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PHYLOGENETIC RELATIONSHIPS AMONG LINEAGES OF THE CERAMIACEAE (CERAMIALES, RHODOPHYTA) BASED ON NUCLEAR SMALL SUBUNIT rDNA SEQUENCE DATA[1]

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Phylogenetic relationships among 69 species of the Ceramiales (51 Ceramiaceae, six Dasyaceae, seven Delesseriaceae, and five Rhodomelaceae) were determined based on nuclear SSU rDNA sequence data. We resolved five strongly supported but divergent lineages among the included Ceramiaceae: (i) the genus *Inkyuleea*, which weakly joins other orders of the Rhodymeniophycidae rather than the Ceramiales in our analyses; (ii) the tribe Spyridieae, which is sister to the remainder of the included ceramialean taxa; (iii) the subfamily Ceramioideae, weakly including the tribe Warrenieae; (iv) the subfamily Callithamnioideae; and (v) the subfamily Compsothamnioideae, which emerges as sister to the Dasyaceae/Delesseriaceae/Rhodomelaceae complex, thus rendering the Ceramiaceae sensu lato unequivocally paraphyletic, as has been argued separately on anatomical grounds by Kylin and Hommersand. Our data support a restricted concept of the Ceramiaceae that includes only one of the five lineages (Ceramioideae) that we have resolved. In addition to failing to ally with the Ceramiales in our molecular analyses, species of *Inkyuleea* differ substantially from other Ceramiaceae sensu lato in details of pre- and postfertilization development. The genus *Inkyuleea* is here assigned to the Inkyuleeaceae fam. nov., which we provisionally retain in the Ceramiales. Species of *Spyridia* also differ from the remaining Ceramiaceae in their postfertilization development, and, in light of our molecular data, the genus *Spyridia* is assigned to the Spyridiaceae. The Callithamnioideae is strongly monophyletic (100% in all analyses), which, in combination with key anatomical differences, supports elevation to family status for this lineage as the Callithamniaceae. Similarly, the Compsothamnioideae is solidly monophyletic in our molecular trees and has a unique suite of defining anatomical characters that supports family status for a complex that we consider to include the tribes Compsothamnieae, Dasyphileae, Griffithsieae, Monosporeae, Ptiloteae, Spermothamnieae, Sphondylothamnieae, Spongoclonieae, and Wrangelieae, for which the reinstated family name Wrangeliaceae is available.

Key index words: **Callithamniaceae; Ceramiaceae; Ceramiales; Inkyuleeaceae fam. nov.; nuclear small subunit rDNA; phylogeny; Rhodophyta; Spyridiaceae; systematics; Wrangeliaceae**

Abbreviations: ***rbc*L, LSU of RUBISCO gene; SH, Shimodara-Hasegawa**

The red algal family Ceramiaceae includes >120 genera and is represented by at least some members in virtually every suitable marine habitat throughout the world (Athanasiadis 1996, 2002; Table 1), as well as by at least a half dozen freshwater species. It is distinguished from sister families of the Ceramiales (Dasyaceae, Delesseriaceae, Rhodomelaceae, and the recently proposed Sarcomeniaceae [Womersley 2003]) by the absence of true pericentral cells and the lack of consolidated pericarps (as distinct from

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TABLE 1. List of families, subfamilies, tribes, and genera of the Ceramiaceae sensu lato according to Kylin (1956), Hommersand (1963), Itono (1977), Athanasiadis (1996, 2002), and this study.

Kylin (1956)	Hommersand (1963)	Itono (1977)	After Athanasiadis (1996, 2002)	This study (only taxa used in the molecular investigation)
				Inkyuleeaceae fam. nov.— *Inkyuleea*
	Ceramioideae	Antithamnioideae	Ceramioideae	Ceramiaceae sensu stricto
	Antithamnieae *Acrothamnion,* *Antithamnion,* *Antithamnionella,* *Ballia,* *Bracebridgea* (now synonymized with *Wrangelia*), *Grallatoria,* *Heterothamnion,* *Ptilocladia,* *Warrenia*	Antithamnieae *Acrothamnion,* *Antithamnion,* *Platythamnion*	Antithamnieae *Acrothamnion,* *Antithamnion,* *Hollenbergia,* *Macrothamnion,* *Perikladosporon*	Antithamnieae *Antithamnion*
Ceramium Gruppe *Campylaephora,* *Carpoblepharis,* *Centroceras,* *Ceramium,* *Ceramothamnion,* *Corallophila,* *Herpochondria,* *Microcladia,* *Reinboldiella,* *Syringocolax*	Ceramieae *Campylaephora,* *Carpoblepharis,* *Centroceras,* *Ceramium,* *Corallophila,* *Herpochondria,* *Microcladia,* *Reinboldiella,* *Syringocolax*	Ceramieae *Campylaephora,* *Carpoblepharis,* *Centroceras,* *Ceramiella,* *Ceramium,* *Ceramothamnion,* *Herpochondria,* *Microcladia,* *Reinboldiella*	Ceramieae *Amoenothamnion,* *Campylaephora,* *Carpoblepharis,* *Centroceras,* *Centrocerocolax,* *Ceramium,* *Corallophila,* *Episporium,* *Herpochondria,* *Leptoklonion,* *Microcladia,* *Reinboldiella,* *Sympodothamnion,* *Syringocolax*	Ceramieae *Carpoblepharis,* *Centroceras,* *Ceramium*
Crouania Gruppe *Acrothamnion,* *Antithamnion,* *Antithamnionella,* *Ballia, Crouania,* *Heterothamnion,* *Gattya,* *Grallaria,* *Gulsonia,* *Platythamnion,* *Ptilocladia,* *Warrenia*		Crouanieae *Crouania,* *Gattya,* *Ptilocladia*	Crouanieae *Crouania,* *Crouaniella,* *Crouanophycus,* *Dasyphila,* *Euptilocladia,* *Gattya,* *Gulsonia,* *Gulsoniopsis,* *Muellerena,* *Ptilocladia*	
		Delesseriopseae *Balliella,* *Delesseriopsis*		
Dohrniella Gruppe *Actinothamnion,* *Callithamnionella,* *Dohrniella*	Dohrnielleae *Callithamniella,* *Dohrniella*	Dohrnielleae *Dohrniella*	Dohrnielleae *Antithamnionella,* *Callithamniella,* *Dohrniella,* *Irtugovia,* *Trithamnion*	Dohrnielleae *Antithamnionella*
			Griffithsieae *Anotrichium,* *Baldockia,* *Bornetia,* *Griffithsia,* *Halurus*	

naked or involucrate carposporophytes) around the gonimoblasts (Bold and Wynne 1985, Maggs and Hommersand 1993, Womersley 1998). The genera *Lejolisia* (Gordon 1972, Itono 1977) and *Spyridia* (Phillips 1924, Hommersand 1963, Womersley and Cartledge 1975, Womersley 1998) are the only exceptions to this latter generalization, although their pericarps have certainly arisen independently as analogous, rather than homologous, structures (Bornet and Thuret 1867, Hommersand 1963).

