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SYSTEMATICS OF THE DELESSERIACEAE (CERAMIALES, RHODOPHYTA) BASED ON LARGE SUBUNIT rDNA AND *rbc*L SEQUENCES, INCLUDING THE PHYCODRYOIDEAE, SUBFAM. NOV.[1]

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The present classification of the Delesseriaceae retains the essential features of Kylin's system, which recognizes two subfamilies Delesserioideae and Nitophylloideae and a series of "groups" or tribes. In this study we test the Kylin system based on phylogenetic parsimony and distance analyses inferred from two molecular data sets and morphological evidence. A set of 72 delesseriacean and 7 additional taxa in the order Ceramiales was sequenced in the large subunit rDNA and *rbc*L analyses. Three large clades were identified in both the separate and combined data sets, one of which corresponds to the Delesserioideae, one to a narrowly circumscribed Nitophylloideae, and one to the Phycodryoideae, subfam. nov., comprising the remainder of the Nitophylloideae sensu Kylin. Two additional trees inferred from *rbc*L sequences are included to provide broader coverage of relationships among some Delesserioideae and Phycodryoideae. Belonging to the Delesserioideae are the Caloglosseae with *Caloglossa*; an expanded Hemineureae that includes *Hemineura*, *Patulophycus*, *Marionella*, *Laingia*, *Botryocarpa*, and *Pseudophycodrys*; the Delesserieae with *Delesseria* and *Membranoptera*; the Apoglosseae with *Apoglossum* and a group of southern hemisphere species presently placed in *Delesseria* that belong in *Paraglossum*; the Hypoglosseae with *Hypoglossum*, *Branchioglossum*, *Zellera*, and *Bartoniella*; and the Grinnellieae with *Grinnellia*. The revised Nitophylloideae contains the Nitophylleae with *Nitophyllum*, *Valeriemaya*, *Polyneuropsis*, and *Calonitophyllum* and the Martensieae with *Opephyllum* and *Martensia*. A new subfamily, Phycodryoideae, is proposed to include the Phycodryeae with *Phycodrys*, *Polyneura*, *Nienburgia*, *Cladodonta*, *Heterodoxia*, and *Womersleya*; the Cryptopleureae with *Cryptopleura*, *Hymenena*, *Acrosorium*, and *Botryoglossum*; the Myriogrammeae with *Myriogramme* and *Haraldiophyllum*; and the Schizoserideae with *Schizoseris*, *Neuroglossum*, *Drachiella*, *Abroteia*, and species from South America placed in *Platyclinia*. This research promotes the correlation of molecular and morphological phylogenies.

Key index words: **Ceramiales; Delesseriaceae; LSU rDNA; *rbc*L; Phycodryoideae subfam. nov.; Delesserioideae; Nitophylloideae; Rhodophyta; systematics; phylogeny**

Abbreviations: **LSU, large subunit**

The Delesseriaceae is a large family of nearly 100 genera found in intertidal and subtidal environments around the world. Kylin (1924) originally recognized 11 groups in the Delesseriaceae that he assigned to two subfamilies: Delesserioideae (as Delesserieae) and Nitophylloideae (as Nitophylleae) based on the location of the procarps (whether restricted to primary cell rows or scattered over the thallus surface), the presence or absence of midribs with rhizoidal filaments, and the presence or absence of intercalary cell divisions in the primary cell rows.

The Delesserioideae were further divided by Kylin into groups as follows: (1) intercalary cell divisions absent in all cell rows and all third-order cell rows reaching the blade margin (Hypoglossum group), (2) intercalary cell divisions absent in all cell rows but not all third-order cell rows reaching the blade margin (Membranoptera group), (3) intercalary cell divisions present in second- and higher order cell rows with the procarp consisting of one carpogonial branch (Delesseria group), (4) as above, but the procarp consisting of two carpogonial branches (Hemineura group), and (5) intercalary cell divisions present in second- and higher order cell rows with the procarps produced on minute bladelets immersed in the surface of the parent blade (Grinnellia group).

Groups in the Nitophylloideae were characterized as follows: (1) growth by means of a transversely dividing apical cell and midribs with downward coursing rhizoids (Pseudophycodrys group), (2) as above, but midribs lacking rhizoids (Phycodrys group), (3) as in *Phycodrys*, but branching from the midrib (Ruprechtiella group), (4) growth by marginal meristematic cells, microscopic veins present (Cryptopleura group), (5) growth by marginal meristematic cells, microscopic veins absent (Myriogramme group), and (6) as above,

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but the procarp with only one sterile group (Nitophyllum group).

