Small-subunit rDNA sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). 3. Delineating the Gigartinales sensu stricto

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Abstract: Nuclear small-subunit ribosomal DNA sequences were determined for 65 members of the Gigartinales and related orders. With representatives of 15 families of the Gigartinales sensu Kraft and Robins included for the first time, our alignment now includes members of all but two of the ca. 40 families. Our data continue to support ordinal status for the Plocamiales, to which we provisionally transfer the Pseudoanemoniaceae and Sarcodiaceae. The Halymeniales is retained at the ordinal level and consists of the Halymeniaceae (including the Corynomorphaceae), Sebdeniaceae, and Tsengiaceae. In the Halymeniaceae, *Grateloupia intestinalis* is only distantly related to the type species, *Grateloupia filicina*, but is closely affiliated with the genus *Polyopes*. The Nemastomatales is composed of the Nemastomataceae and Schizymeniaceae. The Acrosymphytaceae (now including *Schimmelmannia*, formerly of the Gloiosiphoniaceae) and the Calosiphoniaceae (represented by *Schmitzia*) have unresolved affinities and are considered as incertae sedis among lineage 4 orders. We consider the Gigartinales sensu stricto to include 29 families, although many contain only one or a few genera and mergers will probably result following further investigation. Although the small-subunit ribosomal DNA was generally too conservative to resolve family relationships within the Gigartinales sensu stricto, a few key conclusions are supported. The Hypneaceae, questionably distinct from the Cystocloniaceae on anatomical grounds, is now subsumed into the latter family. As recently suggested, the Wurdemanniaceae should be incorporated into the Solieriaceae, but the latter should not be merged with the Areschougiaceae. The **Corynocystaceae Kraft**, fam. nov., is described and added to the Gigartinales sensu stricto.

Key words: Corynocystaceae, Cryptonemiales, Florideophyceae, Gigartinales, Rhodymeniales, systematics.

Résumé : Les auteurs ont déterminé les séquences de la petite sous-unité de l'ADN ribosomique nucléique, chez 65 membres des Gigartinales et ordres associés. Avec les 15 familles de Gigartinales sensu Kraft et Robins comprises pour la première fois, l'alignement présenté par les auteurs inclut maintenant des membres des quelque 40 familles, sauf deux. Les données continuent de supporter un statut ordinal pour les Plocamiales, à lesquellles les auteurs transfèrent provisoirement les Pseudoanemoniaceae et les Sarcodiaceae. On maintient au niveau ordinal les Halymeniales, qui comportent les Halymeniaceae (incluant les Corynomorphaceae), les Sebdeniaceae et les Tsengiaceae. Au sein des Halymeniaceae, le *Grateloupia intestinalis* n'est que faiblement relié à l'espèce type, le *Grateloupia filicina*, mais étroitement relié au genre *Polyopes*. Les Nemastomales comportent les Nemastomataceae et les Schizymeniaceae. Les Acrosymphytaceae (incluant maintenant les *Schimmelmannia*, anciennement un Gloiosiphoniaceae) et les Calosiphoniaceae représentées par les *Schmitzia*) sont d'affinités irrésolues, et on les considère comme incertae sedis au sein des ordres de la Lignée 4. Les auteurs considèrent que les Gigartinales sensu stricto comportent 29 familles, bien que plusieurs contiennent seulement un ou quelques genres, et des regroupements sont à prévoir suite à de nouvelles recherches. Bien que la petite sous-unité de l'ADN ribosomique soit généralement trop conservatrice pour résoudre les relations familiales au sein des Gigartinales sensu stricto, elle supporte quelques conclusions déterminantes. Les Hypneaceae, possiblement distinctes des Cystocloniaceae sur des bases anatomiques, sont incluses maintenant dans cette dernière famille. Comme on l'a suggéré récemment, les Wurdemanniaceae devraient être incorporées dans les Solieriaceae, mais non pas regroupées avec les Areschougiaceae. Les auteurs décrivent les **Corynocystaceae Kraft**, fam. nov., et les ajoutent aux Gigartinales sensu stricto.

Mots clés : Corynocystaceae, Cryptonemiales, Florideophyceae, Gigartinales, Rhodymeniales, systématique.

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Introduction

Families and genera of the red algal class Florideophyceae are undergoing substantial taxonomic reorganization as a result of ultrastructural, biochemical, and molecular approaches (see review by Saunders and Kraft 1997). This is perhaps a "modern" echo of an earlier revolution that began in the late 19th century, one centered around detailed anatomical observations and interpretations of fertilization, zygote-formation and embryogenesis events that set the standard for decades of systematic thought. Schmitz (1883, 1892) led this earlier shift away from classification based on mainly vegetative structure and gross cystocarp features, recognizing four orders: (1) Nemaliales (as the Nemalionales), for species with direct carposporophyte development from fertilized carpogonia; (2) Gigartinales, for species with a consistent spatial association (a "procarpic" relationship) between fertilized carpogonia and diploidized auxiliary cells from which the carposporophyte developed toward the thallus interior; (3) Rhodymeniales, for procarpic species with outward carposporophyte direction of development; and (4) Cryptonemiales, for species with spatially nondeterministic associations between carpogonia and auxiliary cells (a "nonprocarpic" relationship). Oltmanns (1904–1905) introduced an even more subtle refinement by segregating the Ceramiales from the Rhodymeniales for species in which auxiliary cells are produced only after, rather than before or in the absence of, fertilization.

Kylin (1923) added a sixth order by segregating the Gelidiales from the Nemaliales, arguing that gelidialean carposporophyte anatomy was distinct from other Nemaliales and showing that auxiliary cells served a strictly nutritive function in the Gelidiaceae, unlike those of any other florideophyte order. Kylin (1928) later noted that the Nemaliales and Gelidiales also differed significantly in life-history patterns, those of the former being haplobiontic, whereas those of the latter were diplobiontic and isomorphic (Kylin 1932, 1956). At least in part because of the eventual revelation (e.g., Magne 1961, 1967) that life histories in the Nemaliales were actually also diplobiontic (although for the most part heteromorphic), arguments arose as to the validity of the Gelidiales, with Dixon (1973) arguing for its return to the Nemaliales and Papenfuss (1966) advocating its continued recognition. Subsequent ultrastructural (Pueschel and Cole 1982), anatomical (Hommersand and Fredericq 1988), and molecular studies (Ragan et al. 1994; Saunders and Bailey 1997) have all strongly supported the autonomy of the Gelidiales and its quite distant phylogenetic position relative to the Nemaliales.

Relationships among families apportioned by Kylin (1956) between the orders Cryptonemiales and Gigartinales have had a particularly involved history. Kylin (1925) proposed the Nemastomatales (as Nemastomales) for nonprocarpial species that had auxiliary cells intercalary in unmodified cortical filaments, in contrast with members of the Cryptonemiales, in which they were borne on or within modified lateral branch systems. Sjöstedt (1926) then removed the Sphaerococcaceae and the genus *Plocamium*, both of the Rhodymeniales, to the new order Sphaerococcales, defined as containing procarpic algae in which the supporting cell of the carpogonial branch functioned as the auxiliary cell. Kylin (1928) rejected his student's proposal of the Sphaerococcales and included the procarpic Sphaerococcaceae in his nonprocarpic Nemastomales, arguing that the situation seen in *Calosiphonia*, in which the carpogonium first fuses with the supporting cell of its branch before issuing connecting filaments that extend to distant auxiliary cells, was an intermediate step on the path toward sphaerococcacean procarpy. Kylin (1932) ultimately merged the Nemastomales and Gigartinales, thus abandoning procarpy versus nonprocarpy as an ordinal taxonomic criterion, and emphasized the nonaccessory versus the accessory nature of the auxiliary-cell branch in his revised concepts of the Gigartinales and Cryptonemiales. This distinction was maintained in Kylin's (1956) posthumously published systemization of red-algal suprageneric taxonomy, part of a paradigm that would be almost universally regarded as the classification standard for the next 25–30 years.

Despite general acceptance of the Cryptonemiales, Gigartinales, and Rhodymeniales as defined by Kylin (1932) for algae in which generative auxiliary cells are present before or in the absence of fertilization, questions were raised as to the meaning and applicability of his most critical criterion for distinguishing the Cryptonemiales from the Gigartinales: determination of the sometimes ambiguously displayed position of the auxiliary cell as either in a "normal" vegetative filament (the Gigartinales) or an "accessory" structure (the Cryptonemiales). The order-level significance of this feature was questioned by phycologists such as Fritsch (1945), Drew (1951), Searles (1968; 1983), and Dixon (1973), whereas Kraft (1975) was openly puzzled about what was actually meant by such a distinction. Kraft and Robins (1985) linguistically analyzed the various definitions and contexts in which the word "accessory" was used by phycologists and by botanists generally, arguing that these broke down when applied to some paradigm gigartinalean and cryptonemialean taxa in which "accessory" filaments appeared to be "normal" vegetative components of the thalli (cf. Saunders and Kraft 1996). In a move that had been foreshadowed by Searles (1968, 1983), Kraft and Robins (1985) formally advocated submerging the Cryptonemiales into the Gigartinales and suggested that the Rhodymeniales might be vulnerable to a similar fate. Nevertheless, possibly owing to the fact that Kylin's distinction between the Gigartinales and Cryptonemiales could be made with little ambiguity for a large number of European and North American species, it continued to be maintained by some authors (Moe 1985; Silva and Johansen 1986). Other phycologists, however, recognized the merger as a necessary, but interim, step towards the total phylogenetic reappraisal of the families included in these three orders, which most considered to be para- and (or) poly-phyletic (Lindstrom and Scagel 1987; Garbary and Gabrielson 1990; Hommersand 1990; Womersley 1994).

The Gigartinales sensu lato (s.l.) had thus become a rather unwieldy order of some 40 families, but new studies completed even prior to the proposed ordinal merger quickly reduced this number as discordant elements were systematically removed. Pueschel and Cole (1982) had established the distinctness of the Hildenbrandiaceae, which they elevated to ordinal status, and the Corallinaceae was soon removed to its own order by Silva and Johansen (1986), as had already been generally anticipated (Kraft and Robins 1985). Heterogeneity was further reduced when Fredericq and Hommersand (1989) provided detailed anatomical observations as justification for removing the agarophyte family Gracilariaceae to the new order Gracilariales. A combination of life-history elucidation, careful anatomical observations, and new ultrastructural data supported removal of another agarophyte, the genus *Ahnfeltia*, from the Phyllophoraceae to a new family and order, Ahnfeltiaceae and Ahnfeltiales (Maggs and Pueschel 1989). Saunders and Kraft (1994) then combined previously underemphasized features of reproductive anatomy with molecular systematic analyses to remove the Plocamiaceae, as well as provisionally the Pseudoanemoniaceae, to the new order Plocamiales. In a subsequent study (Saunders and Kraft 1996), they assessed the phylogenetic affinities of eight additional families of the Gigartinales s.l., including four each from the former Cryptonemiales and the revised Gigartinales sensu stricto (s.s.), bringing the total number of families for which small-subunit ribosomal DNA (SSU) data were available to ca. 20. They concluded that six of the families were correctly included in the Gigartinales but that the Halymeniaceae and Sebdeniaceae, paradigm members of the Cryptonemiales and Gigartinales, respectively, sensu Kylin (1956), grouped together as an independent lineage for which they proposed the new order Halymeniales. In that study Saunders and Kraft (1996) also provided molecular support for the Rhodymeniales as distinct from both the Gigartinales and Halymeniales. Most recently, Saunders and Kraft (2002) have added the new family Tsengiaceae to the Halymeniales in the course of removing the Nemastomataceae and Schizymeniaceae to a resurrected and emended Nemastomatales.

Our present report incorporates 65 newly determined SSU sequences that provide data for all of the families generally recognized in the Gigartinales s.l. save for two, the rare and difficult-to-obtain Blinksiaceae and Haemeschariaceae. The results modify the familial composition of the Halymeniales and Plocamiales and result in the removal of discordant elements from the Gigartinales s.l. such that a monophyletic construct is finally emerging for this order.

Materials and methods

The sources for samples and sequences used in this study are provided in Appendix Table A1. Samples for which SSU data were generated were processed, and DNA was extracted as previously published (Saunders 1993). The SSU was amplified as two to four overlapping fragments with previously published primer combinations (Saunders and Kraft 1994, 1996). The Wizard™ PCR Preps DNA purification system (Promega, Madison, Wis.) was used to purify PCR products for subsequent DNA sequencing. The dRhodamine Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems (ABI), Foster City, Calif.) was used for the sequencing of PCR products, and reactions were electrophoresed in an ABI Prism 310 genetic analyzer. Complete (excluding the 5′ and 3′ PCR primer regions) sequences were determined in both directions for all taxa.

Four alignments were constructed with the assistance of the program SeqPup (Gilbert 1995). The master alignment contained 145 taxa and 2991 sites, including most of the SSU sequences available for members of the Gigartinales s.l. (extra species from some genera were removed), as well as representation from all of the orders of florideophyte lineage 4 (Saunders and Bailey 1997). A preliminary phylogenetic analysis (distance with bootstrap as detailed below) of this alignment was used to design the remaining three alignments. (1) Gigartinales s.l.: This alignment contained representation from all of the currently recognized orders of lineage 4 (including the Gigartinales s.s.), as well as all of the rogue lines of Gigartinales resolved during analyses of the master alignment. The resulting alignment contained 53 taxa and 1821 characters, with *Ahnfeltia* (lineage 3; Saunders and Bailey 1997, 1999) as the designated outgroup. (2) Halymeniales: This alignment contained 19 taxa resolved as members of the Halymeniales during analyses of the master alignment, as well as 17 sequences from species of related orders, for a total of 36 taxa and 1795 characters. Members of the Plocamiales were used to root the trees generated from this alignment. (3) Gigartinales s.s.: This alignment included 84 species representing the ca. 29 families recognized as belonging to the Gigartinales s.s. during analyses of the master alignment. The alignment had a total of 87 sequences with 1822 characters, the Bonnemaisoniales being included to root the resulting phylogenetic trees.

Prior to phylogenetic inference the 5′ and 3′ primer regions, as well as ambiguously aligned areas, were removed from the alignments (alignment 1 — 53 taxa and 1722 nucleotide sites; alignment 2 — 37 taxa and 1721 nucleotide sites; alignment 3 — 87 taxa and 1758 nucleotide sites). Analyses (except Bayesian inference, below) were completed in PAUP 4.0b4a for the Macintosh (Swofford 2001). Maximum likelihood was implemented under the heuristic search option (10 random additions) with tree bisection–reconnection branch swapping. The program Modeltest v. 3.06 was used to determine the parameters for the maximum likelihood analyses (Posada and Crandall 1998). In all cases the general time reversible model with gamma distribution for unequal rates of evolution at sites was selected, although the actual values for change from one nucleotide type to another, as well as the proportion of invariant sites and the gamma shape, differed for each alignment. Distance analyses used the maximum likelihood parameters calculated previously, and the trees were constructed with neighbor joining. Parsimony analyses were completed under a heuristic search with 50 random additions, gaps treated as missing data, and the tree bisection–reconnection branch-swapping option in effect. Parsimony was completed with an unweighted approach for all three alignments, as well as with transversions weighted 2:1 over transitions for alignments 1 and 2. Distance (2000 replicates) and parsimony (1000 replicates for unweighted and 500 replicates for weighted, with random additions set to 10) analyses were subjected to bootstrap resampling to estimate robustness (Felsenstein 1985). With the model parameters identified previously, MrBayes (v. 2.01; Huelsenbeck and Ronquist 2001) was used to complete a Bayesian inference of phylogeny. Four Markov chains were used, the temperature was set to 0.2, and 10^6 generations were run with sampling every 100 generations. Log-likelihood values stabilized around 25 to 30 thousand generations and the final 6000 trees (4000 burnin) were used to estimate the posterior probabilities.

Results

Phylogenetic analyses of alignment 1 were completed to resolve relationships among the ordinal assemblages of lineage 4, as well as among the various lines of the Gigartinales s.l. The maximum likelihood result (Fig. 1) is presented (–ln = 10 234.07 783). Neighbor joining, unweighted parsimony (eight trees, length = 1549, consistency index = 0.419, retention index = 0.644) and weighted parsimony (15 trees, length = 2096, consistency index = 0.43, retention index = 0.64) all generated results (not shown) similar to the maximum likelihood topology, and the bootstrap results for these three analyses are appended to the likelihood tree (Fig. 1).

Weak to moderate support was acquired for a monophyletic Ceramiales (including *Inkyuleea*), whereas the Bonnemaisoniales, Gelidiales, Gracilariales, Nemastomatales, Plocamiales, and Rhodymeniales were all relatively strongly supported. The component families of the Halymeniales were all associated solidly as sister taxa to the Rhodymeniales, but failed to resolve as a monophyletic group in the current lineage 4 SSU-based analyses. The included Gigartinales s.l. essentially resolved as five lineages: Gigartinales s.s.; Peyssonneliaceae; Calosiphoniaceae (*Schmitzia*); Acrosymphytaceae (including *Schimmelmannia*); and, a weakly supported assemblage for Pseudoanemoniaceae (*Hummbrella*) and Sarcodiaceae, which allied without support to the Plocamiales.

The analyses variably allied the Peyssonneliaceae relative to the Bonnemaisoniales and Gigartinales s.s. Under maximum likelihood the Bonnemaisoniales and Peyssonneliaceae were the first and second divergences, respectively, among the lineage 4 taxa (Fig. 1), whereas distance allied the latter to the Gigartinales s.s. Both parsimony analyses positioned the Peyssonneliaceae as the earliest divergence in lineage 4 and placed the Bonnemaisoniales well within this lineage. Published SSU (Saunders and Bailey 1997, 1999), (large-subunit ribosomal DNA) LSU, and combined (Harper and Saunders 2001) phylogenies generally associate the Bonnemaisoniales with either the Gigartinales s.s. or the Gelidiales. The long branches leading to the included Peyssonneliaceae and the outgroup Ahnfeltiales may be causing the branches to attract, thus confounding efforts at phylogenetic inference. This becomes a particular problem when distant outgroups are used (Lyons-Weiler et al. 1998), an unavoidable situation in this case as the only suitable outgroup for lineage 4 is the distant and species-poor Ahnfeltiales (Saunders and Bailey 1999). To test this possibility, all analyses were completed on alignment 1 excluding the Ahnfeltiales as outgroup (essentially resulting in an unrooted tree). The resulting maximum likelihood solution (–ln = 9 632.38 494; Fig. 2) was similar in most respects to the previous result (Fig. 1), except that both the Bonnemaisoniales and Peyssonneliaceae were allied with the Gigartinales s.s. Bootstrap analyses under distance and weighted (three trees, length = 1872, consistency index = 0.422, retention index = 0.661) parsimony positioned the Peyssonneliaceae as sister to the Gigartinales s.s. with weak to moderate support (Fig. 2). However, if the root to this tree is placed along the branch leading to the Bonnemaisoniales or Peyssonneliaceae, then the topology is very similar to the previous outgroup rooted tree.