Table 1. (Continued)

Kylin (1956)	Hommersand (1963)	Itono (1977)	After Athanasiadis (1996, 2002)	This study (only taxa used in the molecular investigation)
		Heterothamnieae *Antithamnionella*	Heterothamnieae *Heterothamnion,* *Elisiella,* *Tetrathamnion*	Heterothamnieae *Heterothamnion*
			Perithamnieae *Perithamnion,* *Scageliopsis*	
			Pterothamnieae *Inkyuleea,* *Pterothamnion*	Pterothamnieae *Pterothamnion*
			Scagelieae *Scagelia*	
			Scagelothamnieae *Scagelothamnion*	
			Sphondylothamnieae *Diplothamnion,* *Drewiana,* *Involucrana,* *Medeiothamnion,* *Shepleya,* *Sphondylothamnion,* *Vickersia,* *Wollastoniella*	
Spyridia Gruppe *Spyridia*		Spyridieae *Spyridia*	Spyridieae *Spyridia,* *Spyridiocolax*	Spyridiaceae *Spyridia*
		Warrenieae *Warrenia*		
Wrangelia Gruppe *Wrangelia*		Wrangelieae *Wrangelia*	Wrangelieae *Grallatoria,* *Wrangelia*	
Callithamnion Gruppe *Aglaothamnion,* *Aristothamnion,* *Callithamnion,* *Pseudospora,* *Seirospora*		Callithamnioideae Callithamnieae *Aglaothamnion,* *Callithamnion,* *Seirospora*	Callithamnioideae Callithamnieae *Aglaothamnion,* *Callithamnion,* *Carpothamnion,* *Pseudospora,* *Seirospora*	Callithamniaceae Callithamnieae *Aglaothamnion,* *Callithamnion,* *Diapse*, *Euptilota,* *Seirospora*
				Crouanieae *Crouania*
				Euptiloteae *Euptilota, Seirospora*
				Rhodocallideae *Rhodocallis*
		Compsothamnioideae	Compsothamnioideae	Wrangeliaceae
Compsothamnion Gruppe *Compsothamnion,* *Dasythamnion,* *Haloplegma,* *Lophothamnion,* *Mesothamnion,* *Pleonosporium,* *Spongoclonium*	Compsothamnieae *Compsothamnion,* *Dasythamnion,* *Haloplegma,* *Lophothamnion,* *Mesothamnion,* *Pleonosporum,* *Spongoclonium*	Compsothamnieae *Compsothamniella,* *Haloplegma,* *Mesothamnion,* *Pleonosporum*	Compsothamnieae *Antarcticothamnion,* *Compsothamniella,* *Compsothamnion,* *Dasythamniella,* *Gymnophycus,* *Haloplegma,* *Lophothamnion,* *Rhododictyon*	Compsothamnieae *Compsothamnion,* *Dasythamnionella*
Dasyphila Gruppe *Dasyphila,* *Psilothallia,* *Rhodocallis*	Dasyphileae *Dasyphila,* *Muellerena,* *Psilothallia*	Dasyphileae *Dasyphila*		Dasyphileae *Dasyphila,* *Muellerena*
Griffithsia Gruppe *Corynospora,* *Halurus,* *Griffithsia*	Griffithsieae *Corynospora,* *Griffithsia*	Griffithsieae *Griffithsia*		Griffithsieae *Anotrichium,* *Griffithsia,* *Halurus*

Schmitz (1889) recognized 39 genera distributed among 14 informal groups in the Ceramiaceae but later increased this to 40 genera in 24 unranked infrafamilial taxa (Schmitz and Hauptfleisch 1897, occasionally referred to as ''Gruppe''). De Toni (1903) treated these informal groups as subfamilies,

Table 1. (Continued)

Kylin (1956)	Hommersand (1963)	Itono (1977)	After Athanasiadis (1996, 2002)	This study (only taxa used in the molecular investigation)
			Halosieae *Halosia*	
			Monosporeae *Anisoschizus*, *Desikacharyella*, *Deucalion*, *Guiryella*, *Mazoyerella*, *Monosporus*, *Tanakaella*	Monosporeae *Monosporus*
Ptilota Gruppe *Diapse*, *Euptilota*, *Falklandiella*, *Georgiella*, *Gymnothamnion*, *Plumariopsis*	Ptiloteae *Dasyptilon*, *Delesseriopsis*, *Diapse*, *Euptilota*, *Georgiella*, *Gymnothamnion*, *Neoptilota*, *Plumaria*, *Plumariella*, *Plumariopsis*, *Ptilota*, *Rhodocallis*	Ptiloteae *Euptilota*, *Gymnothamnion*	Ptiloteae *Diapse*, *Dasyptilon*, *Euptilota*, *Falklandiella*, *Georgiella*, *Gymnothamnion*, *Neoptilota*, *Plumaria*, *Plumariopsis*, *Psilothallia*, *Ptilota*, *Rhodocallis*, *Tokidaea*	Ptiloteae *Neoptilota*, *Plumaria*, *Ptilota*
			Radiathamnieae *Laurenciophila*, *Radiathamnion*	
Spermothamnion Gruppe *Bornetia*, *Lejolisia*, *Ptilothamnion*, *Spermothamnion*, *Sphondylothamnion*, *Vickersia*	Spermothamnieae *Bornetia*, *Lejolisia*, *Ptilothamnion*, *Spermothamnion*, *Sphondylothamnion*, *Tiffaniella*, *Vickersia*	Spermothamnieae *Gordoniella*, *Lejolisia*, *Lomathamnion*, *Ptilothamnion*, *Tiffaniella*	Spermothamnieae *Gordoniella*, *Interthamnion*, *Lejolisia*, *Lomathamnion*, *Ptilothamnion*, *Ptilothamniopsis*, *Rhipidothamnion*, *Spermothamnion*, *Tiffaniella*	Spermothamnieae *Lejolisia*, *Spermothamnion*
	Crouanioideae Callithamnieae *Aglaothamnion*, *Callithamnion*, *Seirospora*	Sphondylothamnieae *Tanakaella*		Sphondylothamnieae *Involucrana*, *Shepleya*
	Crouanieae *Crouania*, *Gattya*, *Gulsonia*, *Gulsoniopsis*		Spongoclonieae *Mesothamnion*, *Pleonosporium*, *Spongoclonium*	Spongoclonieae *Pleonosporium*, *Spongoclonium*
	Spyridieae *Spyridia*			
	Wrangelieae *Wrangelia*			Wrangelieae *Wrangelia*
Uncertain position *Bracebridgea*, *Delesseriopsis*, *Lasiothalia*, *Mortensenia*, *Müllerella*, *Perischelia*, *Spencerella*, *Thamnocarpus*	Uncertain position *Chalicostroma*, *Mortensenia*, *Perischelia*, *Ptilocladiopsis*, *Spencerella*		Uncertain position Delesseriopseae—*Ballia*, *Balliella*, *Delesseriopsis*, *Plumariella*; Lasiothalieae—*Lasiothalia* Liagorothamnieae— *Liagorothamnion*; Warrenieae—*Warrenia*; Other genera *Mortensenia*, *Perischelia*, *Ptilocladiopsis*, *Scagelonema*, *Spencerella*	Uncertain position Warrenieae—*Warrenia*; *Tetrathamnion* in the Ceramiaceae sensu stricto; *Muellerena* and *Ptilota hannafordii* in the Wrangeliaceae

although using the termination ''-ieae'' rather than ''-ioideae'' as is now required. Feldmann-Mazoyer (1940) regarded Schmitz's taxa as tribes and added four additional tribes. Kylin (1956) employed the designation ''Gruppe,'' of which he recognized 11 containing 61 genera, plus eight unascribed genera that he considered to be of uncertain taxonomic position (Table 1). Kylin (1930, 1937) had earlier divided the Ceramiaceae into two developmental lines: in the first, which included the Ceramieae, Crouanieae, and Wrangelieae, procarps are borne on indeterminate axes; in the second, containing the Callithamnieae, Griffithsieae, Monosporeae, Ptiloteae, and Spermothamnieae, procarps are formed only on determinate axes. Hommersand (1963), however, pointed out that the position of procarps is highly variable, although in most tribes they tend to be restricted to subapical supporting cells at the tips of the axes or to be localized (often on basal cells) on either modified or unmodified determinate laterals. On the basis of types of vegetative branches, the consistent arrangement of particular cells associated with the carpogonial branch (i.e., components of the procarp) and uniform patterns of postfertilization events, Hommersand (1963) divided the Ceramiaceae (Table 1) into the two subfamilies Crouanioideae (including the tribes Callithamnieae, Crouanieae, Spyridieae, and, possibly, the Wrangelieae); and Ceramioideae (containing the tribes Antithamnieae, Ceramieae, Compsothamnieae, Dasyphileae, Dohrnielleae, Griffithsieae, Ptiloteae, and Spermothamnieae). Itono (1977) also emphasized procarp and postfertilization features but differed from Hommersand in recognizing (Table 1) the three subfamilies Antithamnioideae (including the Antithamnieae, Ceramieae, Crouanieae, Delesseriopseae, Dohrnielleae, Heterothamnieae, Spyrideae, Warrenieae, and Wrangelieae), Callithamnioideae (containing only the Callithamnieae), and Compsothamnioideae (for the Compsothamnieae, Dasyphileae, Griffithsieae, Ptiloteae, Spermothamnieae, and Spondylothamnieae). Moe and Silva (1979), however, simply suggested that the various component taxa of Ceramiaceae had undergone a recent explosive radiation, with the present members all having diverged from a common ancestor. They rejected subfamilial rank for the ceramiacean lineages but did argue that they group naturally into 18 tribes. Most recently, Athanasiadis (1996, 2002) has renewed arguments for recognizing Itono's (1977) three subfamilies (the Antithamnioideae [as the Ceramioideae], Callithamnioideae, and Compsothamnioideae) in the Ceramiaceae (Table 1).