Taxonomic concepts used in the current classification of the Delesseriaceae have changed little since the first proposals by Kylin (1924). Kylin (1956) added the Sarcomenia group, the Claudea group, the Botryocarpa group, the Papenfussia group, and the Martensia group and renamed the Ruprechtiella group as the Yendonia group based on a suite of vegetative characters and procarp architecture. To these Wynne (1983) added four additional groups to the Delesserioideae: the Congregatocarpus group with intercalary divisions in primary cell rows and three sympodially branched groups, the Sympodophyllum group with intercalary divisions absent, the Cumathamnion group with intercalary cell divisions present only in second-order cell rows, and the Kurogia group with intercalary cell divisions also present in first-order cell rows. The Yendonia group was merged with the Phycodrys group. Wynne (1996) published a revised key to genera of Delesseriaceae together with a list of the genera, type species, and recent references and added the Valeriemaya group (Millar and Wynne 1992) to the subfamily Nitophylloideae based on the presence of a persistent apical cell. Three tribes have been proposed or emended since 1996: the Dicroglosseae (Millar and Huisman 1996), the Myriogrammeae (Hommersand and Fredericq 1997a), and the Schizoserideae (Hommersand and Fredericq 1997b) (Table 1). Recently, Wynne (2001) extended formal recognition at the tribal level to all 23 groups and tribes presently identified in the Delesseriaceae.

A main goal of this study was to test the Kylin (1956) and Wynne (1996, 2001) systems (Table 1) and to evaluate phylogenetic relationships at subfamilial, tribal, and generic levels based on large subunit (LSU) rDNA and *rbc*L molecular data sets and a reassessment of the morphological evidence.

MATERIALS AND METHODS

Algal samples used in molecular studies were desiccated in silica gel, air dried, or preserved in 95% alcohol in the field. Voucher specimens and materials for morphological studies were fixed in 10% formalin/seawater for at least 24 h or longer and stored in 5% formalin/seawater or pressed as herbarium sheets and deposited in the Herbarium of the University of Louisiana at Lafayette and/or the Herbarium of the University of North Carolina at Chapel Hill. Whole-mount slides and cross-sections were treated with Wittmann's aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted in 50% Hoyer's mounting medium (Stevens 1981) or placed in an alcohol/xylene series after staining and mounted in Piccolyte (Wards Natural Science Establishment, Inc., Rochester, NY), which clears the tissues and reveals the internal structures (Lin et al. 2001). Silica gel-dried specimens and extracted DNA samples were deposited in the Seaweed Laboratory at the University of Louisiana at Lafayette and stored at −20° C. Herbarium abbreviations follow those of Holmgren et al. (1990). Photomicrographs (Fig. 6, A–I) were taken on an Olympus BX60 microscope (Olympus, Melville, NY) with a Polaroid DMC Ie digital camera (Polaroid, Inc., Cambridge, MA). Digital images were edited and assembled in plates using Photoshop v.4.0. Photographic plates were printed on an Epson Stylus Color 900 inkjet printer (Epson, Tokyo, Japan). Genera of Delesseriaceae sequenced in this study are listed in Table 1, third column. Vouchers extracted for DNA analysis include all taxa sequenced in this study, which are listed in Table 2, together with their GenBank accession numbers.

DNA samples were prepared using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA) or were submitted to a hexadecyltrimethylammonium bromide (CTAB)-cesium chloride DNA procedure (Freshwater et al. 1994). The addition of 0.5×10^{-3} to 1×10^{-3} mg of proteinase K to each extraction when grinding the samples using the Qiagen Minikit often improved the DNA yield (Hughey and Hommersand 1999).

The genes selected to infer the phylogeny of the Delesseriaceae are chloroplast- encoded *rbc*L and the nuclear-encoded LSU rDNA gene. The *rbc*L primers used in this study are as listed in Freshwater and Rueness (1994) and Hommersand et al. (1994), and the LSU rDNA primers used in this study are listed in Freshwater et al. (1999). The entire *rbc*L-coding region was sequenced except the first 84 base pairs, whereas the first 300 base pairs and the last 1200 base pairs of the LSU rDNA-coding region were not sequenced due to lack of informative signal. Additional internal sequencing primers designed specifically for the Delesseriaceae include

LSU-F449 (5′-CCCGAAAGA TGGTGAACTATG-3′)
LSU-R831 (5′-GAATGCCAAGTA GGGCATAGC-3′)
*rbc*L-F64 (5′-CCATATGCAAAAATGGGATAC-3′)
*rbc*L-F645 (5′-ATGCGTTGG AAAGAAAGATTCT-3′).