Bayesian inference (not shown) including and excluding the outgroup Ahnfeltiales produced topologies virtually identical with the respective maximum likelihood results, but provided no posterior probability values (<50%) for resolution among the major assemblages Bonnemaisoniales, Ceramiales–Acrosymphytaceae–Calosiphoniaceae, Gelidiales, Gigartinales s.s., Peyssonneliaceae, and a line including the remaining orders. Thus, all analyses consistently indicate that the SSU fails to resolve adequately relationships among the major assemblages of lineage 4.

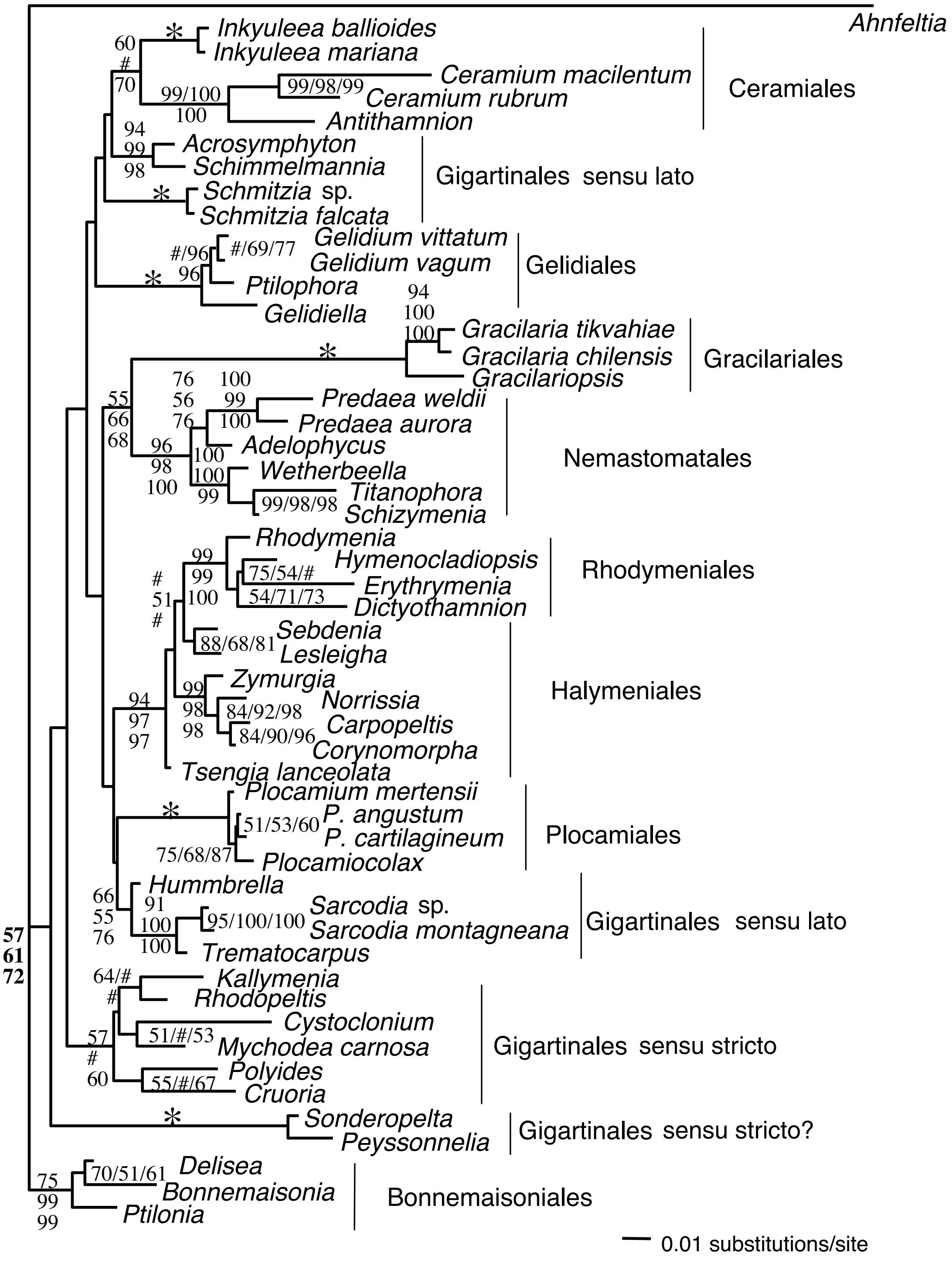
Alignment 2 was generated to explore relationships among the component lineages of the Halymeniales (Halymeniaceae, Sebdeniaceae, Tsengiaceae) relative to one another and to the monophyletic Rhodymeniales. In all analyses the Halymeniales and Rhodymeniales grouped solidly together, but the lineages of the former failed to form a monophyletic sister to the Rhodymeniales, their relationships varying with the method of analysis (maximum likelihood tree provided, –ln = 6 195.29 785; Fig. 3). Reasonable support was gained for a monophyletic Sebdeniaceae, including the yet to be published *Lesleigha* and an unidentified alga from Lord Howe Island. The Halymeniaceae was solidly resolved as monophyletic, with *Zymurgia* weakly positioned as the earliest divergence (Fig. 3). *Grateloupia intestinalis* solidly joined the two included species of *Polyopes* in all analyses (Fig. 3) and failed to join the generitype, *Grateloupia filicina*. *Corynomorpha*, the sole member of the Corynomorphaceae, was unequivocally resolved as a recent divergence among the genera of the Halymeniaceae.

Alignment 3 was designed to emphasize relationships among the Gigartinales s.s. Unfortunately the SSU failed to resolve relationships among many of the included taxa, the gene being too conservative at this level. Only distance (Fig. 4) and unweighted parsimony were completed for this large contingent. Despite the overall lack of resolution this alignment serves to identify those 29 families that should be included in the Gigartinales s.s. In addition, a few important taxonomic conclusions can be framed. A cluster of families including the Dumontiaceae, Gainiaceae, Kallymeniaceae, and Rhizophyllidaceae was resolved in which *Dasyphloea* and *Dudresnaya* (Dumontiaceae) were closely associated with *Gainia* (Gainiaceae) and the Kallymeniaceae (Fig. 4), respectively, echoing published results of Tai et al. (2001). *Hypnea* associated solidly with *Calliblepharis* of the Cystocloniaceae, into which family the Hypneaceae should be subsumed. The Solieriaceae s.s. was solidly supported and included *Wurdemannia* (the sole member of the Wurdemanniaceae), but failed to join the genera of the Areschougiaceae s.s., which have been placed in the former family in some recent taxonomic treatments. Finally, *Austroclonium* allies with the Areschougiaceae (albeit with only weak support) rather than the Cystocloniaceae, where it had recently been placed (Fig. 4).

Discussion

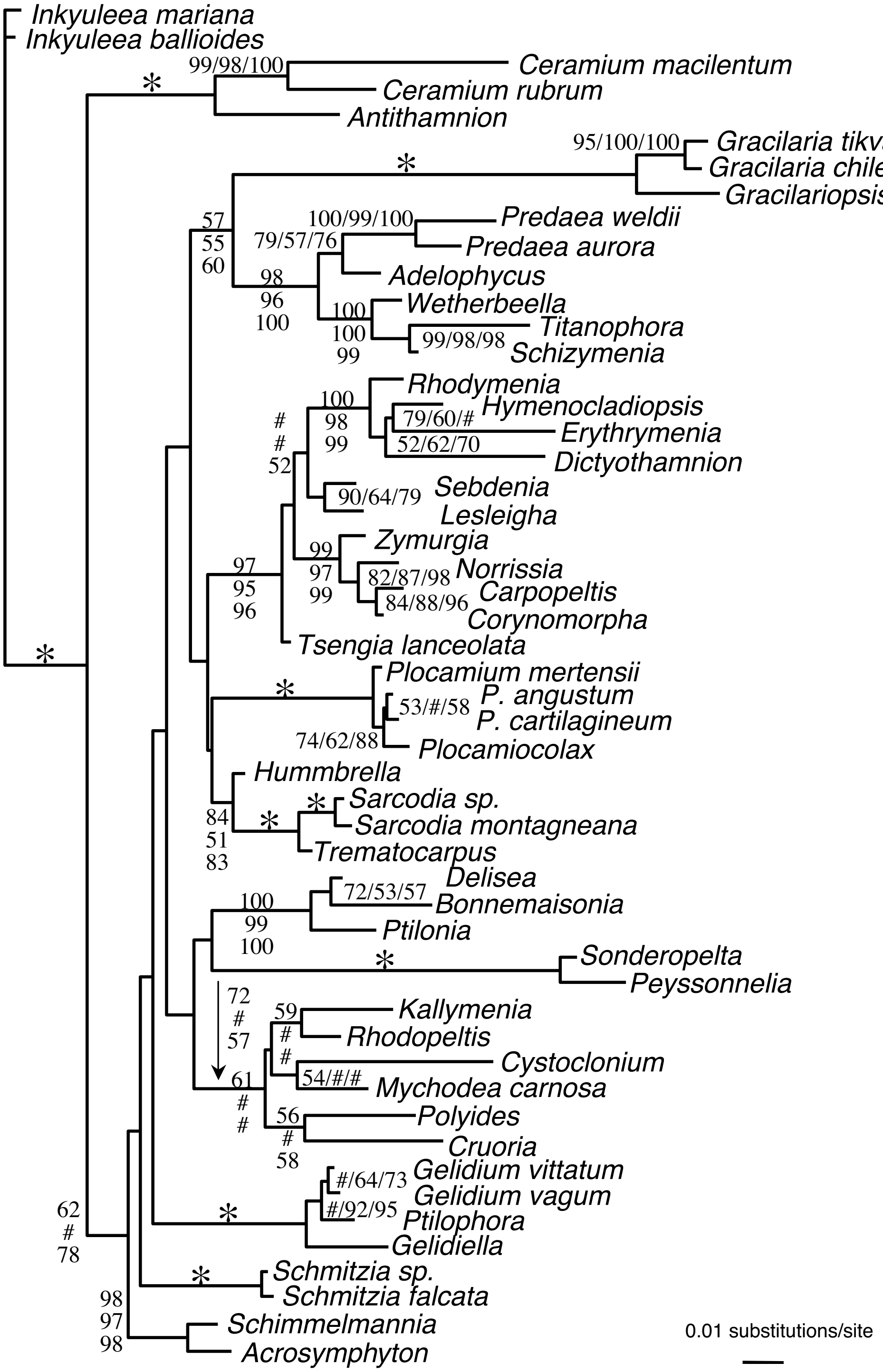
The merger of the Gigartinales and Cryptonemiales by Kraft and Robins (1985) generated a broadly circumscribed order of ca. 40 families. Their proposal was accepted largely as an interim stage in the construction of a more natural system of classification for the included families (Garbary and Gabrielson 1990). The first steps toward a monophyletic

Fig. 1. Maximum likelihood tree derived from alignment 1. Values at internal nodes represent percent bootstrap support under distance, and unweighted and weighted parsimony, respectively. *, 100% support in all analyses; #, <50% support for a specific analysis. Values in bold indicate that Peyssonneliaceae joins the Gigartinales s.s. under distance (57% support) and falls to the base of lineage 4 under both unweighted (61%) and weighted (72%) parsimony.



Gigartinales witnessed the discordant elements included in the Corallinaceae (Silva and Johansen 1986) and Gracilariaceae (Fredericq and Hommersand 1989) removed to their own respective orders on the basis of anatomical interpretations. Following these reports a series of molecular studies have had a dramatic impact on our understanding of familial composition and relationships among gigartinalean algae. A number of papers using the *rbc*L gene have contributed to this revolution, and this is the third (cf. Saunders and Kraft 1994, 1996) in a series of SSU-based investigations directed specifically at the issue of resolving a monophyletic Gigartinales. The present effort includes representatives of

Fig. 2. An unrooted tree constructed under maximum likelihood for alignment 1 with the outgroup Ahnfeltiales removed. Symbols and values as per Fig. 1 caption. Arrow indicates that Peyssonneliaceae joined the Gigartinales s.s. in distance and both parsimony analyses.



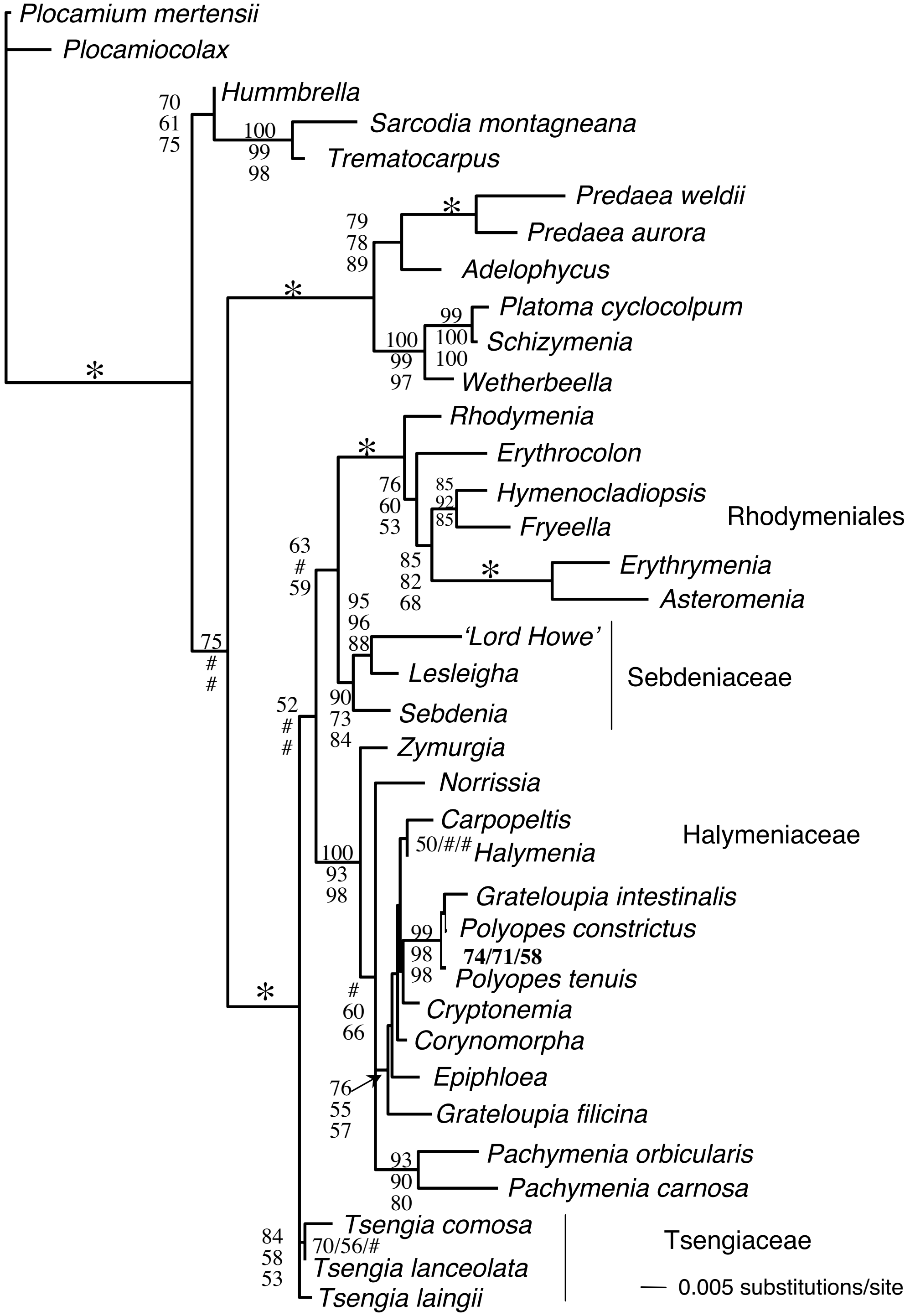
all but two of the ca. 40 families included in the order by Kraft and Robins (1985), as well as *Corynocystis*, a putatively gigartinalean taxon for which family placement has until now been obscure. The results of our analyses of additional and already-published sequences include both new taxonomic proposals (such as the establishment of the Corynocystaceae) and support for previous molecular phylogenetic inferences (such as the positioning of the Tsengiaceae and Pseudoanemoniaceae). Figure 5 provides a summary of the orders and families currently recognized in lineage 4, Florideophyceae.