Systematists have largely agreed that the Dasyaceae, Delesseriaceae, Rhodomelaceae, and Sarcomeniaceae (DDRS) all originated within the Ceramiaceae, thus rendering the latter paraphyletic. There is, however, disagreement as to whether these supposedly advanced families were derived from a single common ancestor (Papenfuss 1944) or from independent lines within this family (Kylin 1956, Hommersand 1963). Previous molecular studies (Freshwater et al. 1994, Saunders et al. 1996, de Jong et al. 1998, Choi et al. 2000, 2002, 2004) have confirmed that the Ceramiaceae is paraphyletic, the three advanced families having evolved from a single common ancestor in this family [although Freshwater et al. (1994) and de Jong et al. (1998) do not agree]. These studies, however, included only a limited number of species from the Ceramiaceae, and phylogenetic relationships between its subfamilies and/or tribes could not be adequately assessed, nor could the most likely source groups for the DDRS complex be pinpointed.

The aim of our study was to assess paraphyly of the Ceramiaceae relative to the other included families of the order, as well as to establish the phylogenetic affinities of its major lineages relative to one another by generating an extensive phylogeny for the family based on SSU rDNA sequence data from a wide variety of common and rare (mostly Australian) taxa. The results are interpreted in conjunction with a review of vegetative and reproductive attributes of ceramiacean genera, with the result that a new system of taxonomy is proposed for the entities currently included in this lineage.

MATERIALS AND METHODS

Material analyzed has come from numerous localities in Europe, North America, Korea, Japan, Australia, and South Africa (Table S1 in the supplementary material). To determine SSU rDNA sequences, samples were processed and genomic DNA was extracted as previously described (Saunders 1993). The SSU rDNA was PCR-amplified from total genomic DNA using the primer combinations of Saunders and Kraft (1994, 1996). Agarose gel-purification with the Wizard^{TM} PCR Preps DNA Purification System (Promega, Madison, WI, USA) or direct purification with High Pure^{TM} PCR Product Purification Kit (Roche Diagnostics, Indianapolis, IN, USA) was used to clean PCR products. DNA cleaned by these methods was sequenced with the dRhodamine^{TM} or BigDye^{TM} Terminator Cycle Sequencing Ready Reaction Kit [PE Applied Biosytems (ABI), Foster City, CA, USA]. Sequence data were collected with the ABI PRISM 310 Genetic Analyzer or 3730 DNA Analyzer. Editing of sequence data was accomplished with the SeqEd DNA sequence Editor (ABI) Software Package. Edited sequences were aligned relative to one another using the SeqPup multiple alignment program (Gilbert 1995).

The final alignment consisted of 84 species, including 48 previously published red algal SSU sequences (Table S2 in the supplementary material). The 1917 aligned nucleotide positions of SSU data were edited to remove the 5′ and 3′ PCR primer regions (G01 and G07, Saunders and Kraft 1994), as well as ambiguously aligned regions, to yield 1,597 bp for phylogenetic inference. Bayesian phylogenetic analyses were performed using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001) using default settings for priors, proposal probabilities, and chain temperature. The GTR + Γ + I model (see below) was used, and 5,000,000 generations were run with four chains and sampling every 100 generations. Four independent runs of analyses were completed, and all gave virtually identical results. Burn-in was identified for each run by plotting likelihood values against generations.

Maximum-likelihood (ML), distance, and parsimony analyses were completed in PAUP* 4.0b10 for the Macintosh (Swofford 2002). For ML and distance analyses, we used Modeltest 3.06 (Posada and Crandall 1998) to determine an appropriate model for our data. The model identified was a general time reversible (GTR) model with a gamma correction for among-site variation (Γ) and invariant sites (I). Distance analyses were completed with neighbor joining (Saitou and Nei 1987) and were subjected to 2,000 rounds of bootstrap resampling (Felsenstein 1985). ML and parsimony analyses (unweighted, gaps treated as missing data) were completed under a heuristic search (5 and 100 random additions, respectively) with tree-bisection-reconnection (TBR) branch swapping in effect. To estimate the robustness of internal nodes, bootstrap resampling was completed for the parsimony analysis (2,000 replicates; 10 random addition replicates per bootstrap replicate). In all analyses, unrooted trees were calculated, and the ingroup taxa subsequently rooted on *Ahnfeltia plicata* (Ragan et al. 1994, Saunders and Bailey 1997, Choi et al. 2000, Harper and Saunders 2001).

The Shimodaira and Hasegawa (1999) test (SH test), as implemented in PAUP*, was used to assess statistically a series of alternative phylogenetic hypotheses among the five resolved lineages of the Ceramiaceae. The following backbone (i.e., taxa were confined to the monophyletic group indicated, but no other constraints within or between lineages were enforced) constraint topologies were constructed:

1. Monophyletic order Ceramiales sensu lato, that is, including *Inkyuleea* (outgroups, [*Inkyuleea*, Spyridieae, Ceramioideae, Callithamnioideae, Compsothamnioideae, DDRS complex]).
2. Monophyletic family Ceramiaceae sensu stricto, that is, excluding *Inkyuleea* but including all other ceramiacean lineages (outgroups, *Inkyuleea*, [Spyridieae, Ceramioideae, Callithamnioideae, Compsothamnioideae], DDRS complex).
3. Monophyletic family Ceramiaceae excluding Compsothamnioideae (outgroups, [*Inkyuleea*, Spyridieae, Ceramioideae, Callithamnioideae], Compsothamnioideae, DDRS complex).
4. Monophyletic family Ceramiaceae excluding *Inkyuleea* and Compsothamnioideae (outgroups, *Inkyuleea*, [Spyridieae, Ceramioideae, Callithamnioideae], Compsothamnioideae, DDRS complex).
5. Monophyletic family Ceramiaceae including only Ceramioideae and Callithamnioideae (outgroups, *Inkyuleea*, Spyridieae, [Ceramioideae, Callithamnioideae], Compsothamnioideae, DDRS complex).
6. Monophyletic family Ceramiaceae excluding *Inkyuleea* and Spyridieae (outgroups, *Inkyuleea*, Spyridieae, [Ceramioideae, Callithamnioideae, Compsothamnioideae], DDRS complex).
7. Monophyletic lineage including only Callithamnioideae and Compsothamnioideae (outgroups, *Inkyuleea*, Spyridieae, Ceramioideae, [Callithamnioideae, Compsothamnioideae], DDRS complex).

The best tree for the full SSU alignment was determined for each of the constraints listed above following precisely the ML analyses protocol outlined above for the full alignment without topological constraints invoked. The best tree obtained when each constraint was enforced was then compared in turn against the best ML tree when no constraints were enforced using the SH test (RELL approximation, 1,000 replicates).

RESULTS

The 36 SSU sequences newly completed for this study ranged from 1,763 bp (*Spyridia elongata* and *Wrangelia plumosa*) to 1,807 bp (*Warrenia comosa*) in length and have been deposited in GenBank (Table S1). For taxonomic authors, see Tables S1 and S2. No ambiguities were observed in the SSU data. The final alignment consisted of 84 species, including 51 species representing 38 genera of the currently circumscribed Ceramiaceae (Tables S1 and S2).

