H. Hommersand, 2.i.1993	70	U03081
Mazzaella 'affinis'	[non (Harvey) Fredericq in Hommersand *et al.* 1993]	Caleta Errazuriz, Antofagasta, Chile, coll. M. E. Ramírez, 27.xi.97	91	AF146209
Mazzaella californica	(J. Agardh) G.B. DeToni f. 1936	Jalama Beach State Park, Santa Barbara Co., California, coll. M. H. Hommersand, 19.v.1992	94	U03082
Mazzaella cobinae	(Dawson) Fredericq in Hommersand *et al.* 1993	Punta María, Baja California, Mexico, coll. J. R. Hughey, 4.vi.1996	94	AF146210
Mazzaella convoluta	(Areschoug ex J. Agardh) Hommersand in Hommersand *et al.* 1994	Kommetjie, Cape Peninsula, South Africa, coll. J. Bolton, 23.ii.1993	99	U03084
Mazzaella coriacea	(Dawson) Hughey comb. nov.	Pacific Grove, Monterey Co., California, coll. J. R. Hughey, 14.vii. 1996	85	AF146211
Mazzaella cornucopiae	(Postels et Ruprecht) Hommersand in Hommersand *et al.* 1993	Perevalnie Passage, Shuyak I., coll. G. Hansen, 20.viii.1993	90	AF146212
Mazzaella flaccida	(Setchell et Gardner) Fredericq in Hommersand *et al.* 1993	Pigeon Point, San Mateo Co., California, coll. M. H. Hommersand, 21.xii.1992	98	U03378
Mazzaella heterocarpa	(Postels *et* Ruprecht) Fredericq in Hommersand *et al.* 1993	Seal Rock, Lincoln Co., Oregon, coll. E. Henry, 24.v.1993	92	U03379
Mazzaella japonica	(Mikami) Hommersand in Hommersand *et al.* 1993	Cape Todogasaki, Miyako-wan, Iwate Pref., Japan, coll. M. H. Hommersand, 13.vi.1994	94	AF146213
Mazzaella laminarioides	(Bory) Fredericq in Hommersand *et al.* 1993	Quintay, Valparaiso Prov., central Chile, coll. M. E. Ramírez, 7.iv.1993	92	U03380
Mazzaella leptorhynchos	(J. Agardh) Leister in Hommersand *et al.* 1993	Jalama Beach State Park, Santa Barbara Co., California, coll M. H. Hommersand, 19.v.1992	95	U03381
Mazzaella linearis	(Setchell et Gardner) Fredericq in Hommersand *et al.* 1993	Drift, Moss Beach, Monterey Co., California, coll. F. Shaughnessy, 23.vii.1996	88	AF148520
Mazzaella membranacea	(J. Agardh) Fredericq in Hommersand *et al.* 1993	Punta Daniel Este, Magellanes, Chile, coll. S. Fredericq & M. E. Ramírez, 19.ii.1994	98	AF146214
Mazzaella rosea	(Kylin) Fredericq in Hommersand *et al.* 1993	Pacific Grove, Monterey Co., California, coll. J. R. Hughey, 14.vii.1996	93	AF146215
Mazzaella sanguinea	(Setchell et Gardner) Hommersand in Hommersand *et al.* 1994	Drift, Horseshoe Cove, Bodega Head, Sonoma Co., California, coll. M. H. Hommersand, 22.xii.1992	96	U03384
Mazzaella splendens	(Setchell et Gardner) Fredericq in Hommersand *et al.* 1994	Pigeon Point, San Mateo Co., California, coll. M. H. Hommersand, 21.xii.1992	97	U03385
Ostiophyllum sonderopeltidis	Kraft (mscr.)	SCUBA 20–30 ft. on *Sonderopelta coriacea*, Ninepins Point, south of Hobart, Tasmania, coll. G. T. Kraft, 22.xii.1992	93	AF146221
Phyllophora crispa	(Hudson) Dixon 1964	Spidall, Co. Galway, Ireland, coll. M. D. Guiry, 7.iii.1993	92	U02990
Rhodoglossum gigartinoides	(Sonder) Edyvane et Womersley 1993	Flinders Jetty, Victoria, Australia, coll. G. W. Saunders, I4.V.1993	92	U02991
Rhodoglossum 'gigartinoides'	(Sonder) Edyvane et Womersley 1993	Horseshoe Bay, Stewart I., New Zealand, coll. W. A. Nelson, viii.1994	92	AF146216
Sarcothalia circumcincta	(J. Agardh) Hommersand in Hommersand *et al.* 1993.	Brighton Beach, Otago, New Zealand, coll. C. Hurd, 4.xi.1998	93	AF146219
Sarcothalia crassifolia	(C. Agardh) Edyvane et Womersley in Womersley 1994	Evans Cave, Cape Lannes, South Australia, Australia, coll. H. B. S. Womersley, 31.x.1993	93	AF 146218
Sarcothalia crispata	(Bory) Leister in Hommersand *et al.* 1993.	Playa San Antonio, Bahía de Ancud, Chiloé, Chile, coll. M. E. Ramírez, 14.v.1993	99	U03085
'Sarcothalia' decipiens	(J. D. Hooker et Harvey) Hommersand in Hommersand *et al.* 1993	Muritai, Wellington Harbor, New Zealand, coll. W. A. Nelson, 4.v.1993	98	U03086
Sarcothalia livida	(Turner) Hommersand in Hommersand *et al.* 1993	Horseshoe Bay, Stewart I., New Zealand, Coll. W. A. Nelson, viii.1994	98	AF146220
'Sarcothalia' scutellata	(Hering) Leister in Hommersand *et al.* 1993	Kommetjie, Cape Peninsula, South Africa, coll. J. Bolton, 23.ii.1993	98	U03088
Sarcothalia stiriata	(Turner), Leister in Hommersand *et al.* 1993	Kommetjie, Cape Peninsula, South Africa, coll. J. Bolton, 24.ii.1993	92	U03089

[a]See Benson *et al.* (1994) for taxa analyzed in this study.