The following sections highlight the orders, families, or family complexes for particular attention and discussion:

The Plocamiales: the Plocamiaceae, plus (provisionally) the Pseudoanemoniaceae and Sarcodiaceae

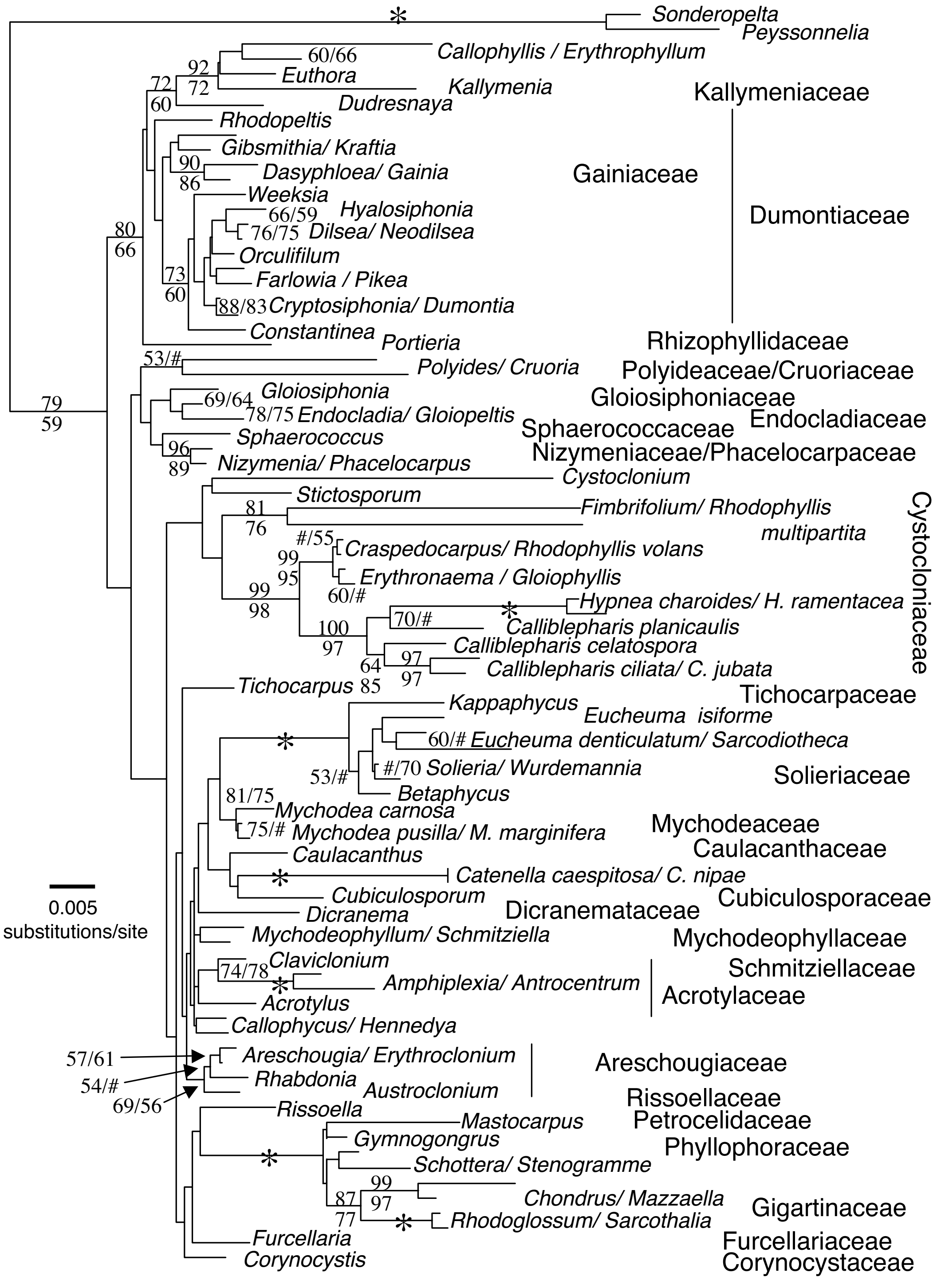
In their first SSU-based study, Saunders and Kraft (1994) combined anatomical and molecular data to remove the Plo-

Fig. 3. Maximum likelihood tree derived from alignment 2, emphasizing Halymeniales. Symbols and values as per Fig. 1 caption. Values in bold indicate that the two *Polyopes* spp. grouped together with bootstrap support in distance and both parsimony analyses.



camiaceae from the Gigartinales to the new order Plocamiales, at the time saying of the monogeneric Pseudoanemoniaceae (containing only the genus *Hummbrella*) that "although seeming an unlikely candidate at first glance…[it] shares many of the unique features that distinguish the Plocamiaceae from the Gigartinales". They thus provisionally included it in the new order. In addition to some similarities to *Plocamium* (Fig. 6) in vegetative structure, *Hummbrella* (Fig. 7) has comparable procarps consisting of three-celled carpogonial branches subtended by an intercalary supporting cell that functions as the auxiliary cell; a single outwardly oriented gonimoblast initial that develops into a lobed carposporophyte, most cells of which become carposporangia; and a similar pattern of nutritive-cell development. Unfortunately, tetrasporangial features, a key to distinguishing the Plocamiales from the Gigartinales, are not known for *Hummbrella*, which Hawkes

Fig. 4. Neighbor-joining tree for alignment 3, emphasizing the Gigartinales s.s. Values at internal branches indicate percentage of bootstrap support under distance and unweighted parsimony, respectively. Symbols as per Fig. 1 caption. The outgroup Bonnemaisoniales have been pruned from the base of the tree to facilitate presentation.



and Johnson (1981) have determined from cultures to probably undergo somatic meiosis.

Our molecular results do not ally *Hummbrella* to the Gigartinales but rather tend to group it, albeit weakly, with the Plocamiaceae, thus providing the first molecular indications of the ordinal affiliations of this bizarre, hydra-shaped organism so different in appearance from any member of the Plocamiaceae. Stranger and more counter-intuitive yet, however, is the somewhat stronger link inferred by the data between the Pseudoanemoniaceae and the widespread family Sarcodiaceae. In this case not only do sarcodioid algae (Fig. 8) differ in being multiaxial rather than uniaxial, but in form and texture they are far removed from the often membranous, sympodially organized Plocamiaceae and the soft, vermiculiform Pseudoanemoniaceae.

Kylin (1932) defined the Sarcodiaceae for a group of five

Fig. 5. A summary of lineage-4 classification following this study. Nine orders are recognized with one lineage incertae sedis. Twenty-nine families are currently included in the Gigartinales s.s. *, families only provisionally assigned to that order; taxa in parentheses are subsumed and (or) transferred into the corresponding family.

Florideophyte Lineage 4

Bonnemaisoniales
Bonnemaisoniaceae
Naccariaceae

Ceramiales
Ceramiaceae
Dasyaceae
Delesseriaceae
Rhodomelaceae

Gelidiales
Gelidiaceae

Gracilariales
Gracilariaceae
Pterocladiophyllaceae

Halymeniales
Halymeniaceae
(Corynomorphaceae)
Sebdeniaceae
Tsengiaceae

Nemastomatales
Nemastomataceae
Schizymeniaceae

Plocamiales
Plocamiaceae
Pseudoanemoniaceae*
Sarcodiaceae*

Rhodymeniales
Champiaceae
Faucheaceae
Lomentariaceae
Rhodymeniaceae

Gigartinales sensu stricto

Acrotylaceae
Areschougiaceae
Caulacanthaceae
Corynocystaceae fam. nov.
Cruoriaceae (Blinksiaceae?)
Cubiculosporaceae
Cystocloniaceae (Hypneaceae)
Dicranemataceae
Dumontiaceae
Endocladiaceae
Furcellariaceae
Gainiaceae
Gigartinaceae
Gloiosiphoniaceae
Haemeschariaceae
Kallymeniaceae
Mychodeaceae
Mychodeophyllaceae
Nizymeniaceae
Peyssonneliaceae*
Phacelocarpaceae
Phyllophoraceae (Petrocelidaceae)
Polyideaceae
Rhizophyllidaceae
Rissoellaceae
Schmitziellaceae
Solieriaceae (Wurdemanniaceae)
Sphaerococcaceae
Tichocarpaceae

Incertae sedis
Acrosymphytaceae
(*Schimmelmannia*)
Calosiphoniaceae

genera with fleshy to cartilaginous thalli and large, protuberant, thick-walled cystocarps that contain hemispherical carposporophytes of complex anatomy basally anchored to layers of specialized gametophyte tissue, the inner gonimoblasts sterile and arising from a fusion cell, the outer layers producing chains of carposporangia released through prominent ostioles. Free-living phases are isomorphic, the tetrasporangia being zonate. Details of procarp structure and gonimoblast initiation in *Sarcodia* were misinterpreted by Rasmussen (1964) but correctly elucidated by Searles (1968), who showed that three-celled carpogonial branches were borne on an intercalary cortical supporting cell that functioned on diploidization as the auxiliary cell. Norris (1987) later confused this accurate interpretation by regarding the strongly reflexed trichogyne of the carpogonium as a connecting filament in a species of *Sarcodia*, which led him to characterize the family as nonprocarpic. As a result, he concluded that the almost entirely Australian-endemic Dicranemataceae was not distinct at the family level and should be sunk into the Sarcodiaceae. The unrelatedness of the two families was persuasively demonstrated by Liao et al. (1993), who showed that Searles' interpretation of the sarcodiaceous procarp was correct and demonstrated very different nonfibrillar wall polysaccharides in members of the two families. Our SSU data (Fig. 4) confirm the conclusions of Liao et al. (1993).

At this time we only tentatively ally the Sarcodiaceae to the Plocamiales and regard this proposal as an interim step, the major thrust of which is to exclude the family from the Gigartinales s.s. Only the general procarp structure, outward orientation of the gonimoblast, and zonate tetrasporangia appear at all anatomically indicative of an association with the Plocamiales, as features such as the multiaxial apical structure, confinement of carposporangia to surface chains on a central mass of sterile gonimoblasts, incorporation of large fusion cells, and wide basal placentation are unlike anything seen in either *Plocamium* or *Hummbrella*. These three morphologically disparate groups, however, may prove to be additionally linked by the complex molecular structure of their outer-wall polysaccharides. In contrast with the conclusion reached in an earlier study (Whyte et al. 1984) that the backbone structure of the extracellular polysaccharides of British Columbian *Plocamium cartilagineum* comprised predominantly 3-linked galactopyranosyl (Gal*p*) residues, Falshaw et al. (1999) recently showed by chemical analysis and ^{13}C nuclear magnetic resonance (NMR) spectroscopy of the native and desulfated galactans from New Zealand *Plocamium costatum* (C. Agardh) Hooker et Harvey that the galactans were composed of alternating 3- and 4-linked galactosyl residues, with the 4-linked residues occurring in approximately equal proportions of D- and L-isomers. These observations demonstrated that the *Plocamium costatum* polysaccharides are a hybrid or mixture of carrageenans and agarocolloids. ^{13}C NMR spectroscopy of native and chemically modified polysaccharides of New Zealand specimens of two species of *Trematocarpus*, the genus that allies most strongly with *Sarcodia* in our analyses (Figs. 1 and 2), indicated they were complex galactans mainly of the agarocolloid group but with significant (ca. 20 mol%) carrageenan structure (Miller 2002). In common with the sulfated galactans of New Zealand *Plocamium cartilagineum*, these polysaccharides had very little 3,6-anhydrogalactose and a heterogeneous pattern of sulfation. The sulfate esters were proposed to be predominantly at O-2 of 3-linked residues and at O-3 and, to a lesser extent, O-2 of 4-linked residues of the *Trematocarpus* galactans (Miller 2002). Unlike the *Plocamium cartilagineum* galactans, however, the *Trematocarpus* galactans were enriched in pyruvate. ^{13}C NMR analysis of alkali-modified and desulfated polysaccharides from two New Zealand *Sarcodia* species indicated they were mainly galactans of the agar type, with only very low levels of carrageenan (Miller 2003). Although there were minor differences between them, the galactans from these two *Sarcodia* species contained very little AnGal but were relatively enriched in pyruvate and had heterogeneous sulfation patterns comparable with those of the *Trematocarpus* galactans. Compositional analyses and infrared (IR) spectroscopy (Liao et al. 1993) suggested the polysaccharides extracted with hot water from two Australian *Sarcodia* species were complex sulfated xylogalactans. However, further analyses of the *Sarcodia* polysaccharides are required to clarify the source of the xylose and to determine the relative content of carrageenan and agar structure.

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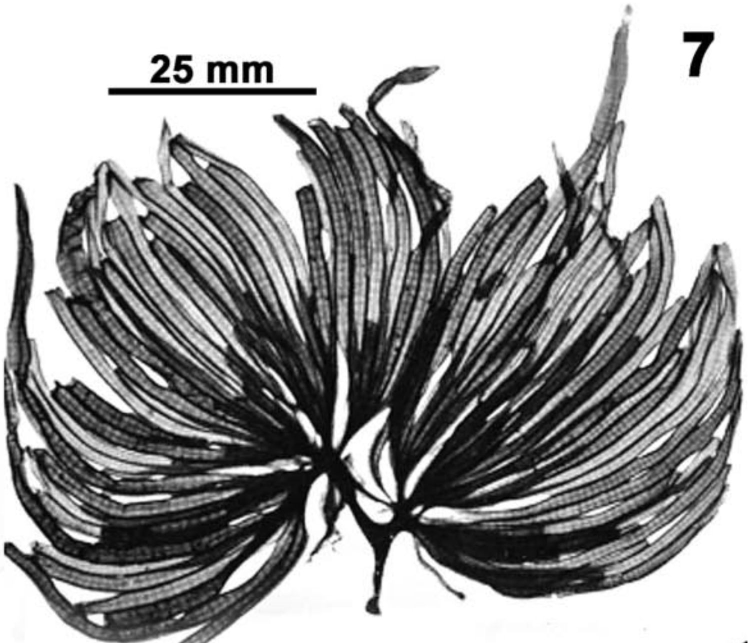

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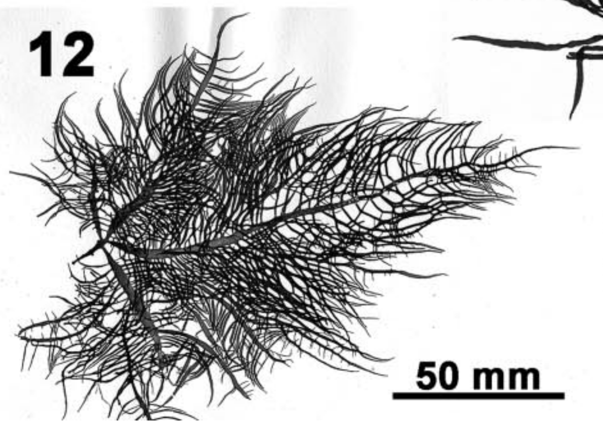

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Figs. 6–13. Plocamiales (Plocamiaceae (6), Pseudoanemoniaceae (7), Sarcodiaceae(8)); Halymeniales (Halymeniaceae (9–13)). Fig. 6. *Plocamium coccineum* var. *pacificum* (Kylin) Dawson. Santa Barbara, California; "ca. 1885". Coll.: "Mrs. Sherman". BISH 537980. Fig. 7. *Hummbrella hydra* Earle. Leigh, New Zealand. Coll.: M.. Hawkes. WELT A11444. Fig. 8. *Sarcodia* sp. Denpassar, Bali, Indonesia; 6.vii.1976. Coll.: M.. Doty. BISH 544386. Fig. 9. *Norrissia setchellii* (Kylin) Balakrishnan. Cape Beale, Vancouver Island, British Columbia, on rocks at low tide mark; 4.vii.2000. Coll.: V. Lehmkuhl. UNB GWS001231. Fig. 10. *Zymurgia chondriopsidea* (J. Agardh) J.A. Lewis et Kraft. Warrnambool, Victoria, drift; 6.xi.1989. Coll.: G. & R. Kraft. MELU, A38175. Fig. 11. *Grateloupia intestinalis* (Hooker fil. et Harvey) Setchell ex Parkinson in Chapman et Parkinson. Kaikoura, New Zealand, lower eulittoral rocks; 16.xi.1972. Coll.: Kraft & Parsons. MELU, GEN-4760. Fig. 12. *Grateloupia filicina* (Lamouroux) C. Agardh. Williamstown, Victoria, on shallow subtidal rocks; 24.ii.1975. Coll.: J.A. Lewis. MELU, KA-00225. Fig. 13. *Polyopes constrictus* (Turner) J. Agardh. Wilsons Promontory, Victoria, in a lower eulittoral rockpool; 11.i.1962. Coll.: S. Ducker. MELU, WP226.

The Halymeniales: the Halymeniaceae (including the Corynomorphaceae), Sebdeniaceae, and Tsengiaceae

In the second of their SSU-based studies, Saunders and Kraft (1996) attributed only the Halymeniaceae and Sebdeniaceae to their proposed new order Halymeniales, a group established for multiaxial species with filamentous medullas and triphasic life histories with an alternation of isomorphic gametophytic and tetrasporophytic generations. Carpogonial branches are two- to four-celled and outwardly directed, with carpogonia producing multiple, septate, branched connecting filaments that diploidize intercalary auxiliary cells in often widely separated cortical branch systems that may be either part of the "normal" cortical structure or lateral filaments of highly modified morphology. Gonimoblasts arise thallus-outwardly from single initials and produce lobed to globular cystocarps composed mainly of carposporangia buried within rudimentary pericarps in the outer layers of the frond. Tetrasporangia are cruciate or decussate. A considerable amount of work has been done on the polysaccharides from representatives of the Halymeniaceae, with galactans from species of *Aeodes*, *Grateloupia* (including *Phyllymenia*), and *Pachymenia* studied in substantial detail (cf. Miller et al. 1995, 1997 and references therein). The prevailing picture of halymeniacean polysaccharides is one of highly sulfated galactans predominantly with an alternating backbone of 3-linked and 4-linked D-galactosyl residues (as in carrageenans) but containing relatively low levels of 3,6-anhydrogalactose and with some (up to one-third of the total polysaccharide) of the 4-linked residues replaced with the L-enantiomers (as in agars). Halymeniacean galactans bear sulfate ester substitution predominantly on the 3-linked galactosyl residues, usually at O-2 but also, to lesser extents, at O-4 and O-6. The polysaccharides of some species have also been reported to contain small amounts of pyruvate acetal, terminal xylose, and (or) terminal mono-*O*-methylgalactose. Compositional analyses, optical rotation, and IR spectroscopy also indicated that the polysaccharides from an Indian specimen of *Sebdenia flabellata* were nongelling sulfated galactans consisting predominantly of D-galactose, low levels of 3,6-anhydrogalactose, and a heterogeneous sulfate substitution pattern (Doshi et al. 1988, as *S. polydactyla*), but further analyses are required to clarify the structure.

Although subsequent work by ourselves and others confirms the wide phylogenetic distance between the Halymeniales and Gigartinales, SSU phylogenies remain equivocal on monophyly of the Halymeniales relative to the order Rhodymeniales, a result consistent with the trees presented here (Figs. 1 and 3) and those given by Saunders and Kraft (2002). The few reports of rhodymenialean polysaccharides indicate that they, like those of the Halymeniaceae, tend to be highly sulfated with low levels of 3,6-anhydrogalactose and have both 4-linked D- and L-residues but, unlike the Halymeniaceae, the agar-type backbone predominates (Usov and Klochkova 1992; Takano et al. 1994; Miller et al. 1996). Small amounts of pyruvate acetal, terminal xylose, and *O*-methylgalactose have been reported (Usov and Klochkova 1992; Miller et al. 1996), as well as unusual substitution patterns, such as terminal D-glucose and D-glucuronic acid residues in the polysaccharides of *Lomentaria catenata* Harvey (Takano et al. 1994). However, many more rhodymenialean polysaccharides must be investigated to assess both the distribution of polysaccharide structures within the order and whether these polysaccharides represent a continuum of structures with those of the Halymeniales. We nevertheless continue to recognize the Halymeniales at the ordinal level until new data unequivocally resolve the issue of either maintaining it as separate or combining it with the Rhodymeniales.