The tree generated by Bayesian inference is presented with posterior probabilities and bootstrap results from the distance and maximum-parsimony analyses appended (Fig. 1). Our analyses resolved five distinct lineages for current members of the Ceramiaceae: (i) species of *Inkyuleea* failed to join the Ceramiales, instead grouping with the Gracilariales and Plocamiales, although the relationships among these three lineages were unresolved (Fig. 1); (ii) the Spyrideae was strongly supported as a distinct lineage, but its sister relationship to the remaining Ceramiales was unresolved; (iii) the tribe Warrenieae and the subfamily Ceramioideae were weakly allied as sister lineages, the latter moderately supported and including the tribes Antithamnieae, Ceramieae, Dohrnielleae, Heterothamnieae, and Pterothamnieae; (iv) the subfamily Callithamnioideae was solidly resolved as being monophyletic and consists of the tribes Callithamnieae, Crouanieae, Euptiloteae, and Rhodocallideae; and (v) the subfamily Compsothamnioideae, composed of the tribes Compsothamnieae, Dasyphileae, Griffithsieae, Monosporeae, Ptiloteae, Spermothamnieae, Spondylothamnieae, Spongoclonieae, and Wrangelieae, was moderately resolved as monophyletic and unequivocally allied to the DDRS complex (Fig. 1).

The distance tree differed from the Bayesian result in (i) the relative positioning of *Inkyuleea* spp. among the Gracilariales, Halymeniales/Rhodymeniales, and Plocamiales; (ii) failing to associate *Warrenia* with the Ceramioideae; (iii) associating *Muellerena* with the Dasyphileae rather than the Ptiloteae; and (iv) the affinities of *Tetrathamnion*, which allied to *Antithamnionella* spp. and *Heterothamnion* within the Ceramioideae, and *Aglaothamnion feldmanniae*, which joined *Aglaothamnion tenuissimum* and *Callithamnion* spp. within the Callithamnieae. However, none of these relationships received bootstrap support.

Unweighted parsimony generated four trees (length = 2,944; consistency index = 0.315; retention index = 0.659). A strict consensus of four equally parsimonious solutions differed from the Bayesian tree in the relative positioning of *Inkyuleea* spp. among the Gracilariales, Halymeniales/Rhodymeniales, and Plocamiales; in failing to associate *Warrenia* with the Ceramioideae; and for associations of *Pterothamnion* spp. and *Tetrathamnion* within

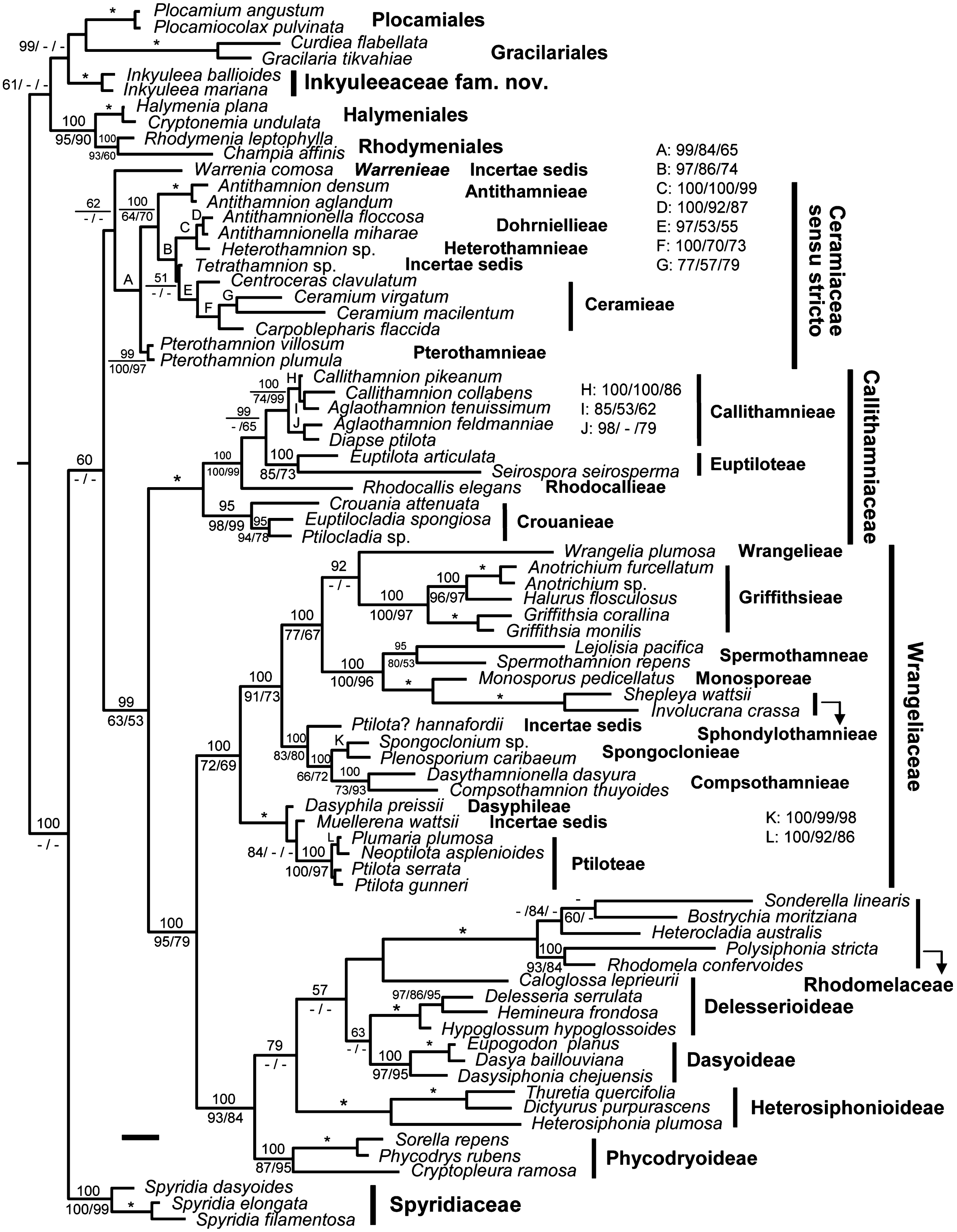

Fig. 1. Tree constructed with Bayesian inference for the SSU alignment. Taxonomic labels are based on the system of classification presented in this study (Table 1). Values at branches represent Bayesian posterior probabilities (top value), and 2,000 bootstrap replicates each for distance and parsimony (lower left and right values, respectively). Branches marked with an asterisk received 100% support in all three analyses, whereas those lacking values received <50% support. Scale bar = 0.01 substitutions/site.

the Ceramioideae and *Muellerena* and *Wrangelia* within the Compsothamnioideae. Again, there was no support for any of these relationships.

ML (−Ln likelihood = 16762.84) produced a topology identical to that resolved under Bayesian inference (Fig. 1). A series of phylogenetic hypotheses (Table 2) was tested under likelihood with the Shimodaira and Hasegawa (1999) test. Our results indicate that the best tree that includes *Inkyuleea* within the Ceramiales is not statistically different from the best ML result. Similarly, multiple hypotheses regarding various monophyletic groupings of the five resolved lineages of the Ceramiaceae were not rejected, with the exception of hypotheses including the Compsothamnioideae, which were statistically worse than the best tree (Table 2).

In light of previous research (Choi et al. 2000), we recognized the possibility that *Inkyuleea* may not be a member of the Ceramiales, which necessitated the use of an outgroup external to the subclass Rhodymeniophycidae. The closest, and thus most appropriate, lineage is the Ahnfeltiophycidae (Le Gall and Saunders 2007), which nonetheless is only distantly allied raising the probability of tree construction artifacts [see Withall and Saunders (2006) for a discussion of this issue relative to resolving relationships among lineages of Rhodymeniophycidae]. Therefore, based on the analyses performed here, we completed a second round of Bayesian inference excluding the Ahnfeltiophycidae as a distant outgroup and rooting the resulting topology at the base of the Ceramiales sensu stricto (i.e., excluding *Inkyuleea*) to ascertain if significant topological or support differences would be uncovered among the key lineages in this taxon. The only notable change was enhanced posterior probability support (62% in Fig. 1 to 83%) for the equivocal association of *Warrenia* with the Ceramioideae (data not shown).

DISCUSSION

Several authors have argued in the past on the basis of morphological interpretations that the Ceramiaceae is a paraphyletic family within the Ceramiales (Papenfuss 1944, Kylin 1956, Hommersand 1963), a proposition strongly supported by recent molecular studies (Freshwater et al. 1994, Saunders et al. 1996, Choi et al. 2000, 2002, 2004). Our analyses unequivocally support this perspective by resolving the Compsothamnioideae as sister to the DDRS complex (Choi et al. 2002), although the Sarcomeniaceae has not yet been included in our molecular analyses. Although our molecular analyses do result in a paraphyletic Ceramiaceae (albeit only weakly with the exception of the Compsothamnioideae), they are not consistent with the proposals of Kylin (1956), Hommersand (1963), and published *rbc*L data (de Jong et al. 1998), all of which conclude that the three supposedly ''advanced'' families are derived from independent lines rather than from a common ancestor within the Ceramiaceae. Although our statistical tests did not reject a common ancestor for the remaining lineages of Ceramiaceae resolved here (viz., *Inkyuleea*, Spyridieae, Ceramioideae and Callithamnioideae), these taxa do not form a monophyletic group in our best trees, and all can be defined by a unique suite of anatomical characters. In fact, there is no single known shared derived character that currently unites the taxa presently included in the Ceramiaceae. Previous studies usually refer to the absence of true pericentral cells and the absence of a consolidated pericarp as features that unite the Ceramiaceae as distinct from the other families (e.g., Hommersand 1963, Kraft 1981), but it is also acknowledged that these are most likely the ancestral states for these features, thus rendering them of no taxonomic value in defining the family. It is therefore an inevitable conclusion of our research that the Ceramiaceae is not a natural taxon as currently circumscribed.

The Ceramiales as now constituted is incompatible with contemporary systematic practices because the families of the DDRS complex are sister to a subfamily of a paraphyletic Ceramiaceae. We recognize four alternative options to deal with this problematic situation: (i) leave the Ceramiaceae as currently circumscribed (i.e., an arbitrary collection of taxa); (ii) accept a paraphyletic family Ceramiaceae within the Ceramiales (probably excluding *Inkyuleea*, which may not be affiliated with the order at all and which, by its inclusion, would clearly render the family polyphyletic); (iii) merge the four families of the DDRS complex into a single subfamily that would be of equivalent taxonomic rank to the other major lineages of the Ceramiaceae; or (iv) recognize each of the five divergent lineages of the Ceramiaceae at the family level. The first two options are not consistent with current taxonomic practices, whereas the third would result in a widely diverse (anatomically, reproductively, and, to a lesser extent, molecularly) assemblage of algae being grouped together within a single subfamily. For practical purposes, the last option seems clearly preferable as it is supported by key anatomical differences between the five lineages of the Ceramiaceae (as discussed below) and the divergence between them in SSU sequences.

Taxonomic proposals, including discussions of key anatomical features. 1. **Inkyuleeaceae** H.-G. Choi, Kraft, H.-S. Kim, Guiry et G. W. Saunders fam. nov.

Diagnosis: Plantae erectae, uniaxiales. Cellula axialis unaquaeque ramulos tres verticillatos ferens, ramulo majore alternanti, duobus ramulis minoribus opposito. Cellulae gladulae ignota. Cellulae uninucleata. Gametophyta dioecia; spermatangia fasciculata, terminalia in divisionbus ultimis ramulorum verticillatorum; rami carpogoniales quadricellulares, adaxiales in pagina superiore cellulis basalibus ramulorum verticillatorum majorum. Fecundatio auctu rami tricellularis auxiliari-cellularis secuta; diploidisatio cellulae auxiliaris ex cellula conjunctiva inter carpogonium et cellulam secundam-formatam rami auxiliari-cellularis dffecta. Tetrasporangia decussata-cruciata divisa, in filamentis cellulis basalibus ramulorum verticillatorum majorum minorumque orientibus portata.

Plants erect, uniaxial. Each axial cell bearing three whorl-branchlets, with an alternating major branchlet opposite two minor whorl-branchlets. Gland cells absent. Cells uninucleate. Gametophytes dioecious; spermatangia clustered, terminal on ultimate divisions of the whorl-branchlets; carpogonial branches four-celled, adaxial on the upper sides of basal cells of major whorl-branchlets. Fertilization followed by development of a three-celled auxiliary-cell branch; diploidization of the auxiliary cell effected by a connecting cell between the carpogonium and the subapical cell of the auxiliary-cell branch. Tetrasporangia decussately to cruciately divided, borne on filaments arising on basal cells of major and minor whorl-branchlets.

Type genus: *Inkyuleea* H.-G. Choi, Kraft et G. W. Saunders 2000, pp. 284–5.

Comments: This family contains a single genus *Inkyuleea* and three species (Choi et al. 2000). Wollaston's (1968, 1974, 1984) detailed anatomical studies form the bases of our familial characterization. Recently, we collected *I. beckeri* from Rocky Bay, Durban, South Africa, and completed the SSU rDNA sequence for the species, which shows it to differ in 18 and 14 bp between those of *I. ballioides* and *I. mariana*, respectively, and to group strongly together with them in phylogenetic analyses (data not shown).

Although Wollaston (1974, p. 25) characterizes the procarps and gonimoblast development, particularly those displayed by *I. mariana* (as *Ballia mariana*), as ''broadly similar to those of [the Antithamnieae of the Ceramiaceae],'' the position and behavior of the auxiliary cells are very anomalous. The procarps are borne singly on the upper sides of basal cells of successive major whorl-branchlets, and the auxiliary cells are apparently intercalary in three-celled branches on which the gonimoblast initial arises terminally, although nuclear studies are yet to determine how the separate sites of diploidization and gonimoblast initiation are bridged.

These reproductive features serve to distinguish the Inkyuleeaceae from any member of the Ceramiales (including the Ceramiaceae sensu lato) or of the other orders belonging to the Rhodymeniophycidae (Saunders and Bailey 1997, Saunders and Hommersand 2004). Inclusion of this family in the Ceramiales is considered an interim step until its phylogenetic affinities are better (Fig. 1 and Table 2) resolved among the Ceramiales and related orders.

2. **Spyridiaceae** J. Agardh (1851: vii, 337, ''Ordo Spyridieae'').

Plants erect, uniaxial, radially branched. Each axial cell bearing an indeterminate branch, from each cell of which one or more determinate branchlets (ramelli) develop laterally or in whorls, the ramelli unbranched and monosiphonous but encircled at each node by narrow bands of cortication that leave the bulk of their axial cells exposed. Primary axes and indeterminate laterals completely corticated, without internodal spaces. Gland cells absent. Cells multinucleate. Gametophytes dioecious; male gametophytes forming confluent cylinders of spermatangia around several successive cells of monosiphonous laterals. Carpogonial branches four-celled, borne singly on one of two or three periaxial cells in each fertile segment on small uncorticated lateral branchlets with restricted growth, each periaxial cell forming an auxiliary cell on fertilization but bearing no sterile cells. Two or three connecting cells arising on the hypogynous cell, fusing with usually two auxiliary cells. Carposporophyte surrounded by pericarpic filaments developed from the segments above and below the fertile-axial cell, cystocarps nonostiolate. Tetrasporangia tetrahedrally divided, sessile on corticating nodal cells of ramelli, naked, and mostly adaxial.

Type genus: *Spyridia* Harvey 1833, pp. 259, 336.

Comments: The family contains the single genus *Spyridia* and ~20 species (Hommersand 1963, Guiry and Guiry 2007), most, excepting the type species [*S. filamentosa* (Wulfen) Harvey], being of limited geographical distribution. Detailed anatomical studies of Phillips (1924), Hommersand (1963), and Womersley and Cartledge (1975) form the bases of our familial characterization. Development of the procarp and cystocarp in the type species have been

TABLE 2. Results of the Shimodaira and Hasegawa (1999) tests used to evaluate alternative hypotheses among the five resolved lineages of the Ceramiaceae for our SSU alignment.