Saunders and Kraft (2002) have recently added the genus *Tsengia* and the new family Tsengiaceae to the Halymeniales, removing *Tsengia* from the Nemastomataceae where Masuda and Guiry (1995) had provisionally left it in the course of analyzing that family and establishing the segregate family Schizymeniaceae. As treated by Masuda and Guiry, the three genera of the Schizymeniaceae were highly homogeneous in regard to the characters that defined the family (gland cells and nutritive auxiliary cells present, heteromorphic life histories with diminutive, zonately tetrasporangial tetrasporophytes), whereas the five genera of the Nemastomataceae were inconsistent in gland cell, life history, and tetrasporangial features. The major discordant element within the Nemastomataceae had been *Tsengia* itself, as its five species lack the gland cells that the other genera all have (at least in part), display isomorphic rather than heteromorphic life-history stages, and produce cruciate rather than zonate tetrasporangia. In regard to these features *Tsengia* conforms to those of the Halymeniales, where the molecular data repeatedly indicate the genus should be placed. IR spectroscopy suggests the polysaccharides of *Tsengia comosa* are complex (Chopin et al. 1999), but detailed analyses are required to elucidate their structure. The removal of *Tsengia* leaves the Nemastomataceae (see below) a much more homogeneous group.

As treated by Kylin (1956) and is still the case today, the family Sebdeniaceae is monogeneric. Kylin distinguished *Sebdenia* from the Halymeniaceae (as Grateloupiaceae) by its nonampullar carpogonial and auxiliary-cell branch systems and its "normal" versus "accessory" auxiliary-cell branches. This made the genus a paradigm representative of the Gigartinales sensu Kylin, which is nonetheless only distantly related to that order (Saunders and Kraft 1996) and more correctly included in the Halymeniales. Recent collections from island localities in the Northern and Southern hemispheres have been sequenced and found to constitute new genera closely allied to *Sebdenia*. Among these are "*Lesleigha*" gen. ined. Kraft, from the Hawaiian Islands, and an unnamed species from Lord Howe Island. Work is continuing to elucidate the anatomical features of this group of species and decide whether one or two genera will need to be described for these recent collections. The two entities are, however, as distinct from one another in SSU sequences as, for example, *Platoma* is from *Schizymenia*, or *Halymenia* is from *Carpopeltis*, *Cryptonemia*, or *Corynomorpha*.

Within the large family Halymeniaceae itself, the SSU is generally too conservative to resolve many of the relationships among particular taxa, although some significant species–genus associations do emerge. *Zymurgia* (Fig. 10) was described as an anomalous new genus of the Halymeniaceae by Lewis and Kraft (1992), who considered it to either represent a link between a closely related Halymeniaceae and Dumontiaceae or be a member of the former family that displayed many examples of parallel evolution to the latter. Saunders and Kraft (1996) clearly established that the Halymeniaceae and Dumontiaceae are so remotely related as to be members of separate orders, and although the rarely collected *Zymurgia* was not included in the molecular trees at that time, it was later shown by Saunders and Kraft (2002) that Lewis and Kraft (1992) were correct to posit it as an early lineage of the Halymeniaceae on the basis of its nonampullar carpogonial branches, a feature it also shares with the North Pacific genera *Norrissia* (Fig. 9) and *Isabbottia* (Lewis and Kraft 1992). We have sequenced *Norrissia* and found that it also forms an early lineage of the Halymeniaceae. Wang et al. (2000), although using the *rbc*L gene and with a limited generic taxon sample, indicated that the typically halymeniaceous genus *Pachymenia* resolves at the base of the Halymeniaceae, a result consistent with the relatively early divergence of this genus in our SSU tree (Fig. 3), and in a subsequent study (Wang et al. 2001) added *Aeodes* to that basal grouping. Wang et al. 2001 also advocated the merger of *Prionitis* and *Grateloupia*, but we cannot comment on this suggestion, as no members of *Prionitis* were included in our analyses, and in any case the SSU is far too conservative to resolve successfully such an issue. We hope to include these and many additional genera in future analyses of the Halymeniales using a more informative gene system such as the LSU (Harper and Saunders 2001).

One striking inconsistency picked up by our SSU trees is the failure of the New Zealand – Tasmanian *Grateloupia intestinalis* (Fig. 11) to join the generitype, *Grateloupia filicina* (Fig. 12), allying instead with the genus *Polyopes* (Fig. 13). Kraft (1977*a*) had previously illustrated the anomalously bushy auxiliary-cell ampullae in *G. intestinalis* and showed that this species was far more akin to Chiang's (1970) *Aeodes* group of genera than to typical *Grateloupia*. He made no recommendations for generic change, however, because of the typically grateloupioid vegetative structure of the species. This decision brought with it a recommendation, incorrect as it has turned out, to downplay the taxonomic importance of Chiang's (1970) ampullar features in characterizing genera and positing intergeneric relationships in the family. The combination of morphological and SSU data now available strongly support the removal of *G. intestinalis* to a new genus related to *Polyopes*, as substantial anatomical differences between it and the type species of the latter, *Polyopes constrictus* (Fig. 13) (soft versus cartilaginous consistency; irregular versus strictly dichotomous branching; scattered versus sorally aggregated cystocarps and tetrasporangia), would seem to preclude transferring to that genus. That would be our opinion, ordinarily, but a genus of almost equal anatomical dissimilarity to *Polyopes*, *Sinkoraena* H.-B. Lee et al. (Lee et al. 1997), has just been transferred to it by Kawaguchi et al. (2002) on the basis of *rbc*L affinities, and those authors foreshadow that the same fate awaits *Grateloupia intestinalis*.

The monogeneric Corynomorphaceae was established by Balakrishnan (1962) for *Corynomorpha prismatica*, which was then included in the Halymeniaceae (as the Cryptonemiaceae). Balakrishnan argued that its polycarpogonial supporting cells and the procarpic association of auxiliary cells in the carpogonial ampullae distinguished it at the family level from the monocarpogonial, nonprocarpic Halymeniaceae. Based on similarities of the procarp components, Balakrishnan allied the Corynomorphaceae to the Endocladiaceae of the Gigartinales, but our molecular data unequivocally place *Corynomorpha* solidly within the Halymeniaceae. As separation of the Corynomorphaceae renders the Halymeniaceae paraphyletic, we advocate that the Corynomorphaceae no longer be recognized and that *Corynomorpha* be returned to the Halymeniaceae.

The Nemastomatales: the Nemastomataceae and Schizymeniaceae

As was recently established on the basis of SSU analyses, these two families continue to form a strongly supported monophyletic clade in our trees (Fig. 1), one coequivalent to other orders and thus designatable at this level. Consistent within the order are multiaxial, nonprocarpic thalli in which secondary pit connections are lacking (for the most part); carpogonial branches that are three celled and form (except in *Nemastoma* itself) as a substitute for a fascicle of cortical filaments on inner-cortical supporting cells; auxiliary cells that are intercalary in either cortical vegetative filaments or within unbranched rhizoids; gonimoblast initials that arise either laterally or are directed thallus outwardly on auxiliary cells contacted by lengthy, branched, and septate connecting filaments or from the connecting filaments themselves at or adjacent to their points of fusion with auxiliary cells; carposporophytes that consist almost wholly of carposporangia; and tetrasporophytes (where known) that are either diminutive clusters of filaments or tightly adhesive crusts bearing zonate tetrasporangia. The latest addition to the group is the new genus *Wetherbeella* Saunders et Kraft (Sanders and Kraft 2002) for two Australian-endemic species that consist of leafy thalli that differ significantly from *Platoma* in SSU nucleotide sequences, but which at present appear to only signal their identity morphologically by a lack of cortical gland cells.

The polysaccharides extracted from Sicilian *Schizymenia dubyi* were distinctive for their relatively high levels of uronic acid. Compositional analyses showed they essentially lacked 3,6-anhydrogalactose and contained galactose, glucuronic acid, and sulfate in the molar ratio 1:0.75:1.3 (Bourgougnon et al. 1993, 1996). Enzymic assay indicated that 45% of the galactose occurred as the L-enantiomer. Linkage analysis of the native and desulfated polysaccharides (Bourgougnon et al. 1996) provided evidence for a backbone consisting of 3-linked and 4-linked galactosyl residues and a heterogeneous pattern of substitution with sulfate ester and terminal Gal*p*. The glucuronic acid residues were presumed to be interspersed throughout the polysaccharide, since anion-exchange chromatography gave only a single peak from the sample, and the polysaccharides were therefore proposed to be sulfated glucuronogalactans (Bourgougnon et al. 1996). Component sugar and IR analyses of polysaccharides obtained from limited samples of New Zealand *Nemastoma laciniata* J. Agardh suggested they were galactans that had little or no 3,6-anhydrogalactose with heterogeneous patterns of sulfation like "λ-type carrageenans" (Adams et al. 1988). More detailed studies are required, however, to understand the structure of *Nemastoma* polysaccharides.

Incertae sedis: the Acrosymphytaceae (including *Schimmelmannia*) and Calosiphoniaceae

For both of these families our molecular analyses match published results for SSU (e.g., Tai et al. 2001), LSU, and combined (Harper and Saunders 2001) trees, which position them as unresolved early clades among lineage 4 taxa (weak affinities with Ceramiales in some analyses). Unfortunately, the taxon sampling is still low for both families and their phylogenetic exclusion from the Gigartinales in our molecular trees may be resulting from taxon-sampling artifacts. As such it is premature to remove these two families to a new order or orders, although the move may soon be necessary. For now we can only conclude that SSU and LSU data sets do not position these lines within the Gigartinales s.s.

Lindstrom (1987) established the monogeneric family Acrosymphytaceae when she removed the genus *Acrosymphyton* (Fig. 14) from the Dumontiaceae, arguing that female reproductive structures and postfertilization development were only superficially similar in the two taxa. Typical Dumontiaceae display unbranched carpogonial branches rather than the pinnately branched counterparts of *Acrosymphyton*. The dumontiacean auxiliary cell is intercalary and usually medial or proximal in the auxiliary-cell branch, as opposed to being terminal in *Acrosymphyton*. *Acrosymphyton* additionally has distinctly moniliform carpogonial and auxiliary-cell branch cells and usually a basally coiled trichogyne. In the Acrosymphytaceae one or more primary connecting filaments from the fertilized carpogonium fuse with nutritive auxiliary cells that terminate pinnae on the carpogonial branch, rather than the nutritive auxiliary cell or cells being intercalary within the carpogonial branch itself.

Lindstrom (1987) speculated that the new family might in fact be more closely allied to families of the Gigartinales (such as the Calosiphoniaceae) or Bonnemaisoniales (such as the Naccariaceae) than to the Dumontiaceae. Tai et al. (2001) provided molecular support for Lindstrom's Acrosymphytaceae and additionally concluded that it was probably not a member of the Gigartinales. The molecular data that we present indicate a strong association of *Acrosymphyton* with *Schimmelmannia*, although an alliance with *Schmitzia* of the Calosiphoniaceae is also weakly suggested by published LSU data (Harper and Saunders 2001).

Schimmelmannia (Fig. 15) is traditionally included in the Gloiosiphoniaceae of the Gigartinales. It shares with the generitype, *Gloiosiphonia*, a uniaxial construction with four or five periaxial cells, a close association of the carpogonial and auxiliary cell branches, a single primary gonimoblast initial, and a mature gonimoblast consisting almost entirely of carposporangia (Sjöstedt 1926; Kylin 1930; Abbott 1961; Acleto 1972; Abbott and Hollenberg 1976). In *Schimmelmannia*, a four- to six-celled carpogonial branch is produced from the supporting cell, which itself is borne on the abaxial surface of a periaxial cell. Following formation of the carpogonial branch an auxiliary-cell branch is formed from the same supporting cell, with the terminal cell differentiating into an auxiliary cell. Following fertilization the carpogonium undergoes one or two transverse divisions, with either the terminal or intercalary cell (respectively) fusing with the auxiliary cell. The tetrasporangial generation is unknown for *Schimmelmannia* (Abbott and Hollenberg 1976). In *Gloiosiphonia,* although carpogonial and auxiliary-cell branches are also borne on the same supporting cell, the two or three connecting filaments arising from the fertilized carpogonium do not necessarily fuse with the contiguous auxiliary cell but can diploidize auxiliary cells of other cortical branch systems. Furthermore, the auxiliary cell is intercalary in the branch rather than terminal (Sjöstedt 1926; Abbott and Hollenberg 1976), and *Gloiosiphonia* is also known to produce cruciate tetrasporangia on a heteromorphic diploid generation. In summary, there is no compelling anatomical evidence to support inclusion of *Schimmelmannia* in the Gloiosiphoniaceae, and molecular results reported above further cast doubt on such a taxonomic construct. The close association of *Schimmelmannia* and the Acrosymphytaceae determined in our molecular trees is reflected morphologically by the terminal position of the auxiliary cell in both these taxa. Reports of auxiliary-branch initiation subsequent to carpogonial-branch formation in *Schimmelmannia*, as well as putatively tetrahedral tetrasporangia in *Acrosymphyton*, indicate that the weak positioning of this lineage as sister to the Ceramiales in the molecular trees is worthy of further study.

The Calosiphoniaceae fails to join either the Gigartinales or Halymeniales in our analyses and has an unresolved position in the SSU tree. It does associate weakly with the Bonnemaisoniales in some analyses, a position consistent with the possibility of a putative alliance between this family and the Naccariaceae (not in our trees to date), as well as possibly also the Acrosymphytaceae as discussed by Lindstrom (1987). Perhaps all of these families, along with the genus *Schimmelmannia*, will ultimately form a new red algal order (where known, all have an alternation of heteromorphic generations and similar vegetative constructions). Additional analyses using a more informative gene system will hopefully soon clarify these relationships. Female reproductive anatomy and postfertilization development in *Schmitzia* (Fig. 16) and *Calosiphonia,* however, are not much like those of *Acrosymphyton* and *Schimmelmannia,* which more than likely indicates that two independent ordinal lines (cf.

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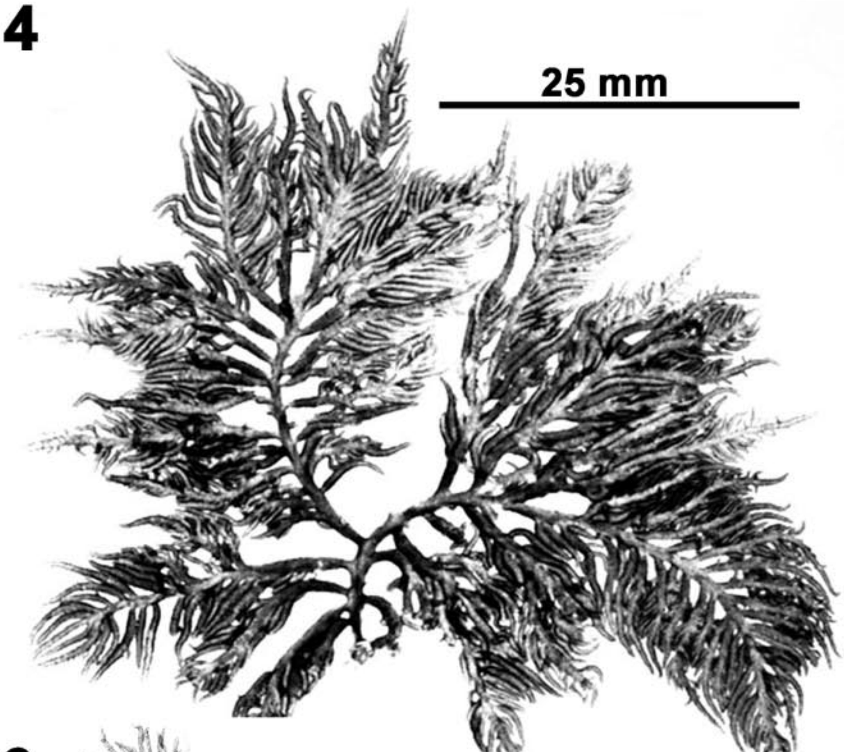

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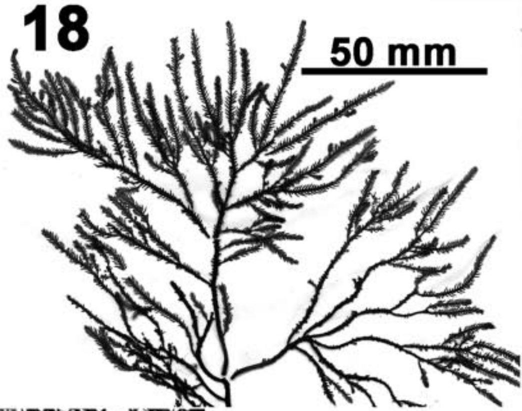

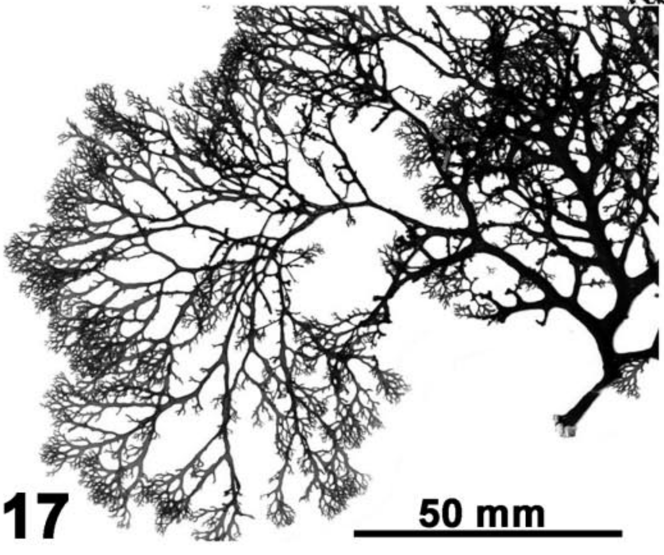

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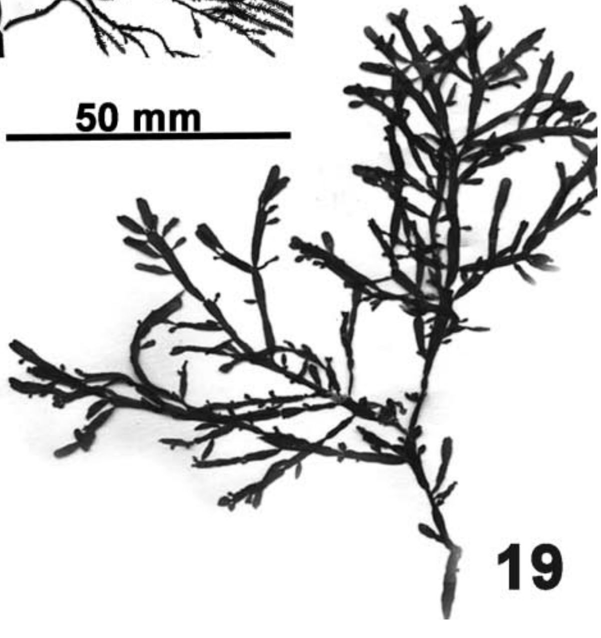

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Figs. 14–19. Acrosymphytaceae (14, 15); Calosiphoniaceae (16); Sphaerococcaceae (17); Phacelocarpaceae (18); Nizymeniaceae (19). Fig. 14. *Acrosymphyton taylorii* Abbott. One Tree Island, Great Barrier Reef, Australia, 26–28 m depths on a coral flat; 21.x.1979. Coll.: Kraft, F. Scott, A. Larkum. MELU, GBR-15406. Fig. 15. *Schimmelmannia plumosa* (Setchell) Abbott. Monterey Peninsula, California, on lower eulittoral vertical rock faces; 3.v.1942. Coll.: M. Doty. BISH 539906. Fig. 16. *Schmitzia 'falcata'* sp. ined. Lord Howe Island, Australia, 14–17 m, on cobbles of a sloping reef platform; 15.xii.1986. Coll.: Kraft & Millar. MELU, LHI-10754. Fig. 17. *Sphaerococcus coronopifolius* Stackhouse. Plymouth, England; 9.iii.1970. Coll.: G. Forster. BISH 540031. Fig. 18. *Phacelocarpus peperocarpos* (Poiret) Wynne, Ardré et Silva. Victoria, Australia, drift; 1880s. Coll.: F.V. Mueller. BISH 537597. Fig. 19. *Nizymenia australis* Sonder. Port Elliot, South Australia, drift; 10.viii.1957. Coll.: M. Doty. BISH 537327.