Phylogenetic constraint tested[a]	−ln *L*	*P*-value
None = best tree from ML analysis of SSU alignment	16,762.84	–
1. Monophyletic order Ceramiales sensu lato, that is, including *Inkyuleea*	16,772.98	0.248
2. Monophyletic family Ceramiaceae sensu stricto, that is, excluding *Inkyuleea*, but including all other ceramiacean lineages	16,809.40	0.023*
3. Monophyletic family Ceramiaceae excluding Compsothamnioideae	16,781.97	0.154
4. Monophyletic family Ceramiaceae excluding *Inkyuleea* and Compsothamnioideae	16,764.84	0.426
5. Monophyletic family Ceramiaceae including only Ceramioideae and Callithamnioideae	16,768.13	0.307
6. Monophyletic family Ceramiaceae excluding *Inkyuleea* and Spyridieae	16,810.65	0.011*
7. Monophyletic lineage including only Callithamnioideae and Compsothamnioideae	16,788.65	0.027*

*Significant difference. ML, maximum likelihood.

[a] Phylogenetic constraints employed are outlined in detail in the Materials and Methods section.

studied in detail by Phillips (1924), Hommersand (1963), Womersley and Cartledge (1975), and Womersley (1998). According to Phillips (1924), a fertile segment on short, adventitious indeterminate branches consists of four periaxial cells (as pericentral cells), one of which bears the four-celled carpogonial branch. Hommersand (1963), however, reported only three periaxial cells per fertile-axial cell, each producing an auxiliary cell following fertilization of the associated carpogonium, with connecting cells arising from the hypogynous cell and usually fusing with just two of the three auxiliary cells formed, resulting in two separate but oppositely directed gonimoblasts. The whole structure becomes enveloped in a reticulum of pericarp filaments derived from the sterile segments above and below the fertile-axial cell. Phillips (1924) suggested that *Spyridia* has no near affinity with the Ceramiaceae or any Rhodymeniales and should be given ordinal status alongside the Wrangeliaceae in the cohort Gigartinales (sensu Oltmanns). Feldmann-Mazoyer (1940) agreed that if Phillips's observations were correct, *Spyridia* should probably be placed in a separate order. Hommersand (1963), however, corrected a number of errors in earlier studies (e.g., Cramer 1864, Phillips 1924, Feldmann and Feldmann 1940), and he placed *Spyridia* in the subfamily Crouanioideae along with the Crouanieae and the Callithamnieae on the basis that the supporting cell bears a single carpogonial branch, sterile groups are absent, and a connecting cell is evident as a process containing its own nucleus extending from the auxiliary cell after fusion with it. Krishnamurthy (1969), however, suggested that *Spyridia* shows affinities with the Wrangelieae in vegetative organization and with the Callithamnieae in features of reproduction.

Development of the spermatangia in *Spyridia* (Hommersand 1963, Womersley and Cartledge 1975, Womersley 1998) in confluent cylinders of mother cells that traverse several cells of monosiphonous laterals is another feature with no counterparts in the Ceramiaceae, although members of the Dasyaceae and the Heterocladieae and Lophothalieae of the Rhodomelaceae can be superficially similar in anatomy (Phillips et al. 2000, Choi 2001).

The Spyridiaceae is thus distinct from all recognized families of the Ceramiales in several vegetative and reproductive characteristics (Table 3 and Fig. 2), as well as in our molecular data (Fig. 1). Nevertheless, we provisionally retain the Spyridiaceae in the Ceramiales until additional data resolve the phylogenetic affinities of the family within the Rhodymeniophycidae.

3. The genus *Warrenia*, a sister of the Ceramiaceae sensu stricto.

Wollaston (1971) regarded *Warrenia comosa* (Harvey) Kützing, the only member of the tribe Warrenieae Schmitz, as a phylogenetically primitive member of the Ceramiaceae, one characterized by irregular and variable branching in which most cells of either determinate or indeterminate axes may act as supporting cells of carpogonial branches that arise singly in an abaxial position and, when fertilized, diploidize the auxiliary cell via a connecting cell. Three gonimoblast initials and gonimolobes composed entirely of carposporangia then develop within a lax involucre of sterile filaments derived from axial cells proximal to the supporting cell. Athanasiadis (2002) has suggested that either *Warrenia* or *Balliella* could be potential sister-taxa of the subfamily Ceramioideae, as both of these genera share the seemingly pleisiomorphic character of direct conversion of axial cells to supporting cells (i.e., supporting cells are not periaxial cells).

Our SSU (Fig. 1) and anatomical data (Table 3 and Fig. 2) indicate that the Warrenieae is a sister of the Ceramiaceae sensu stricto, but the phylogenetic relationships among the Spyridiaceae, Ceramiaceae sensu stricto, and other families of the Ceramiales are generally unresolved. It is possible that the Warrenieae could form a new taxon at the family level, and recently completed SSU sequences from two species of *Balliella* and a species of *Plumariella* from Korea and South Africa show that they group together with *Warrenia* with strong support. This assemblage will probably ultimately warrant independent familial status. We remain conservative with regard to this decision and retain *Warrenia* as sister to the Ceramioideae in a restricted Ceramiaceae pending further study. From the molecular perspective, removal of the distant outgroup Ahnfeltiophycidae resulted in enhanced, albeit not significant, support for this alliance, indicating that additional anatomical and molecular investigations are warranted prior to formal taxonomic proposals.

4. Redefining the Ceramiaceae sensu stricto.

Our restricted definition of the Ceramiaceae is based on work by Kylin (1923), Hommersand (1963), Itono (1977), Womersley (1978, 1998), Maggs and Hommersand (1993), and Athanasiadis (1996, 2002), coupled with the indications of our molecular investigations.

Ceramiaceae Dumortier (1822, pp. 73, 100)

Plants usually erect, uniaxial. Each axial cell bearing two to numerous normal or reduced determinate laterals or whorl-branchlets. Gland cells frequently present. Cells uninucleate. Gametophytes dioecious; spermatangia terminal on cells of normal or reduced whorl-branchlets; carpogonial branches four-celled, abaxial on the lower lateral sides of basal cells of normal or reduced whorl-branchlets; sterile pericentral cells or cells on the basal cell absent from the procarp; auxiliary cell cutting off a single gonimoblast initial. Cystocarps composed of one to several rounded gonimolobes of compact to linear carposporangia, the carposporophytes naked or involucrate. Tetrasporangia decussately, cruciately

TABLE 3. Comparison between Inkyuleeaceae fam. nov., Spyridiaceae, *Warrenia*, Ceramiaceae sensu stricto, Callithamniaceae, Wrangeliaceae, and the DDRS (Dasyaceae, Delesseriaceae, Rhodomelaceae, and Sarcomeniaceae) complex.

Character	Inkyuleeaceae fam. nov.	Spyridiaceae	*Warrenia*	Ceramiaceae sensu stricto	Callithamniaceae	Wrangeliaceae	DDRS complex
Nuclei per vegetative cell	Uninucleate	Multinucleate	Multinucleate	Mostly uninucleate[a]	Mostly uninucleate[b]	Uni- or multinucleate	Multinucleate
Transverse ramification	Present	Present	Absent	Present	Present	Present	Present
"Gland" cells	Absent	Absent	Present	Usually present[c]	Usually absent[d]	Usually absent[e]	Absent
Position of the supporting cell	The basal cell of a major determinate lateral	The periaxial cell of an indeterminate lateral branch of restricted growth	Any axial cell of a determinate or indeterminate axis	The basal cell of a "normal" or reduced whorl-branchlet	A periaxial cell of a fertile-axial cell of an indeterminate axis	A subapical cell of a short fertile axis with two or three periaxial cells	A pericentral cell of a fertile axial cell or (in the Nitophylloideae) a thallus cortical cell
Position of carpogonial branch	Adaxial on the upper side of the supporting cell	Abaxial on the lateral side of the supporting cell	Abaxial on the lower lateral side of the supporting cell	Abaxial on the lower lateral side of the supporting cell	Abaxial on the lower lateral side of the supporting cell	Abaxial on the lower lateral side of the supporting cell	Abaxial on the lower lateral side of the supporting cell
Sterile-cell group(s) on the supporting cell in procarp	Absent	Absent	Absent	Absent	Absent	One[f]	Usually two[g]
Position of the auxiliary cell	Intercalary in a three-celled auxiliary-cell branch on the supporting cell	Directly on supporting cell of the procarp, plus secondary auxiliary cells on each of two sterile periaxial cells	Directly on the supporting cell of the procarp	Directly on the supporting cell of the procarp	Directly on the supporting cell of the procarp, in some also a secondary auxiliary cell on a sterile periaxial cell[h]	Directly on the supporting cell of the procarp, in some also a secondary auxiliary cell on a sterile periaxial cell[i]	Directly on the supporting cell of the procarp
Multicellular fusion cell	Absent	Absent	Absent	Absent	Absent	Present in most tribes	Present
Carposporophyte investment	Two sterile involucral filaments arising on the supporting cell	A nonostiolate pericarp developed from the segments above and below the procarp	Numerous involucral filaments from cells below the supporting cell	Lacking altogether, composed of involucral filaments, or flanked by one or more adventitious laterals	Lacking altogether or composed of involucral filaments	Lacking altogether, composed of involucral filaments	An ostiolate pericarp developed from sterile pericentral cells
Cleavage pattern of sporangia	Decussate-cruciate or cruciate	Tetrahedral	Decussate-cruciate or cruciate	Decussate-cruciate, cruciate, or tetrahedral	Tetrahedral or polyhedral	Tetrahedral or polyhedral	Tetrahedral
Cover cells associated with tetrasporangial mother cells	Absent	Absent	Absent	Absent	Absent	Absent	Post- and/or presporangial cover cells present

[a] Multinucleate in *Perithamnion muelleri* (Womersley 1998).

[b] Multinucleate in *Callithamnion* spp. (Maggs and Hommersand 1993, Womersley 1998).

[c] Absent in some species of *Ceramium* (Womersley 1998).

[d] Present in *Ptilocladia australis*, *P. crouanioides*, and *P. vestita* (Womersley 1998).

[e] Present in *Muellerena wattsii* (Womersley 1998).

[f] The sterile cell group is absent in some *Wrangelia* spp. except the type species of the genus and one other species (Gordon 1972, Womersley 1998).

[g] The second sterile cell group is absent in some *Bostrychia* spp. (Maggs and Hommersand 1993), *Caloglossa leprieurii* (Papenfuss 1961), *Heterocladia australis* (Phillips et al. 2000), and *Nitophyllum punctatum* (Kylin 1956, Maggs and Hommersand 1993).

[h] Two auxiliary cells on two periaxial cells of a fertile axial cell in the Callithamnieae (Womersley 1998).

[i] The auxiliary cell is the supporting cell in *Radiathamnion*, and there are one or two auxiliary cells in the Monosporeae (Huisman and Gordon-Mills 1994, Huisman and Womersley 1998) and Sphondylothamnieae (Gordon 1972, Womersley 1998).

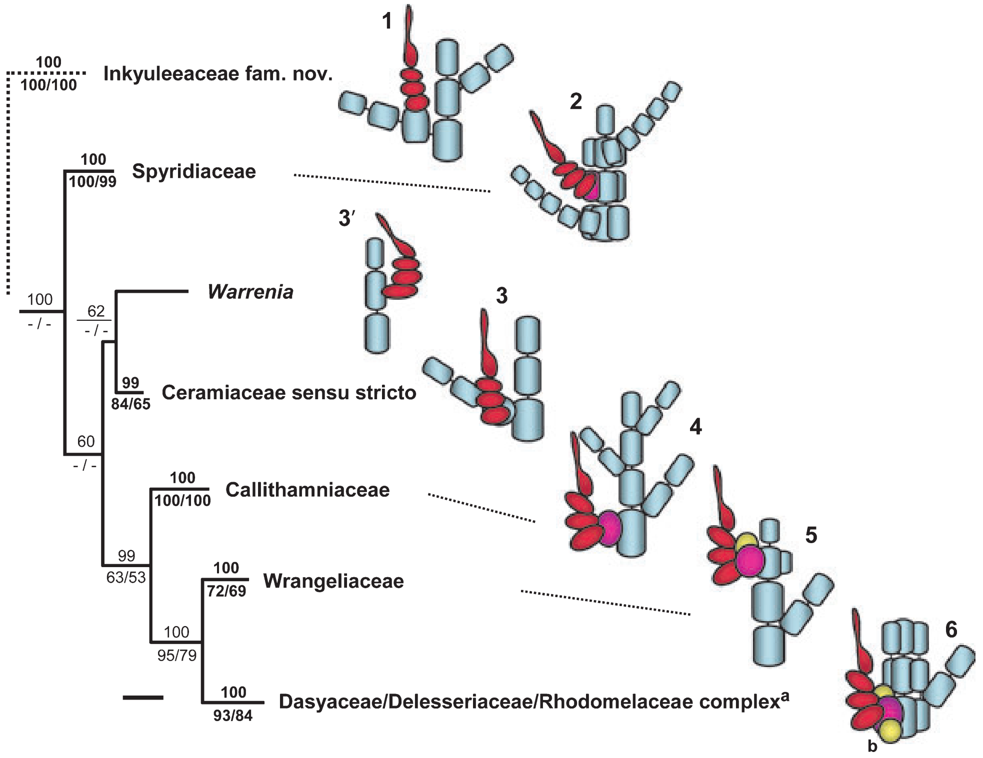

FIG. 2. Putative scenario of procarp evolution for the five major lineages of the Ceramiaceae and the DDRS (Dasyaceae, Delesseriaceae, Rhodomelaceae, and Sarcomeniaceae) complex mapped on the backbone structure of Figure 1. Dashed line represents the putative position for the Inkyuleeaceae. Blue = vegetative cells; red = carpogonial branch cells; pink = an accessory supporting cell; yellow = sterile cell group(s). (1) Procarp borne from the upper side of a basal cell on a determinate branch in *Inkyuleea* spp. (Wollaston 1971, Womersley 1998). (2) Procarp borne on a periaxial cell of an indeterminate lateral branch of restricted growth in the Spyridiaceae (Phillips 1924, Hommersand 1963, Womersley 1998). (3′) Procarp originated from any cell in a lateral branchlet or occasionally on a determinate or an indeterminate branch in *Warrenia* (Wollaston 1971, Womersley 1998). (3) Procarp borne from the lower side of a basal cell of a determinate whorl-branchlet or an indeterminate branch in the Ceramiaceae sensu stricto (Kylin 1956, Hommersand 1963, Womersley 1998, Athanasiadis 2002). (4) Procarp formed from a periaxial cell of a fertile axial cell, lacking a sterile cell on the supporting cell in the Callithamniaceae (Kylin 1956, Womersley 1998). (5) Procarp formed from a periaxial cell of a fertile axial cell, with one sterile cell group on the supporting cell in the Wrangeliaceae (Womersley 1998). (6) Procarp formed from a pericentral cell of a fertile axial cell, with two sterile cell groups on the supporting cell in the DDRS complex (Kylin 1956, Hommersand 1963, Choi 1996, Womersley 2003). [a]Sarcomeniaceae was recently segregated from the Rhodomelaceae (Womersley 2003) and is not included in our molecular analyses. [b]The second sterile cell group is absent in some *Bostrychia* spp. (Maggs and Hommersand 1993), *Caloglossa leprieurii* (Papenfuss 1961), *Heterocladia australis* (Phillips et al. 2000), and *Nitophyllum punctatum* (Kylin 1956, Maggs and Hommersand 1993).

or rarely tetrahedrally divided, borne on cells of normal or reduced whorl-branchlets.

Type genus: *Ceramium* Roth 1797, p. 146.

Comments: The tribes Antithamnieae, Ceramieae, Dohrnielleae, Heterothamnieae, and Pterothamnieae are members of the Ceramiaceae sensu stricto based on anatomical observations (Table 3; Kylin 1923, 1956, Hommersand 1963, Itono 1977, Womersley 1978, 1998, Maggs and Hommersand 1993, Athanasiadis 1996, 2002) and our molecular results (Fig. 1). Procarps in the Ceramiaceae sensu stricto almost always form on the first periaxial cell to be cut off from the central axial cell of the distal fertile axes (with the exception of *Reinboldiella*, where they can occur on any periaxial cell) and consist of the supporting cell and usually a terminal two- or three-celled sterile group that occupies the same position as would a vegetative lateral filament on the basal cell of an unmodified determinate branch (Hommersand 1963, p. 310), the sterile-group initial preceding the carpogonial-branch initial. In a genus like *Carpoblepharis*, the sterile group is several cells long and resembles an ordinary vegetative determinate lateral (Hommersand 1963). This condition seems not to be homologous to that displayed by members of the DDRS complex, in which the fertile pericentral cell is normally the last to be formed on an epibasal fertile-axial cell and the fertile axis extends into a deciduous monosiphonous trichoblast. The first sterile-group initial is cut longitudinally from the supporting cell prior to initiation of the carpogonial branch, followed some time afterward by a second sterile-group initial. We suggest that carpogonial branches borne abaxially on a basal cell of a normal or reduced whorl-branchlet unequivocally demonstrate a synapomorphy for the Ceramiaceae sensu stricto (Table 3 and Fig. 2).