Lindstrom 1987), rather than one, will ultimately be supported by molecular data. In *Calosiphonia* and *Schmitzia* the carpogonium first fuses with the supporting cell, which then initially issues two or three, ultimately up to 10, branched connecting filaments that sequentially diploidize large numbers of intercalary auxiliary cells that function either generatively (as in *Calosiphonia*) or nutritively (as in *Schmitzia*; Hawkes 1982; Maggs and Guiry 1985). Postfertilization development provides no morphological evidence to support the weak alliance between the Calosiphoniaceae and Bonnemaisoniales resolved in our molecular results, and only the presence of possibly analogous, rather than homologous, gland cells and some very general vegetative features serves to ally these lineages.

Gigartinales sensu stricto

We regard the 29 families of Fig. 5, including the Corynocystaceae Kraft, fam. nov. (see below), as belonging to the Gigartinales s.s. A recent proposal to transfer some of the component families to the segregate orders Dumontiales and a resurrected Sphaerococcales by Fredericq et al. (1996*b*) does not seem to us warranted, as these groups, together with the remaining families of the Gigartinales, form a monophyletic lineage equivalent in SSU divergence to the other orders of lineage 4. Unfortunately, the SSU has proven to be too conservative to resolve adequately the precise phylogenetic interrelationships of most of the families that the analyses strongly indicate belong to the included gigartinalean lineages, although several taxonomic issues can be at least preliminarily addressed based on our current molecular results.

The Peyssonneliaceae

This family proved to be highly resistant to joining the Gigartinales s.s. in our SSU trees (Fig. 1), even to the degree of taking up a position at the base of lineage 4 in our initial unweighted and weighted parsimony analyses (data not shown). The branch leading to this family is long, and it is possible its unresolved positioning is an artifact of the analyses. The neighbor-joining results (alignment 1; Fig. 1), using the model determined with Modeltest, did affiliate this family with the Gigartinales. When the distant Ahnfeltiales were excluded, maximum likelihood (model determined by Modeltest) allied the Bonnemaisoniales and Gigartinales s.s., with the Peyssonneliaceae associating with the former, whereas distance (using Modeltest parameters) and weighted parsimony both specifically allied this family to the Gigartinales s.s. Lacking unequivocal molecular data on the affinities of the Peyssonneliaceae, we provisionally retain it in the Gigartinales, although leaving open the possibility that analyses of more discriminating gene systems, as well as consideration of the very complex nonfibrillar wall polysaccharides of its members, may ultimately result in elevation of the family to its own order.

Chemical and linkage analysis combined with IR spectroscopy of the polysaccharides extracted from Mediterranean and Atlantic *Asparagopsis armata* Harvey showed that they were composed predominantly of D-galactose and sulfate, with low levels of L-galactose (inferred from the data), 3,6-anhydrogalactose, xylose, glucose, and uronic acids (typically 3.1%–5.3% *m*/*m* of the dried polysaccharide preparations) and that they were complex with heterogeneous patterns of sulfate ester substitution and glycosyl branching (Haslin et al. 2000). The polysaccharides of the gametophytic *Asparagopsis* and tetrasporophytic *Faulkenbergia* phases had a similar composition, although they showed some variations in substitution patterns. Compared with those of the two dominant life-history phases, polysaccharides of cystocarpic tissues isolated from gametophytes had decreased levels of sulfate (less than half) and increased levels of uronic acids (15.9% *m*/*m*). Preliminary investigations of the polysaccharides from two Australian species of *Peyssonnelia* (N.J. Watt and A. Chiovitti, unpublished data) indicate that they are also predominantly highly sulfated galactans with low levels of 3,6-anhydrogalactose and xylose and have heterogeneous patterns of substitution.

The Dumontiaceae, Gainiaceae, Kallymeniaceae, and Rhizophyllidaceae

The results that we now present for this clade of families are essentially those of Tai et al. (2001), which provided strong support for including it in the Gigartinales s.s. Although the molecular data generally resolve a Dumontiaceae s.s. (including the cold-temperate northern taxa), the many dumontiacean genera of predominately warm-temperate and Southern Hemisphere distribution are shown to be of uncertain taxonomic affinity relative to the northern Dumontiaceae, as well as to the included genera of the other families of this clade (Fig. 4). In particular, the pantropical–temperate genus *Dudresnaya* was resolved as a sister to the strongly supported Kallymeniaceae rather than an in-group member of the Dumontiaceae, whereas the southeastern-Australian-endemic *Dasyphloea* showed a solid alliance to the Antarctic *Gainia*, the sole member of the family Gainiaceae. Although improved resolution among these lineages is required prior to the proposal of any formal taxonomic revisions to either the Dumontiaceae or Gainiaceae (cf. Tai et al. 2001), we can at least conclude for the present that all of these clades fall comfortably within the Gigartinales s.s. If the preliminary SSU indications should prove to hold up under further analyses, the mostly southern group of genera (such as *Dasyphloea*, *Kraftia*, and *Gibsmithia*) could be accommodated in the existing Gainiaceae, whereas a separate family would be required for *Dudresnaya*.

Most of the species in the Gigartinales s.s. known to produce galactans containing substantial amounts of agar structure are representatives of the Kallymeniaceae–Dumontiaceae clade (but see Endocladiaceae below). However, there seems to be no consistent pattern for the relative distribution of agarocolloids and carrageenans within the group, as illustrated by a survey of Russian red algae conducted by Usov and Klochkova (1992). Of seven Kallymeniaceae species investigated, partial reductive hydrolysis yielded carrabiitol from one species, agarobiitol from two species, and both carrabiitol and agarobiitol from the other four species. These results do not exclude the possibility that D- and (or) L-galactose occurs as 4-linked units in the polysaccharides. Generally, where known, Kallymeniaceae and Dumontiaceae polysaccharides are highly sulfated, nongelling galactans containing low to intermediate levels of 3,6-anhydrogalactose, 4-linked residues occurring as either or both D- and L-isomers, and highly heterogeneous patterns of substitution with sulfate ester, methyl ether, and, in some cases, pyruvate acetal (Deslandes et al. 1990; Zinoun et al. 1990; Usov and Klochkova 1992; Sekkal et al. 1993; Chopin et al. 1994, 1999; Miller and Furneaux 1996). Essentially all these structural features were characterized in the complex sulfated galactans of New Zealand *Kallymenia berggreni* J. Agardh (Miller and Furneaux 1996).

Basal to the entire Kallymeniaceae–Dumontiaceae clade, although with only weak to moderate support, is *Portieria*. This is a pantropical member of the Rhizophyllidaceae, a family of three genera defined by Kylin (1956) and Wiseman (1975) as containing uniaxial species in which procarpic gametophytes alternate with isomorphic tetrasporophytes that, like *Dudresnaya* but not the Kallymeniaceae, produce zonate tetrasporangia. Polysaccharides from two Rhizophyllidaceae species were tentatively described as λ-like carrageenans, mainly on the basis of IR spectroscopy (Chopin et al. 1999), but more detailed studies are warranted to clarify their structure.

The Endocladiaceae, Gloiosiphoniaceae, Nizymeniaceae, Phacelocarpaceae, and Sphaerococcaceae

Saunders and Kraft (1994), in their study of the phylogenetic relationships of *Plocamium* and *Plocamiocolax*, included SSU data for the monogeneric families Nizymeniaceae (it became monogeneric when its two component genera were soon afterwards merged by Chiovitti et al. 1995), Phacelocarpaceae and Sphaerococcaceae, as these families had all been allied at various times to the Plocamiaceae. Although molecular analyses showed that they were closely related, the data also strongly indicated that all three were positioned solidly within the Gigartinales s.s. rather than with the new order Plocamiales. Saunders and Kraft (1994) further indicated that the Nizymeniaceae and Phacelocarpaceae were particularly similar in SSU nucleotide sequences, so much so that they should possibly not be separated at the family level despite enormous anatomical dissimilarities between the two in spermatangial and tetrasporangial dispositions. Searles (1968, p. 77) had earlier proposed a possible phylogenetic link between what he concluded on anatomical grounds were the closely allied gigartinalean families Sphaerococcaceae (Fig. 17), Phacelocarpaceae (Fig. 18), and Nizymeniaceae (Fig. 19) and the then cryptonemialean families Endocladiaceae and Gloiosiphoniaceae, all of which are characterized by plants with uniaxial construction and procarps that consist of "clusters of filaments that are produced secondarily and bear both carpogonia and auxiliary cells" (Hommersand and Fredericq 1990). Saunders and Kraft (1996) argued strongly in favor of this association by championing an alternative interpretation of the auxiliary cell position in the Sphaerococcaceae in which this structure is not itself considered the supporting cell, but rather the periaxial cell fulfills this role such that the auxiliary cell is now intercalary in the carpogonial branch and represents a "drastic condensation" of the procarp in the related families (cf. Searles 1968). Saunders and Kraft (1996) included both genera of the Endocladiaceae in their SSU analyses and buttressed this proposal. We have now added SSU sequence data for *Gloiosiphonia* (Fig. 4), the sole member of the Gloiosiphoniaceae with procarpic features consistent with those of the other families of this lineage. The second genus included by Kylin (1956) in the Gloiosiphoniaceae, *Schimmelmannia*, strongly allies to the Acrosymphytaceae in our SSU trees rather than to any member of the Gigartinales s.s. (Fig. 2, and see above).

The apparent discrepancy in the polysaccharides produced by *Endocladia* and *Gloiopeltis* was noted by Craigie (1990) and Fredericq et al. (1996*a*). *Gloiopeltis* species produce agar-type polysaccharides that are predominantly sulfated at O-6 of the 3-linked residues, although they contain other minor variations in sulfation and methylation patterns and, as demonstrated in the case of a Japanese specimen of *Gloiopeltis furcata* (Takano et al. 1998), small amounts of carrageenan structure (Stancioff and Stanley 1969; Lawson et al. 1973; Penman and Rees 1973; Usov 1984; Takano et al. 1995, 1998). By contrast, *Endocladia muricata* produces mainly a hybrid or mixture of κ- and β-carrageenan (Stancioff and Stanley 1969; Whyte et al. 1985), although mild methanolysis of the polysaccharide also yielded small amounts of an agar derivative (Whyte et al. 1985). Interestingly, the polysaccharide from *Phacelocarpus peperocarpos* is mainly a kind of κ-carrageenan that is additionally sulfated at O-6 of the 3-linked residue (Liao et al. 1996), and it therefore shares structural features in common with both *Endocladia* and *Gloiopeltis* polysaccharides. In addition to minor variations in sulfation patterns, the *Phacelocarpus peperocarpos* carrageenan also contained small amounts of terminal xylose, apparently attached at O-3 of 4-linked residues (Liao et al. 1996). *Nizymenia* polysaccharides are predominantly nongelling, highly sulfated xylogalactans with low levels of 3,6-anhydrogalactose (Chiovitti et al. 1995), but further studies employing desulfation or Smith degradation, for example, are required to determine the backbone structure and the sites of xylosylation. A specimen of *Gloiosiphonia capillaris* was reported to yield a nongelling galactan (Usov et al. 1983), but its structure remains to be determined. On the balance, the polysaccharide chemistry of this suite of families displays substantial heterogeneity, but more studies are needed to assess whether these polysaccharides represent extremes along diverse spectra of related structures.

The Cystocloniaceae (including the Hypneaceae)

Kylin (1956) included *Acanthococcus*, *Calliblepharis*, *Craspedocarpus*, *Cystoclonium*, *Erythronaema*, *Grunowiella* (now *Gloiophyllis*), and *Rhodophyllis* in the Cystocloniaceae (as the Rhodophyllidaceae), to which Searles (1968) transferred *Stictosporum* from the monogeneric family Stictosporaceae. Min-Thein and Womersley (1976) added the Australian-endemic genus *Austroclonium* Min-Thein et Womersley, and Hansen (1980) added the north-Atlantic *Fimbrifolium*, to make a final complement of 10 genera in the family.

Chiovitti et al. (1998) surveyed species from the seven genera represented in Australia and found all of them to have similar cell-wall polysaccharides except for *Austroclonium*, which they transferred to the Areschougiaceae (discussed below). We have resolved a monophyletic group (albeit unsupported) for the eight genera of the Cystocloniaceae included in our molecular trees, although a few anomalies can be noted. One is the association of the Australian *Rhodophyllis multipartita* with the Northern Hemisphere *Fimbrifolium* and its failure to join with an Australian congener *Rhodophyllis volans*, which tightly allies to a number of other Australian Cystocloniaceae included in our alignments. Hansen (1980) removed the north-Atlantic *Rhodophyllis dichotoma* (Lepechin) Gobi to the new monotypic *Fimbrifolium* on the basis of a number of reproductive attributes. Clearly more study is needed in this family using a more appropriate (more variable) gene system and especially including the type of the genus, *Rhodophyllis divaricata* (Stackhouse) Papenfuss. At best we can now only conclude that *Fimbrifolium* is generically distinct from the two Australian species of *Rhodophyllis* included in our study, these also being distinct from one another at the genus level.

Two Australian species of *Hypnea* (Hypneaceae) fell solidly within the Cystocloniaceae, where they formed a weak association with *Calliblepharis planicaulis*. Kylin (1930, p. 49) first placed both *Hypnea* and *Calliblepharis* in the Hypneaceae, later (1932) moving *Calliblepharis* to the Cystocloniaceae and distinguishing that family from the Hypneaceae on the basis of the single-terminal, rather than chained, carposporangia in the latter. This family-level criterion was questioned by Min-Thein and Womersley (1976) as being insubstantial given that other vegetative and reproductive features were virtually identical in the two groups. Cystocloniaceae species, including *Calliblepharis* spp., essentially produce ι-carrageenan, whereas Hypneaceae species produce mainly κ-carrageenan (cf. Chiovitti et al. 1998 and references therein). This seems to represent a relatively inconsequential difference in carrageenan chemistry, however, because κ- and ι-carrageenan coexist in the polysaccharides of numerous gigartinalean taxa. Indeed, the κ-carrageenan from *Hypnea musciformis* (Wulfen) Lamouroux also contained a minor ι-carrageenan component and the precursor residues to both carrageenan types as shown by ^{13}C NMR spectroscopy of the oligosaccharides generated by enzymic digestion and the enzyme-resistant fractions (Greer et al. 1984; Knutsen et al. 1995). Phylogenies inferred from both *rbc*L (albeit only weakly; Fredericq et al. 1996*a*) and SSU (much more strongly: Fig. 4) analyses support a merger of these two families. In addition, preliminary indications of the data suggest that the southern-Australian-endemic *Calliblepharis planicaulis*, a species of particularly *Hypnea*-like habit (Womersley 1994; Chiovitti et al. 1998, Fig. 8), may be better accommodated in *Hypnea* than *Calliblepharis*.

The Gigartinaceae and Phyllophoraceae (including the Petrocelidaceae)

These three families consistently ally with one another in published molecular phylogenies (e.g., Freshwater et al. 1994; Saunders and Kraft 1996). In support of their alliance, representatives of these three families consistently show a unique alternation of carrageenan chemistry with life-history phase, irrespective of whether the life-history phases are isomorphic or heteromorphic. The gametophytes produce mainly gelling κ- and (or) ι-carrageenans and the tetrasporophytes produce mainly nongelling "λ-type" carrageenans that are highly sulfated but contain low levels of 3,6-anhydrogalactose and varying amounts of pyruvate acetal (see Craigie 1990 for a review; Falshaw and Furneaux 1994, 1995, 1998).

The widely dispersed Gigartinaceae has been the target of several recent anatomical and molecular-systematic (based on the *rbc*L) investigations that have greatly changed our understanding of its generic makeup and internal phylogenetic alliances. Hommersand et al. (1993) revised the criteria for inclusion in the family and clarified generic concepts based on critical studies of cystocarpic and tetrasporangial features, these efforts resulting in the splitting of the formerly large genus *Gigartina* into four smaller, more internally consistent genera. In companion studies the *rbc*L gene was used to assess phylogenetic relationships among the seven genera attributed to the Gigartinaceae (Hommersand et al. 1994, 1999), including the southeast-Australian-endemic *Ostiophyllum*, which has only just been formally described (Kraft 2003). Our present study includes representatives of four of the genera and is consistent with the *rbc*L data in providing strong support for an association between the Northern Hemisphere genera *Chondrus* and *Mazzaella*, but a contradictory result in solidly allying the Australasian-endemic genus *Rhodoglossum* with an Australian species of the South African – southern Australian *Sarcothalia*. Clearly further investigation is required for this entire complex using additional gene systems.