5. **Callithamniaceae** Kützing (1843, p. 370 ''Callithamnieae'').

Plants uniaxial, usually erect, each axial cell bearing one to four whorl-branchlets or determinate branches. Gland cells normally absent. Cells uninucleate or rarely multinucleate. Gametophytes usually dioecious; spermatangia terminal on cells of the whorl-branchlets or spermatangial filaments on cells of the determinate lateral branchlets; carpogonial branches four-celled, abaxial on the lower lateral sides of either the basal cells (periaxial cells) of whorl-branchlets (most of the tribes) or on intercalary cells that represent the basal cells whorl-branchlets that are reduced to single-celled laterals (i.e., periaxial cells) in the Callithamnieae (Hommersand 1963, p. 313); procarps lacking a sterile-cell group; auxiliary cell cutting off multiple gonimolobes composed of synchronously developing carposporangia, cystocarps naked or involucrate. Putative meiosporangia tetrahedrally or rarely octahedrally divided, sessile on cells of the whorl-branchlets or determinate laterals.

Type genus: *Callithamnion* Lyngbye 1819, p. 123.

Comments: We here propose the reinstatement of the Callithamniaceae, a little-used family name since its introduction by Kützing (1843: 370, ''Callithamneae''). Our concept of the reinstated Callithamniaceae includes the tribes Callithamnieae, Crouanieae, Euptiloteae, and Rhodocallideae (Table 1) based on anatomical data (Table 3; Oltmanns 1922, Kylin 1923, 1956, Feldmann-Mazoyer 1940, Wollaston 1968, Hommersand 1963, Itono 1977, Maggs and Hommersand 1993, Athanasiadis 1996, Hommersand et al. 1998, Womersley 1998, Hommersand et al. 2005) and our molecular results (Fig. 1). The Australian-endemic *Diapse ptilota* and *Euptilota articulata*, which are generally assigned to the tribe Ptiloteae (Kylin 1956, Womersley 1998) based on vegetative anatomy, are here placed in the tribe Callithamnieae and Euptiloteae [recently proposed by Hommersand et al. (2005)] of the Callithamniaceae (Fig. 1), respectively, in line with Kylin's (1956: 390) drawing (fig. 307C) that shows no sterile cell on the supporting cell in *E. articulata*. We suggest that the combination of carpogonial branches borne abaxially on basal cells of whorl-branchlets or determinate branches (i.e., periaxial cells) and procarps lacking a sterile-cell group is synapomorphic for the Callithamniaceae (Table 3 and Fig. 2).

6. **Wrangeliaceae** J. Agardh (1851, p. x; 1852, p. 701 [*bis*] ''Ordo XIV. Wrangelieae'').

Plants usually erect, uniaxial. Each axial cell bearing one to six whorl-branchlets or determinate branches. Gland cells usually absent. Cells multinucleate or rarely uninucleate. Gametophytes usually dioecious; spermatangia surround distinct head-like clusters that are often pinnules of whorl-branchlets; procarps subapical, with 2–3 periaxial cells on the fertile-axial cell, one bearing an abaxial four-celled carpogonial branch, the supporting cell with or without a sterile cell. Diploidized auxiliary cell producing 2–5 gonimolobes of synchronously developing carposporangia, the carposporophytes naked or involucrate. Meiosporangia tetrahedrally divided or polysporangial, sessile or stalked on cells of the whorl-branchlets or determinate branches.

Type genus: *Wrangelia* C. Agardh, 1828, p. 136.

Comments: We here propose the reinstatment of the Wrangeliaceae, a little-used family name since its first introduction by J. Agardh (1851, p. x, ''Ordo XIV. Wrangelieae''; 1852, 701[*bis*] ''Ordo XIV Wrangelieae''). In accordance with Art. 18.2 of the ICBN, as detailed above under Spyridiaceae, ''Wrangelieae'' is treated as a family (see Silva 1980: 81, 88) and corrected to the modern family suffix. The reinstated Wrangeliaceae is here considered to include the genera of the tribes Compsothamnieae, Dasyphileae, Griffithsieae, Monosporeae, Ptiloteae, Spermothamnieae, Sphondylothamnieae, Spongoclonieae, and Wrangelieae (Table 1) based on anatomical data (Table 3; Kylin 1916, 1923, 1930, 1956, Feldmann-Mazoyer 1940, Gordon 1972, Baldock 1976, Itono 1977, Kim 1988, Gordon-Mills and Wollaston 1990, Maggs and Hommersand 1993, Huisman and Womersley 1998) and our molecular data (Fig. 1). *Ptilota hannafordii*, which has been tentatively classified in the Ptiloteae (Womersley 1998), represents an undescribed genus that is probably distinct at the tribal level from the Ptiloteae in the Wrangeliaceae (Womersley 1998, p. 361), but formal taxonomic proposals await a published account of the anatomy of this uncommon southern Australian-endemic species. The Wrangelieae has been variously classified in the Gelidiaceae or the Ceramiaceae (Schmitz 1889, Kylin 1956, Gordon 1972, Womersley 1998). Our results suggest that the tribe is closely related to the Griffithsieae (Fig. 1), although there is no bootstrap support for this association in distance and parsimony analyses. Kylin (1928, figs. 2, A–E) shows the procarp with a terminal sterile-cell group on the supporting cell of *Wrangelia penicillata* (C. Agardh) C. Agardh, the type species of the genus, as well as *W. abietina* Harvey (Gordon 1972, fig. 2, F and G, as *W. princeps* Harvey; Womersley 1998, fig. 4B). We suggest that carpogonial branches borne on a periaxial cell of the whorl-branchlets or determinate branches and procarps that display a sterile-cell group are synapomorphies for the Wrangeliaceae (Table 3). Our survey of female reproductive features in the Ceramiales (Fig. 2) indicates that procarps with a sterile-cell group(s) are a key feature allying the Wrangeliaceae with the DDRS complex.

CONCLUSION

In light of our molecular investigation and review of pertinent anatomical features for taxa traditionally included in the Ceramiaceae, we present a number of general observations and formal taxonomic proposals: (i) five strongly supported lineages, the Inkyuleeaceae fam. nov., Spyridiaceae, Ceramiaceae sensu stricto (tentatively including a single-taxon lineage for *Warrenia comosa*), a reinstated Callithamniaceae, and Wrangeliaceae are resolved; (ii) the Inkyuleeaceae fails to join the Ceramiales showing affinities to the Gracilariales and Plocamiales, although the relationships among these lineages were unresolved; (iii) the Spyridiaceae is only weakly resolved as sister to the remaining Ceramiales; (iv) *Warrenia* and the Ceramiaceae sensu stricto are weakly allied as sister lineages. The Warrenieae may warrant recognition at the family level and also contain the genera *Balliella* and *Plumariopsis*, but adequate molecular data for a sufficient number of related taxa are lacking, and we postpone formal taxonomic proposals; (v) the Callithamniaceae includes the tribes Callithamnieae, Crouanieae, Euptiloteae, and Rhodocallideae; and (vi) the Wrangeliaceae is unequivocally allied to the DDRS complex.

An important additional consequence of our results (and one that gives us great pleasure) is the support they give to the strong emphases on procarp structure advocated by Kylin, Hommersand, Gordon-Mills, Huisman, and others as key indicators of phylogenetic relationships and systematics for families of the Ceramiales and related orders (Fig. 2).

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Collection information for the samples used in this study.

Table S2. Source of additional SSU sequence data included in the multiple alignment.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1529-8817.2008.00554.x.

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