Fredericq and Ramirez (1996) conducted an *rbc*L-based phylogenetic assessment of the Phyllophoraceae and concluded that *Mastocarpus* (Petrocelidaceae) should be moved to it. This proposal is only equivocally supported by SSU data, as relationships between *Mastocarpus* and the three included genera of Phyllophoraceae that we have sequenced are unresolved relative to one another as well as to the four genera that form a monophyletic Gigartinaceae clade in our trees (Fig. 4). Nonetheless, the more variable *rbc*L data are strongly in support of this merger, which we follow here.

The Areschougiaceae (= Rhabdoniaceae), Caulacanthaceae, Cubiculosporaceae, and Solieriaceae (including the Wurdemanniaceae)

Kylin (1925) established the Rhabdoniaceae for nonprocarpic genera previously assigned to the Rhodophyllidaceae (= Cystocloniaceae). Kylin (1928) apparently (fide Searles 1968, p. 44) temporarily abandoned this family, only to resurrect an altered version of it in 1932 to contain only the uniaxial genera *Areschougia*, *Catenella*, *Cystoclonium*, and *Rhabdonia*, moving the multiaxial former members to the new family Solieriaceae. Searles (1968) transferred, albeit with reservation, *Caulacanthus*, *Heringia*, and *Taylorophycus* to the Rhab-

Figs. 20–27. Gigartinales (*Callophycus* (20), Acrotylaceae (21–25), Mychodeophyllaceae (26), Corynocystaceae (2)). Fig. 20. *Callophycus serratus* (Harvey ex Kützing) Silva. Abrolhos Islands, Western Australia, 9–10 m depths on lower Acropora coral tines; 14.x.1990. Coll.: Kraft & Huisman. MELU, GEN-8657. Fig. 21. *Acrotylus australis* J. Agardh. Nora Creina, South Australia, drift; 3.ix.1971. Coll.: Kraft & Womersley. MELU, GEN-3769. Fig. 22. *Hennedya crispa* Harvey. Rottnest Island, Western Australia, 10–12 m; 3.xii.1980. Coll.: Ricker & Kraft. MELU, GEN-7518. Fig. 23. *Claviclonium ovatum* (Lamouroux) Kraft et Min-Thein. Seven Mile Beach, Western Australia, drift; 9.viii.1979. Coll.: Kraft & Allender. MELU, GEN-7077. Fig. 24. *Amphiplexia hymenocladioides* J. Agardh. Kangaroo Island, South Australia, 3–6 m depths on wooden jetty pilings; 3.xii.1971. Coll.: Kraft. MELU, GEN-4082. Fig. 25. *Antrocentrum nigrescens* (Harvey) Kraft et Min-Thein. Aireys Inlet, Victoria, Australia, drift; 21.ii.1976. Coll.: Kraft & Wetherbee. MELU, GEN-5803. Fig. 26. *Mychodeophyllum papillitectum* Kraft. Port Denison, Western Australia, drift; 7.vii.1966. Coll.: Kraft. AD, A44729. Fig. 27. *Corynocystis prostrata* Kraft. Agincourt Reef, Great Barrier Reef, Australia, 9 m at back of reef undercut; 13.i.1994. Coll.: Kraft. MELU, GBR-16254.

doniaceae from the Sphaerococcaceae, to which these genera clearly lacked an affiliation.

The Rhabdoniaceae (a later synonym of both the Areschougiaceae and Caulacanthaceae, families with nomenclatural priority because their generitypes were included in it), as constituted by Kylin (1956) and Min-Thein and Womersley (1976), was considered by Gabrielson and Hommersand (1982) to include several genera (such as *Areschougia*, *Erythroclonium*, and *Rhabdonia*), which, although they were uniaxial rather than multiaxial, belonged on the basis of strong reproductive similarities more naturally in the large multiaxial family Solieriaceae. This proposal left *Caulacanthus*, *Catenella*, *Heringia*, and *Taylorophycus* as the only representatives of a reinstated Caulacanthaceae, a family that had been studied anatomically by Searles (1968) as part of the Rhabdoniaceae. They further argued that within the Solieriaceae there was a particularly close alliance between the genera *Callophycus* (Fig. 20) and *Solieria*. However, Chiovitti et al. (1997) characterized the carrageenans from six species of *Callophycus* and showed that they consisted mainly of pyruvated α-carrageenan, with smaller amounts of α-carrageenan, and were unique for being the most highly pyruvated red algal galactans known. Chiovitti et al. (1998, 2001) argued for the resurrection of the Areschougiaceae after finding that the carrageenans of *Areschougia*, *Erythroclonium*, and *Rhabdonia* were very similar to one another and differed rather markedly, particularly in their high levels of methylation, from those of the Solieriaceae s.s. They also argued that *Austroclonium*, with its highly methylated carrageenans, showed much stronger polysaccharide affinities to the Areschougiaceae than to those of the Cystocloniaceae, in which it was placed by Min-Thein and Womersley (1976). Our molecular results corroborate the carbohydrate-based phylogenetic conclusions of Chiovitti et al. (1998, 2001) rather than the interpretations based strictly on vegetative and reproductive anatomy.

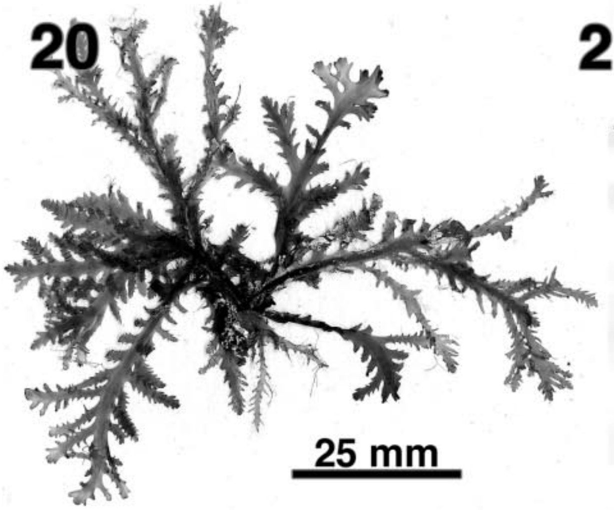
As a result of the previous discussion, we consider the Areschougiaceae, Caulacanthaceae, and Solieriaceae to be distinct at the family level, *Austroclonium* to properly belong in the Areschougiaceae rather than the Cystocloniaceae, and *Callophycus* to be of unresolved (for the moment) family affinity but not a member of the Solieriaceae s.s.

An *rbc*L-based phylogeny of the Solieriaceae s.l. by Fredericq et al. (1999) also strongly segregated the Solieriaceae s.s. (in our sense) from the genus *Callophycus* and the families Areschougiaceae and Caulacanthaceae. Unfortunately, as has also proven to be the case with our own SSU-based phylogenies, the *rbc*L data have failed to resolve relationships between these three indicated lineages, although they lent weak support to the suggestion of Watt et al. (2003) that the ι-, κ-, and β-carrageenans of eucheumoid Solieriaceae may be a molecular marker distinguishing them from the ι-, α-, and pyruvated α-carrageenans of some noneucheumoid Solieriaceae (including *Callophycus*), as well as Areschougiaceae and *Catenella* of the Caulacanthaceae. The *rbc*L trees further failed to include *Rhabdonia* in the Areschougiaceae, an association nevertheless weakly to moderately supported by the SSU results, and was handicapped by being an analysis conducted within an unnatural group (the Solieriaceae s.l.), thus excluding key families that the SSU system indicates must be included in any phylogenetic assessment of these genera (e.g., the Acrotylaceae, Dicranemataceae, and Mychodeaceae, to name but three). The insufficiencies of the two gene systems to resolve relationships of the Solieriaceae and related families stem from somewhat opposite shortcomings: the SSU is too conservative to settle such issues, whereas the *rbc*L can fail owing to not being conservative enough. The ability of the *rbc*L to resolve family and genus interrelationships at the levels we are considering may improve when all of the pertinent taxa are included in the analyses, but we predict that ultimately a third gene system will need to be utilized before the problems are satisfactorily addressed.

The SSU sequences that we have determined for *Solieria robusta* and its adelphoparasite *Tikvahiella candida* were identical, mirroring the observation both species produce similar ι- and pyruvated α-carrageenans (Chiovitti et al. 1999). Previous molecular investigations have generally uncovered a very close relationship between these types of parasites and their hosts (Goff et al. 1996), and our data are consistent with the published results in this regard.

The Wurdemanniaceae is a poorly known monogeneric and monospecific family created by Taylor (1960) for plants that have multiaxial apices and pseudoparenchymatous cross sections, the medullas composed of compact, axially elongated cells. Tetrasporangia are zonate, but as sexual reproduction is poorly known the taxonomic affinities of *Wurdemannia* have remained uncertain (Kraft 1981). Recently generated molecular data have solidly positioned this genus in the Solieriaceae (C. Lane, C. Schneider, and G.W. Saunders, unpublished data), and our results further indicate a putative alliance to *Solieria* itself (Fig. 4). The Wurdemanniaceae should thus be incorporated into the Solieriaceae.

In our trees the Cubiculosporaceae was resolved, albeit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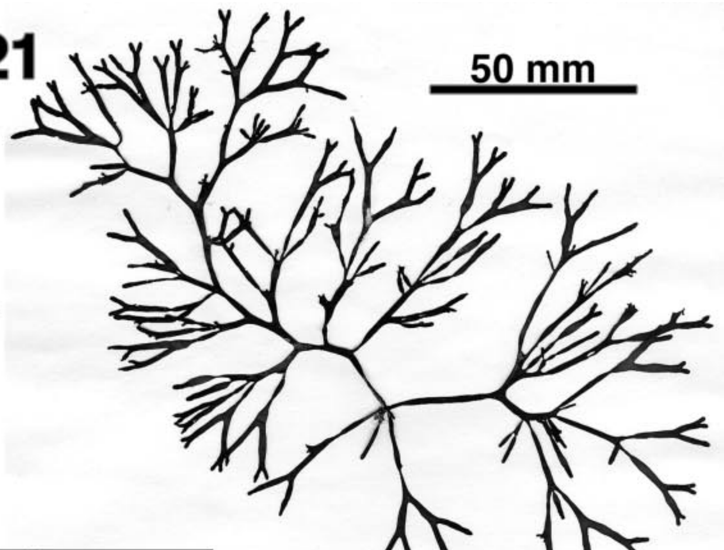
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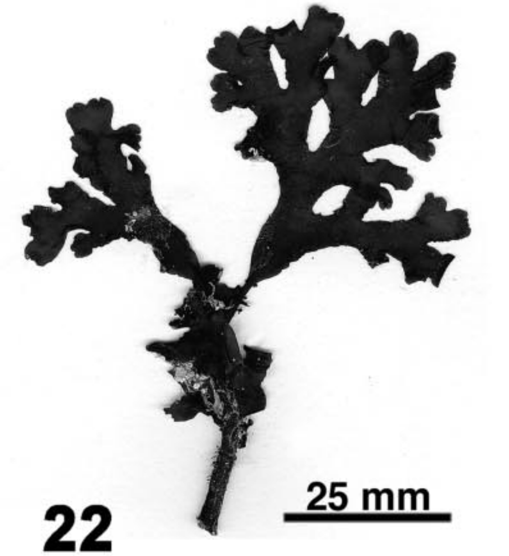
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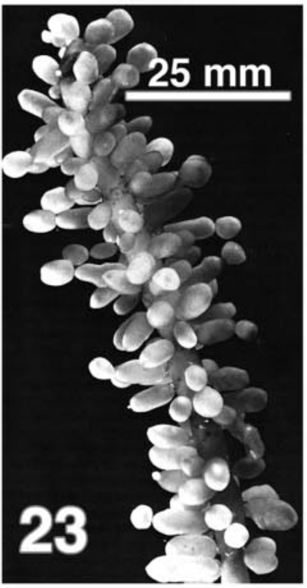
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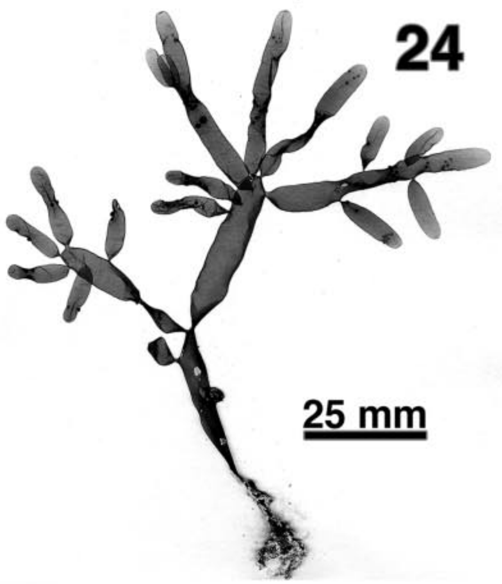
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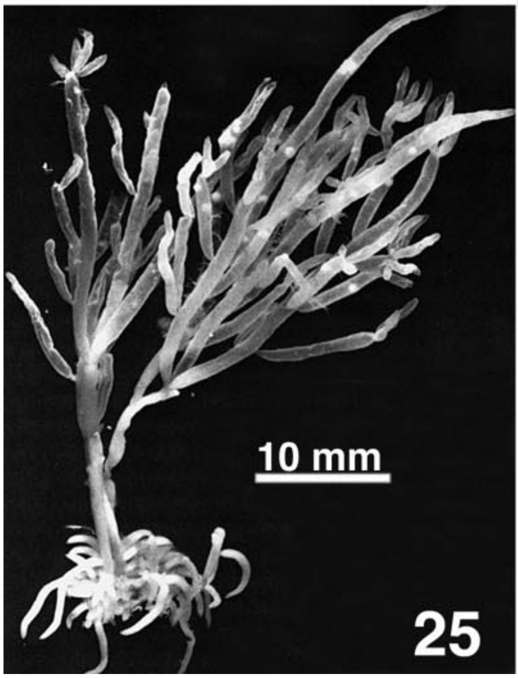
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with no support, within the Caulacanthaceae (Fig. 4). *Cubiculosporum koronicarpus* Kraft (Kraft 1973), the only genus and species of the Cubiculosporaceae, resembles the Caulacanthaceae in its zonate tetrasporangia; intercalary supporting cells; outwardly oriented, generally three-celled carpogonial branches; mostly single, short, and unbranched connecting filaments; initially inward gonimoblast development; multiple fusions of inner gonimoblasts to scattered medullary cells; and outwardly directed spore-producing gonimoblast filaments on which only the terminal few cells produce carposporangia. Differences between the two families include uniaxial versus multiaxial vegetative construction, single versus multiple gonimoblast initials, and nonpartitioned versus partitioned carposporophytes in the Caulacanthaceae relative to the Cubiculosporaceae (Kraft 1973). Although the two families may ultimately warrant being merged, we retain them as separate until a more appropriate gene system and more representatives are brought to bear on the issue.

The Acrotylaceae, Dicranemataceae, Mychodeaceae, and Mychodeophyllaceae

Members of these four families are largely confined to southern Australia (Womersley 1994). Kylin (1956) argued that they, along with the Gigartinaceae and Phyllophoraceae, formed a distinct branch of the Gigartinales in which procarps consist of auxiliary cells that are also the supporting cells of the carpogonial branches, and multiple gonimoblast initials arise laterally and toward the thallus interior (Kraft 1977*b*). Our SSU data solidly ally the Gigartinaceae and Phyllophoraceae with one another, these families sharing the morphological feature of cruciate tetrasporangia, but relationships between those two and the other four families, all of which have zonate tetrasporangia, are equivocal in the SSU analyses. The genera now included in the Acrotylaceae that we have analyzed (*Acrotylus*, *Antrocentrum*, *Amphiplexia*, *Claviclonium*, and *Hennedya*; Figs. 21–25) grouped together along with *Callophycus*, although the SSU provided no support for this particular assemblage.

For those familiar with the genera in this section of the tree, and especially those steeped in kylinian paradigms, the grouping of *Callophycus* with *Acrotylus* and *Hennedya* is not an intuitively felicitous outcome, as few Gigartinales would appear so dissimilar. Although structurally comparable, the centripetally growing gonimoblasts that line hollow cystocarp cavities in the Acrotylaceae (Kraft and Womersley 1994*a*, Figs. 120B, 120D) contrast sharply with the radially expanding carposporophytes anchored to prominent basal fusion cells in *Callophycus* (Womersley 1994, Figs. 109H, 110C, 110G, 110I). In all Acrotylaceae save *Claviclonium,* gametophytes are monoecious, with spermatangia forming in isolated, deeply inset surface clusters (Kraft and Womersley 1994*a*, Figs. 121F, 121L), as opposed to being generally scattered over the frond on surface mother cells (Womersley 1994, Fig. 110D) of dioecious male gametophytes. *Acrotylus* and *Hennedya* are, respectively, polycarpogonial and monocarpogonial (Kraft and Womersley 1994*a*, Figs. 121D, 121K), with supporting cells becoming auxiliary cells on diploidization and issuing multiple gonimoblasts thallus inwardly (Kraft 1977*b*; Kraft and Womersley 1994*a*, Fig. 121E). *Callophycus*, on the other hand, is nonprocarpic, the fertilized carpogonia issuing numerous connecting filaments (Womersley 1994, Figs. 109G, 110B, 110H) that effect diploidization of distant, intercalary auxiliary cells. The possible separation of the solidly allied *Amphiplexia* and *Antrocentrum*, along with the moderately affiliated sister genus *Claviclonium*, from *Acrotylus* and *Hennedya* is somewhat less unexpected, as *Amphiplexia* achieves its hollow cystocarp morphology through seemingly different processes from those of *Acrotylus* and *Hennedya*, *Antrocentrum* is uniaxial rather than multiaxial, and *Claviclonium* does not appear to be monoecious (Kraft and Womersley 1994*a*), as well as being the only member of the group (apart from *Callophycus*) not to produce straightforward κ-carrageenans (M.-L. Liao and A. Chiovitti, unpublished data). Further work using a more discriminating gene system would be desirable to sort out relationships within the fascinating family Acrotylaceae, a group of very unusual carposporophyte ontogeny in which all but one (*Amphiplexia*) of the six genera are monotypic (the east-African *Reinboldia polycarpa* Schmitz is known only from a surviving fragment of the 19th century type collection and is questionably a member of the family) and all but the genus *Ranavalona*, from the southern tip of Madagascar, are confined to southern Australia (Kraft 1977*b*).

The 11 species of *Mychodea*, the sole member of the Mychodeaceae, make it the largest wholly endemic genus of marine algae in Australia. Characterized by a complex internal organization of its uniaxial fronds (Kraft and Womersley 1994*b*, Figs. 160B, 160C), deeply sunken clusters of spermatangia on monoecious gametophytes, polycarpogonial supporting cells that function as auxiliary cells, and a particularly intricate placentation of the carposporophytes (Kraft 1978), its closest relationships were posited by Kraft (1978) on anatomical grounds to be with certain genera of the Cystocloniaceae. The three species of *Mychodea* that we have analyzed formed a monophyletic group sister to the Solieriaceae in both analyses, a position also compatible with the ι-carrageenans that are common to both (M.-L. Liao, unpublished data) and one very much separate from the strongly supported clades of the Cystocloniaceae (Fig. 4).

In his monograph of the Mychodeaceae, Kraft (1978) described a bizarre-looking Western-Australian-endemic species as the genus *Mychodeophyllum* (Fig. 26) and placed it in the new family Mychodeophyllaceae based on differences in axial and carposporophyte structure. Dixon (1982, p. 76) mistakenly portrayed the type and only species, *Mychodeophyllum papillitectum* Kraft, as a former member of *Mychodea* and did not accept the family that had been erected for it. Our molecular data (Fig. 4), however, resolved *Mychodeophyllum* as relatively divergent from *Mychodea*.

The Cruoriaceae (including Blinksiaceae?), Furcellariaceae, Polyideaceae, Rissoellaceae, and Tichocarpaceae

Only a single representative of each of these families was included in our SSU phylogenies, most of the families containing only one or a few genera and four being monospecific. Although nothing can be concluded at the moment about their relationships within the Gigartinales, it can be stated with virtual certainty that all are correctly included in this order.

The Cruoriaceae, with its single genus *Cruoria*, has been the source of considerable taxonomic confusion, as chronicled by Maggs and Guiry (1989). Of the various genera and species included in the past, Maggs and Guiry (1989) accepted only *Cruoria pellita* (Lyngbye) Fries and *Cruoria cruoriaeformis* (Crouan et Crouan) Denizot and argued that the family is a distinct element of the Gigartinales. Interestingly, the initiation of gonimoblasts from connecting filaments, rather than directly on the auxiliary cell, is not commonly seen in the Gigartinales s.s., and is a feature shared with the Polyideaceae, which groups weakly with the Cruoriaceae in our SSU trees (Fig. 4).

The Blinksiaceae is a monospecific family of noncalcified, *Cruoria*-like crusts that appear to be rare, even in the central-Californian type locality of *Blinksia californica* Hollenberg et Abbott (I. Abbott, personal communication). Consequently, we have been unable to secure material for analysis. Tetrasporangia are zonately divided and terminal on perithallial filaments in nemathecia. Carpogonial branches are four celled and directly issue connecting filaments from the carpogonium on fertilization, these effecting the diploidization of auxiliary cells, which are intercalary in perithallial filaments (Hollenberg and Abbott 1968). *Blinksia* shows many similarities to the Cruoriaceae, the main distinction being that gonimoblast initials are produced only outwardly from auxiliary cells in the Blinksiaceae as opposed to both inwardly and outwardly from seemingly nonspecified points along the connecting filaments themselves. This feature alone may well prove insufficient to define a family distinct from the Cruoriaceae (Kraft 1981), but we await molecular data before making any formal taxonomic proposals.

The Furcellariaceae, with three temperate to cold-temperate Northern Hemisphere genera (Kylin 1956), occupies a branch of our trees most closely associated with the Phyllophoraceae and Gigartinaceae (Fig. 4). Kraft (1975) had hypothesized that the family might be intermediary along a line of evolution running from “primitive” nemastomataceous forebears to the higher levels of vegetative and carposporophyte complexity represented by the Solieriaceae, but this scenario gains no support from our molecular evidence. Like the Nemastomataceae, intercalary auxiliary cells in *Furcellaria* and *Halarachnion* are diploidized via lengthy connecting filaments and produce globular carposporophytes composed almost entirely of carposporangia. Unlike the Nemastomataceae, however, the orientations of gonimoblast initials and carposporophytes are thallus inward rather than outward, as is generally also true in the Solieriaceae. The solieriaceous carposporophyte is considerably more anatomically complex than those of the Furcellariaceae or Nemastomataceae, consisting of sterile inner-gonimoblast tissue, often anchored to large basal or central fusion cells, and surface chains or layers of carposporangia. The evolutionary relationships posited by Kraft (1975) are good examples of how misled speculations can be when based on an assumption that evolution in gigartinalean reds is a process by which progressive anatomical complexity moves in incremental steps from the simplest and putatively most ancient to the most elaborately constructed and presumably most recent forms.

The Polyideaceae has been a small family of two genera disjunctly distributed in the North Atlantic (*Polyides*) and the western Pacific (*Rhodopeltis*) from Western Australia to southern Japan. Kylin (1956) originally placed the group in the Cryptonemiales because of its seemingly differentiated auxiliary-cell branches, but Wiseman (1975) transferred it, along with the Rhizophyllidaceae, to the Gigartinales on the grounds that the auxiliary-cell branches are “normal” rather than “accessory” cortical filaments. Our analyses of *Polyides* and *Portieria*, of the Polyideaceae and Rhizophyllidaceae (respectively), confirm the placement of both in the Gigartinales. In a series of publications, Itono and Yoshizaki (1992*a*, 1992*b*) determined that *Rhodopeltis* was not a natural genus, and they retained only *Rhodopeltis australis* Harvey (the type species of the genus) and *Rhodopeltis borealis* in this genus and argued that it should be transferred to the Dumontiaceae. This aspect of their proposal was supported in the earlier study of Tai et al. (2001) and is consistent here (Fig. 4). The remaining species of *Rhodopeltis* were transferred to a new genus, *Stenopeltis*, and retained in the Polyideaceae, a prospect not tested to date in our molecular analyses.

The Rissoellaceae is a kylinian family created for the single Mediterranean species *Rissoella verruculosa*. Seemingly similar to the Solieriaceae in vegetative structure, cystocarp complexity, and zonate tetrasporangia, it differs primarily in the elaborately procarpic association of its multiple but not polycarpogonial carpogonial-branch aggregations (Kylin 1956, Fig. 214). Our analyses of molecular data support placement of the Rissoellaceae in the Gigartinales but position it distant to the Solieriaceae (Fig. 4), again highlighting the lack of intuitive “feel” for picking specific anatomical markers as indicators of close phylogenetic relationships in the Gigartinales.

The Tichocarpaceae is yet another monospecific kylinian construct, this for the cold-water genus *Tichocarpus* from eastern Siberia and northern Japan. Also placed by Kylin (1956) in the Cryptonemiales because of the supposed accessory nature of its auxiliary-cell branches, the genus appears deeply embedded in the Gigartinales.

Observations of carrageenan chemistry may assist in assessing interfamilial affinities, although on their own they are insufficient for drawing conclusions. The extracellular polysaccharides of both *Tichocarpus crinitus* and *Furcellaria lumbricalis* are predominantly hybrids (or mixtures) of κ- and β-carrageenans (Usov et al. 1980; Knutsen and Grasdalen 1987, 1992). As slight variations on this theme, *Furcellaria fastigiata* (Turner) Lamouroux produces mainly κ- and β-carrageenans with small amounts of ι-carrageenan (Lawson et al. 1973; Bhattacharjee et al. 1979; Usov et al. 1980; Peats 1981; Whyte et al. 1985), whereas *Halarachnion ligulatum* (Woodward) Kützing produces essentially κ-carrageenan (Deslandes et al. 1988). The cell-wall galactans of *Rissoella verruculosa* are unique in that they mainly consist of ω-carrageenan (essentially 6′-O-sulfated β-carrageenan) with smaller amounts of κ- and β-carrageenans (Mollion et al. 1986, 1987). ω-Carrageenan is relatively rare but has been reported also as a dominant component in the carrageenans from one member of the Phyllophoraceae, *Phyllophora nervosa* (De Candolle) Greville (synonymous with *Phyllophora crispa*), and as a minor component in the carrageenans from *Phacelocarpus peperocarpos* (Usov and Shashkov 1985; Liao et al. 1996).

The Schmitziellaceae

Schmitziella is a red algal genus with an almost uniquely convoluted taxonomic past. *Schmitziella endophloea* Bornet et Batters in Batters is an endophyte growing within the lamellate walls of the green alga *Cladophora pellucida* (Hudson) Kützing in the northeast Atlantic and Mediterranean Sea (Woelkerling and Irvine 1982; South and Tittley 1986). The prostrate axes of *Schmitziella* branch freely and coalesce in open meshworks, ultimately producing zonate tetrasporangia in protuberant, conceptacle-like sori (Woelkerling and Irvine 1982). The "conceptacles" prompted Batters (1892) to include the genus in the Corallinaceae, a conclusion supported by subsequent morphological investigations that led to its being elevated to tribal (Svedelius 1911) and ultimately subfamilial (Johansen 1969) rank. Woelkerling and Irvine (1982) carefully restudied its anatomy and concluded that *Schmitziella* was not a member of the Corallinaceae but showed much stronger links to the Acrochaetiaceae, a view subsequently accepted (e.g., South and Tittley 1986) or rejected (Garbary 1987) by other researchers. Ultrastructural investigations by Pueschel (1989) virtually eliminated all chance that *Schmitziella* belongs in either the Acrochaetiaceae or Corallinaceae, for it lacks the two cap layers associated with pit plugs that characterize these two families. The capless pit plugs in *Schmitziella* were thus compatible with its placement in the Gigartinales (along with many other orders), and this ultrastructural feature, in combination with the zonate spore tetrads, prompted Pueschel to recommend inclusion in that order. D.J. Garbary and G.W. Saunders (unpublished data) have provided SSU data for *Schmitziella* that resolve it as an unequivocal member of the Gigartinales, one with possible affinities to other families with zonate tetrasporangia such as the Mychodeaceae and Solieriaceae. D.J. Garbary and G.W. Saunders (unpublished data) are recommending familial rank for this lineage (the Schmitziellaceae), although its closest relationships within the Gigartinales remain uncertain.

The Haemeschariaceae: an additional family absent from our molecular data set

Haemeschariaceae is a monogeneric family of two species of noncalcified crusts that are found in the northern Atlantic Ocean (Wilce and Maggs 1989). It is distinguished from other families of noncorallinalean crusts by its catenate rows of cruciate tetrasporangia, postfertilization division of the carpogonium prior to initiation of connecting filaments, production of multiple connecting filaments per fertilized carpogonium, and the initiation of gonimoblasts from the point of fusion of the connecting filament to the auxiliary cell (Wilce and Maggs 1989). For the present we concur that this family almost certainly represents a distinct lineage within the Gigartinales s.s.

The Corynocystaceae Kraft fam. nov.

The genus most recently added to the Gigartinales is *Corynocystis* Kraft (Kraft et al. 1999, Fig. 27), its single species widely distributed in tropical waters from the Philippines to the Great Barrier Reef in the western Pacific and westward to Mauritius in the Indian Ocean. Although similar to members of the Acrotylaceae in its hollow cystocarps and centripetally growing gonimoblasts, as well as its κ- and β-carrageenans (M.-L. Liao, personal communication), it differs in the pattern and arrangement of its spermatangia, in the configurations of its carpogonial branches, and by the strong likelihood that it is nonprocarpic. Our frustration at being unable to secure PCR-amplifiable material of this species, despite having been sent several unfixed dried collections over the years, was at last overcome thanks to the talents of Dr. Wilson Freshwater, who properly prepared living Philippine material given to him by the third author within minutes of collection and later succeeded in obtaining the SSU sequence that he has generously allowed us to incorporate into our analyses. As predicted (Kraft et al. 1999, p. 4), *Corynocystis* appears to be only distantly related to the Acrotylaceae (Fig. 4) and stands as yet another isolated gigartinalean lineage distinct at the family level. As such, we now provide a proposal for a new family to accommodate it:

Corynocystaceae Kraft fam. nov.

Plantae multiaxiales; axes medulla filamentosa et cortice anticlinali e filamentis pseudodichotomis angustis remotis constanti, interstitiis corticis interioris rhizoideis rhizinisque longitudinalibus impletis; conjunctiones foveolatae secundariae in cortice interiori; gametophyta monoica, spermatangiis in soris latis subterminalibus submarginalibusque crescentibus; rami carpogoniales recti, 3- vel 4-celluli, singuli in cellulis sustinentibus undifferentiatis cortices interioris insidentes. Cellulae auxiliares et primi gradus gonimoblasti ignoti. Cystocarpia matura pariete crasso, ostiolate cava; carposporophyta superficies internas cavitatis cystocarpii tegentia; filamenta gonimoblasti centripeta, carposporangia singula terminalia producentia. Tetrasporophyta ignota.

SPECIES TYPICA ET SOLA: *Corynocystis prostrata* Kraft in Kraft, Liao, Millar, Coppejans, Hommersand et Freshwater 1999: 26.

Plants multiaxial; axes with filamentous medulla and anticlinal cortex of narrow, widely separated pseudodichotomising filaments, the intervening inner-cortical spaces filled with longitudinally running rhizoids and rhizines; secondary pit connections present in inner cortex; gametophytes monoecious, spermatangia forming in broad subterminal and submarginal sori; carpogonial branches straight, three- or four-celled, borne singly on undifferentiated inner-cortical supporting cells. Auxiliary cells and early gonimoblast stages unknown. Mature cystocarps thick-walled, ostiolate, hollow; carposporophytes lining inner surfaces of cystocarp cavity, gonimoblast filaments growing centripetally, producing single-terminal carposporangia. Tetrasporophytes unknown.

TYPE AND ONLY SPECIES: *Corynocystis prostrata* Kraft in Kraft, Liao, Millar, Coppejans, Hommersand et Freshwater 1999: 26.

Epilogue

Much progress has been made in the last decade in deciphering the complexities of relationships among members of the large, unwieldy, and artificial ordinal construct left by

Kraft and Robins' (1985) merging of the Cryptonemiales and Gigartinales. The application of SSU-based analyses to increasing numbers of representatives is beginning to reveal a consistent roster of in-group taxa for not only the Gigartinales, but also the sister and segregate orders Halymeniales, Nemastomatales, and Plocamiales. In tandem, molecular-phylogenetic investigations are clarifying the genus and family composition of more distantly related orders such as the Acrochaetiales, Batrachospermales, Bonnemaisoniales, Ceramiales, and Rhodymeniales, so that the goal of achieving clarified concepts of the florideophycean orders appears to be rapidly approaching. At the family and genus levels of interrelationship, however, it can be said that the work has scarcely begun along many branches of the Gigartinales tree. Instances abound, some of which have been highlighted above, where common branches are occupied by genera with little apparent anatomical similarity and where the various lines would appear to be undergoing the supposedly conservative processes of zygote formation and embryogenesis in seemingly no logical or obviously consistent patterns of relatedness. The challenges that we now face are to produce strongly supported phylogenies within the order and then find the visual anatomical clues that point to the synapomorphies linking the descendants, identifying the indicators of common ancestry, as well as the reversions and convergences that make for the morphological confusion that we grapple with as systematists trying to decipher the evolutionary hieroglyphics. Now that the SSU is nearing the end of its work in Florideophyceae systematics, it is time to explore new gene systems (such as the LSU) to resolve more adequately relationships at the family and genus levels of relatedness. Nowhere in the red algae is there a panoply of greater riches spread before the systematist than in the Gigartinales. For many of us with an aesthetic appreciation, as well as a scientific curiosity, it is and will remain an order of particular interest.

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Appendix A.

Appendix appears on the following page.

Table A1. Collection data or published reference, and Genbank numbers (bold indicates sequences newly determined in this study) for species included in our molecular analyses.

Species collected	Collection information* and (voucher), or reference	GenBank
Ahnfeltiales		
Ahnfeltia plicata (Hudson) Fries	Bird et al. 1992*a*	Z14139
Bonnemaisoniales		
Bonnemaisonia hamifera Hariot	Ragan et al. 1994	L26182
Delisea pulchra (Greville) Montagne	Leeman, WA, Australia. 8 Nov. 1995. G.T.K. and G.W.S. (G0370)	**AY437645**
Ptilonia australasica Harvey	Warrnambool, Vic., Australia. 12 Apr. 1997. G.T.K. and R. Kraft. (GWS000160, = MELU-GEN 10570*a*)	**AY437646**
Ceramiales		
Antithamnion sparsum Tokida	Choi et al. 2000	AF236787
Ceramium macilentum J. Agardh	Saunders et al. 1996	U32562
Ceramium rubrum (Hudson) C. Agardh	Choi et al. 2000	AF236793
Inkyuleea ballioides (Sonder) H.-G. Choi, Kraft et G.W. Saunders	Choi et al. 2000	AF236789
Inkyuleea mariana (Harvey) H.-G. Choi, Kraft et G.W. Saunders	Choi et al. 2000	AF236792
Gelidiales		
Gelidiella acerosa (Forsskål) Feldmann et Hamel	Bailey and Freshwater 1997	U60342
Gelidium vagum Okamura	Ragan et al. 1994	L26190
Gelidium vittatum (Linnaeus) Kützing	Saunders and Kraft 2002	AF515300
Ptilophora pinnatifida (J. Agardh) R.E. Norris	Bailey and Freshwater 1997	U60345
Gigartinales, Acrosymphytaceae		
Acrosymphyton purpuriferum J. Agardh	Tai et al. 2001	AF317091
Acrotylaceae		
Acrotylus australis J. Agardh	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0023)	**AY437647**
Amphiplexia hymenocladioides J. Agardh	Coral Patches, WA, Australia. 25 Sept. 1994. J. Huisman. (G0235)	**AY437648**
Antrocentrum nigrescens (Harvey in Hooker f. et Harvey) Kraft et Min-Thein	The Rip, Port Phillip Bay, Vic., Australia. 10 May 1995. G.T.K. and G.W.S. (G0318)	**AY437649**
Claviclonium ovatum (Lamouroux) Kraft et Min-Thein	WA, Australia. Nov. 1994. J. Huisman. (G0252)	**AY437650**
Hennedya crispa Harvey	Mangles Bay, WA, Australia. 16 Feb. 1995. J. Huisman. (G0308)	**AY437652**
Areschougiaceae (in this Appendix including Solieriaceae)		
Areschougia congesta (Turner) J. Agardh	Saunders and Kraft 1994	U09613
Betaphycus speciosum (Sonder) J. Doty	Easter Passage, Easter Group, Abrolhos I., WA, Australia. 10 Nov. 1995. A.C. (T007)	**AY437653**
Callophycus oppositifolius (C. Agardh) P.C. Silva	Port Denison, WA, Australia. 9 Nov. 1995. I. Strachan, A.C., G.T.K., and G.W.S. (T002)	**AY437653**
Erythroclonium angustatum Sonder	Port MacDonnell, SA, Australia. 13 July 1997. G.T.K. (GWS000322)	**AY437655**
Eucheuma denticulatum (N.L. Burman) Collins et Harvey	Lluisma and Ragan 1995	U25439
Eucheuma isiforme (C. Agardh) J. Agardh	Lluisma and Ragan 1995	U25438
Kappaphycus alvarezii (Doty) Doty	Lluisma and Ragan 1995	U25437
Rhabdonia verticillata Harvey	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0022)	**AY437656**
Sarcodiotheca furcata (Setchell et Gardner) Kylin	Goff et al. 1996	U43553
Solieria robusta (Greville) Kylin	Flinders Jetty, Vic., Australia. 23 Apr. 1993. G.T.K. and G.W.S. (G0136)	**AY437657**
Tikvahiella candida Kraft et Gabrielson	Flinders Jetty, Vic., Australia. 23 Apr. 1993. G.T.K. and G.W.S. Sequence identical to *Solieria*. (G0137)	**AY437658**
Calosiphoniaceae		
Schmitzia falcata sp. ined.	NE of White I., Easter Group, Abrolhos I., WA, Australia. 10. Nov. 1995. G.T.K. and G.W.S. (G0397)	**AY437659**

Table A1 (*continued*).

Species collected	Collection information* and (voucher), or reference	GenBank
Schmitzia sp. ined.	Swiss Cheese Reef, Norfolk I., Australia. 12 Dec. 1994. A. Millar and P. Richards. (G0266)	**AY437660**
Caulacanthaceae		
Catenella caespitosa (Withering) L. Irvine in Parke et Dixon	Culture from J. West. 6 May 1993. (G0143)	**AY437661**
Catenella nipae Zanardini	Culture from J. West. 18 Dec. 1991. (G0049)	**AY437662**
Caulacanthus okamurae Yamada	Culture from J. West. 6 May 1993. (G0142)	**AY437663**
Corynocystaceae		
Corynocystis prostrata Kraft in Kraft et al.	Hiluntangan Island, Cebu, Philippines. 15 Apr. 1998. G.T.K. (MELU, K 10938)	**AY437651**
Cruoriaceae		
Cruoria pellita (Lyngbye) Fries	Strangford L., U.K. 25 Feb. 1999. C. Maggs. (GWS000563)	**AY437664**
Cubiculosporaceae		
Cubiculosporum koronicarpis Kraft	Villa Celeste Resort, Danclan, Bulusan, Sorsogon, Philippines. 21 Apr. 1998. W. Freshwater. (GWS000772)	**AY437665**
Cystocloniaceae		
Austroclonium charoides (Harvey) Min-Thein et Womersley	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0038)	**AY437666**
Calliblepharis celatospora Kraft	Pinnaroo Pt., WA, Australia. 7 Nov. 1995. G.T.K. and G.W.S. (G0359)	**AY437667**
Calliblepharis ciliata (Hudson) Kützing	Coral Strand, Carraroe Co., Galway, Ireland. 18 Oct. 1997. C. Maggs. (GWS000324)	**AY437668**
Calliblepharis jubata (Goodenough et Woodward) Kützing	Coral Strand, Carraroe Co., Galway, Ireland. 18 Oct. 1997. C. Maggs. (GWS000323)	**AY437669**
Calliblepharis planicaulis (Harvey) Kylin	Port MacDonnell, SA, Australia. 15 July 1995. G.T.K. (G0334)	**AY437670**
Craspedocarpus ramentaceus (C. Agardh) Min-Thein et Womersley	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0030)	**AY437671**
Cystoclonium purpureum (Hudson) Batters	Pt. Lepreau, N.B., Canada. 7 Oct. 1995. G.W.S. (G0421)	**AY437672**
Erythronaema ceramioides J. Agardh	Point Nepean, Port Phillip Bay, Vic., Australia. 5 Apr. 1995. G.T.K. and G.W.S. (G0304)	**AY437673**
Fimbrifolium dichotomum (Lepechin) Hansen	Sandy Cove, Digby Neck, N.S., Canada. 7 Nov. 1997. G.W.S. (GWS000307)	**AY437674**
Gloiophyllis barkeriae (Harvey) J. Agardh	Port MacDonnell, SA, Australia. 1 Dec. 1991. G.T.K. and G.W.S. (G0033)	**AY437675**
Rhodophyllis multipartita Harvey	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0037)	**AY437676**
Rhodophyllis volans Harvey	Saunders and Kraft 2002	AF515299
Stictosporum nitophylloides (Harvey) J. Agardh	Tarcoola Beach, Geraldton, WA, Australia. 21 Sept. 1995. M.H. and F.C. Hommersand. (Kraft 28)	**AY437677**
Dicranemataceae		
Dicranema revolutum (C. Agardh) J. Agardh	Port MacDonnell, SA, Australia. 1 Dec. 1991. G.T.K. and G.W.S. (G0036)	**AY437678**
Dumontiaceae		
Constantinea subulifera Setchell	Tai et al. 2001	AF317092
Cryptosiphonia woodii (J. Agardh) J. Agardh	Tai et al. 2001	AF317093
Dasyphloea insignis Montagne	Saunders and Kraft 1994	U09614
Dilsea carnosa (Schmidel) Kuntze	Tai et al. 2001	AF317096
Dudresnaya capricornica Robins et Kraft	Tai et al. 2001	AF317098
Dumontia contorta (S.G. Gmelin) Ruprecht	Tai et al. 2001	AF317099
Farlowia mollis (Harvey et Bailey) Farlow et Setchell	Saunders and Kraft 1996	U33129
Gibsmithia dotyi Kraft et Ricker	Tai et al. 2001	AF317108
Hyalosiphonia caespitosa Okamura	Tai et al. 2001	AF317109
Kraftia dichotoma Shepley et Womersley	Tai et al. 2001	AF317110

Table A1 (*continued*).

Species collected	Collection information* and (voucher), or reference	GenBank
Neodilsea borealis (Abbott) Lindstrom	Tai et al. 2001	AF317112
Orculifilum denticulatum Lindstrom	Tai et al. 2001	AF317115
Pikea californica Harvey	Tai et al. 2001	AF317116
Rhodopeltis borealis Yamada	Tai et al. 2001	AF317119
Weeksia coccinea (Harvey) Lindstrom	Tai et al. 2001	AF317120
Endocladiaceae		
Endocladia muricata (Postels et Ruprecht) J. Agardh	Saunders and Kraft 1996	U33127
Gloiopeltis furcata (Postels et Ruprecht) J. Agardh	Saunders and Kraft 1996	U33130
Furcellariaceae		
Furcellaria lumbricalis (Hudson) Lamouroux	Bird et al. 1992*a*	Z14141
Gainiaceae		
Gainia mollis Moe	Tai et al. 2001	AF317107
Gigartinaceae		
Chondrus crispus Stackhouse	Bird et al. 1992*a*	Z14140
Mazzaella laminarioides (Bory) Fredericq	Saunders and Kraft 2002	AF515287
Rhodoglossum gigartinoides (Sonder) Edyvane et Womersley	Flinders Jetty, Vic., Australia. 16 June 1992. G.T.K. and G.W.S. (G0098)	**AY437679**
Sarcothalia crassifolia (C. Agardh) Edyvane et Womersley	Saunders and Kraft 1994	U09615
Gloiosiphoniaceae		
Gloiosiphonia capillaris (Hudson) Carmichael in Berkeley	The Dora, Ireland. 4 May 1998. C. Maggs. (GWS000374)	**AY437680**
Schimmelmannia schousboei (J. Agardh) J. Agardh	Capo Molini, Catania, Italy. 18 May 1993. G. Tripodi. (G0152)	**AY437681**
Hypneaceae		
Hypnea charoides Lamouroux	Pinnaroo Pt., WA, Australia. 7 Nov. 1995. G.T.K. and G.W.S. (G0358)	**AY437682**
Hypnea ramentacea (C. Agardh) J. Agardh	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0020)	**AY437683**
Kallymeniaceae		
Callophyllis rangiferina (Turner) Womersley	Saunders and Kraft 1996	U33123
Erythrophyllum delesserioides J. Agardh	Tai et al. 2001	AF317105
Euthora cristata (C. Agardh) J. Agardh	Maces Bay, Bay of Fundy, N.B., Canada. 18 Apr. 1996. G.W.S. (GWS000026)	**AY437684**
Kallymenia tasmanica Harvey	Tai et al. 2001	AF317111
Mychodeaceae		
Mychodea carnosa Hooker f. et Harvey	Saunders and Kraft 1996	U33135
Mychodea marginifera (Areschoug) Kraft	Port MacDonnell, SA, Australia. 27 Sept. 1992. G.T.K. (G0108)	**AY437685**
Mychodea pusilla (Harvey) J. Agardh	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0040)	**AY437686**
Mychodeophyllaceae		
Mychodeophyllum papillitectum Kraft	Seven Mile Beach, WA, Australia. 13 Nov. 1995. I. Strachan, G.W.S., and G.T.K. (G0385)	**AY437687**
Nizymeniaceae		
Nizymenia australis Sonder	Saunders and Kraft 1994	U09616
Petrocelidaceae		
Mastocarpus stellatus (Stackhouse in Withering) Guiry	Ragan et al. 1994	L26195
Peyssonneliaceae		
Peyssonnelia sp.	Dog Rock, Pelsart Group, Abrolhos I., WA, Australia. 12 Nov. 1995. J. Huisman. (G0418)	**AY437688**

Table A1 (*continued*).

Species collected	Collection information* and (voucher), or reference	GenBank
Sonderopelta coriacea Womersley et Sinkora	Port MacDonnell, SA, Australia. 30 Nov. 1991. G.T.K. and G.W.S. (G0026)	**AY437689**
Phacelocarpaceae		
Phacelocarpus peperocarpos (Poiret) Wynne, André et P.C. Silva	Saunders and Kraft 1994	U09617
Phyllophoraceae		
Gymnogongrus sp.	Maces Bay, Bay of Fundy, N.B., Canada. 18 Sept. 1997. G.W.S. (GWS000280)	**AY437690**
Schottera nicaeensis (Lamouroux ex Duby) Guiry et Hollenberg	Saunders and Kraft 1996	U33137
Stenogramme interrupta (C. Agardh) Montagne ex Harvey	Pt. Lonsdale, Vic., Australia. 31 Mar. 1993. G.T.K. and G.W.S. (G0132)	**AY437691**
Polyideaceae		
Polyides rotundus (Hudson) Greville	Tai et al. 2001	AF317117
Pseudoanemoniaceae		
Hummbrella hydra Earle	North side of Pudding Rock, Mokohinan I., New Zealand. 24 Oct. 1996. D. Crossman. (GWS000134)	**AY437692**
Rhizophyllidaceae		
Portieria hornemanii (Lyngbye) Silva	Tai et al. 2001	AF317118
Rissoellaceae		
Rissoella verruculosa (Bertolini) J. Agardh	Lachea I. (Catania), Italy. 18 May 1993. G. Tripodi. (G0150)	**AY437693**
Sarcodiaceae		
Sarcodia sp.	Sydney Harbour, NSW, Australia. 19 Feb. 1993. A. Millar. (G0128)	**AY437694**
Sarcodia montagneana (Hooker f. et Harvey) J. Agardh	Doubtless Bay, NSW, Australia. 30 Nov. 1993. A. Millar. (G0184)	**AY437695**
Trematocarpus fragilis (C. Agardh) De Toni	Olifantsbos Bay, South Africa. 21 Jan. 1998. M. Guiry. (GWS000346)	**AY437696**
Schmitziellaceae		
Schmitziella endophloea Bornet et Batters	D.J. Garbary and G.W. Saunders, unpublished data	AY437697
Sphaerococcaceae		
Sphaerococcus coronopifolius Stackhouse	Saunders and Kraft 1994	U09622
Tichocarpaceae		
Tichocarpus crinitus (S. Gmelin) Ruprecht	Awaji I., Hyogo prefecture, Japan. 16 Apr. 1996. I. Tan and M. Kamiya. (G0340)	**AY437698**
Wurdemanniaceae		
Wurdemannia miniata (Sprengel) Feldmann et Hamel	Walsingham Pond, Bermuda. 12 Nov. 2001. G.W.S., C. Lane, and C. Schneider. (GWS001246)	**AY437699**
Gracilariales		
Gracilaria chilensis Bird, McLachlan et Oliveira	Bird et al. 1992*a*	L26217
Gracilaria tikvahiae McLachlan	Bird et al. 1990	M33640
Gracilariopsis lemaneiformis (Bory) E.Y. Dawson et al.	Bird et al. 1992*b*	L26214
Halymeniales, Corynomorphaceae		
Corynomorpha clavata (Harvey) J. Agardh	Key Largo, Fla., U.S.A. 19 June 1994. W. Freshwater. (G0301)	**AY437700**
Halymeniaceae		
Carpopeltis phyllophora (Hooker f. et Harvey) Schmitz	Saunders and Kraft 1996	U33124
Cryptonemia undulata Sonder	Saunders and Kraft 1996	U33125

Table A1 (*concluded*).

Species collected	Collection information* and (voucher), or reference	GenBank
Epiphloea bullosa (Harvey) DeToni	Third Sister I., Walabi Group, Abrolhos I., WA Australia. 28 Sept. 1994. J. Huisman. (G0237)	**AY437701**
Grateloupia filicina (Lamouroux) C. Agardh	Saunders and Kraft 1996	U33132
Grateloupia intestinalis (Harvey) Setchell ex Parkinson in Chapman et Parkinson	Los Molinos, Valdivia, Chile. 30 Nov. 1996. A. Peters. (GWS000354)	**AY437702**
Halymenia plana Zanardini	Saunders and Kraft 1996	U33133
Norrissia setchellii (Kylin) Balakrishnan	Botany Bay, Vancouver I., B.C., Canada. 11 July 1995. M. Wynne. (G0336)	**AY437703**
Pachymenia carnosa (J. Agardh) J. Agardh	Saunders and Kraft 2002	AF515289
Pachymenia cf. *orbicularis* (Zanardini) Setchell et Gardner	Penon de Peca, Potter Peninsula, King George I., South Shetland I., Antarctica. 27 Dec. 1997. A. Peters. (GWS000355)	**AY437704**
Polyopes constrictus (Turner) J. Agardh	Point Lonsdale, Vic., Australia. 27 Feb. 1992. G.W.S. and G.T.K. (G0071)	**AY437705**
Polyopes tenuis Womersley et Lewis	Williamstown, Vic., Australia. 28 Apr. 1995. G.T.K. (G0316)	**AY437706**
Zymurgia chondriopsidea (J. Agardh) Lewis et Kraft	Saunders and Kraft 2002	AF515304
Sebdeniaceae		
Lesleigha sp. Kraft mscr.	Saunders and Kraft 2002	AF515286
Lord Howe 'Lesleigha'	Noddy I., Lord Howe I., Australia. 16 Mar. 2001. G.W.S. and G.T.K. (GWS001076)	**AY437707**
Sebdenia flabellata (J. Agardh) P.G. Parkinson	Saunders and Kraft 1996	U33138
Tsengiaceae		
Tsengia comosa (Harvey) Womersley et Kraft	Saunders and Kraft 2002	AF515303
Tsengia laingii (Kylin) Womersley et Kraft	Saunders and Kraft 2002	AF515302
Tsengia lanceolata (J. Agardh) G.W. Saunders et Kraft	Saunders and Kraft 2002	AF515288
Nemastomatales, Nemastomataceae		
Adelophycus corneus (J. Agardh) Kraft	Saunders and Kraft 2002	AF515285
Predaea aurora Kraft et G.W. Saunders	Saunders and Kraft 2002	AF515296
Predaea weldii Kraft et Abbott	Saunders and Kraft 2002	AF515298
Schizymeniaceae		
Platoma cyclocolpum (Montagne) Schmitz	Saunders and Kraft 2002	AF515292
Schizymenia dubyi (Chauvin ex Duby) J. Agardh	Saunders and Kraft 1996	U33136
Titanophora weberae Børgesen	Saunders and Kraft 2002	AF515301
Wetherbeella australica (Womersley et Kraft) G.W. Saunders et Kraft	Saunders and Kraft 2002	AF515290
Plocamiales		
Plocamiocolax pulvinata Setchell	Saunders and Kraft 1994	U09618
Plocamium angustum (J. Agardh) Hooker f. et Harvey	Saunders and Kraft 1994	U09620
Plocamium cartilagineum (Linnaeus) Dixon	St. John Pt., Co. Down, N. Ireland. 14 Nov. 1993. C. Maggs. (G0167)	**AY437708**
Plocamium mertensii (Greville) Harvey	Portsea Jetty, Vic., Australia. 24 Mar. 1992. G.T.K. (G0080)	**AY437709**
Rhodymeniales, Champiaceae		
Dictyothamnion saltatum A. Millar	Saunders et al. 1999	AF085264
Rhodymeniaceae		
Asteromenia peltata (W.R. Taylor) Huisman et A. Millar	West Whale Bay Park, Bermuda. 13 Nov. 2001. G.W.S., C. Lane & C. Schneider. (GWS001252)	**AY437710**
Erythrocolon podagricum (Harvey) J. Agardh	Millar et al. 1996	U23953
Erythrymenia minuta Kylin	Saunders et al. 1999	AF085272
Hymenocladiopsis crustigena R.L. Moe	Saunders et al. 1999	AF085274
Fryeella gardneri (Setchell) Kylin	Saunders et al. 1999	AF085273
Rhodymenia leptophylla J. Agardh	Saunders and Kraft 1994	U09621

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