For gene amplification, 2 μL of the resulting extractions were used as templates for a 50-μL PCR consisting of 10 μL 5 M betaine, 6 μL 10μ PCR buffer (Perkin Elmer Corp., Foster City, CA), 6 μL 25 mM $MgCl_2$ solution, 8 μL of 500 mM dNTP stock, 2 μL each of the appropriate primers at 10 mM, and 0.3–0.5 μL Amplitaq DNA Polymerase (PE Applied Biosystems, Foster City, CA). Amplification conditions for both *rbc*L and LSU rDNA consisted of 4 min at 96° C for denaturation, followed by 35 cycles of 60 s at 94° C, 60 s at either 45° C or 42° C, and 90 s at 72° C, with a final 8-min extension cycle at 72° C, and soak cycle at 4–12° C. The amplification reactions were performed on a PE GeneAmp PCR system 9700 or 2400 (PE Applied Biosystems). Some PCR amplifications that initially failed were successfully amplified under one-half volume conditions by doubling Amplitaq DNA Polymerase or by increasing the PCR to 42–45 cycles.

For automated gene sequencing, amplification products were cleaned of excess primer, enzyme, and dNTPs by PEG precipitation (Hillis et al. 1996). The sequences were determined over both strands using an ABI Prism 310 Genetic Analyzer (PE Applied Biosystems) with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems). Reaction mixtures comprised 4 μL Terminator Ready reaction mix with 4 μL X buffer or 8 μL Terminator Ready reaction mix, 1–2 μL template, 3.2 pmol primer, and deionized water as needed up to a total volume of 20 μL. The cycle sequencing reactions were performed on a PE GeneAmp PCR system 9700 or 2400 for 25 cycles (96° C for 10 s, rapid thermal ramp to 50° C, 50° C for 5 s, rapid thermal ramp to 60° C, 60° C for 4 min, rapid thermal ramp to 4° C). Resulting products were then purified using Centri-Sep spin columns (P/N CS-901, Princeton Separations, Adelphie, NJ) following the manufacturer's instructions.

The generated sequence data were compiled and aligned with Sequencher (Gene Codes Corp., Ann Arbor, MI) and exported for phylogenetic analysis. The *rbc*L data set was aligned manually, whereas the LSU rDNA data set alignment was done first by using the online program ClustalW 1.8 (http://dot.imgen.bcm.tmc.edu:9331/multi-align/multi-align.html), and then this alignment was revised manually. The alignments are available at GenBank. Phylogenetic analyses of the *rbc*L, LSU rDNA, and concatenated LSU rDNA + *rbc*L sequence data were performed using the neighbor-joining program with Kimura 2-parameter distances and maximum parsimony algorithms available in the computer program PAUP (v.4.0b4a*, Swofford 2000). Gaps were treated as a "fifth" base. Missing data and gaps were excluded from pairwise comparisons in these analyses. Initial searches consisted of 100 random sequence additions, MULPARS (but hold-

TABLE 1. List of subfamilies, tribes, and genera of the Delesseriaceae according to Kylin (1956), Wynne (2001), and this article.

Kylin (1956)	Wynne (2001)	This article
Delesserioideae	Delesserioideae	Delesserioideae
Sarcomenia Gruppe	Sarcomenieae	Sarcomenieae
Sarcomenia, *Taenioma*, *Cottoniella*, *Platysiphonia*, *Sonderella*	*Sarcomenia*, *Cottoniella*, *Dotyella*, *Sarcotrichia*, *Malaconema*	*Sarcomenia*
Caloglossa Gruppe	Caloglosseae	Caloglosseae
Caloglossa	*Caloglossa*, *Taenioma*	*Caloglossa*
Claudea Gruppe	Claudeeae	Claudea group
Claudea, *Vanvoorstia*, *Implicaria*	*Claudea*, *Vanoorstia*	*Vanoorstia?*
		Apoglosseae
		Apoglossum, *Paraglossum*,
Hemineura Gruppe	Hemineureae	Hemineureae
Hemineura	*Hemineura*	*Hemineura*, *Patulophycus*, *Marionella*, *Laingia*, *Botryocarpa*, *Pseudophycodrys*
	Dicroglosseae	
	Dicroglossum	
Hypoglossum Gruppe	Hypoglosseae	Hypoglosseae
Hypoglossum, *Branchioglossum*, *Bartoniella*, *Vanassella*, *Phitymophora*, *Botryocarpa*, *Laingia*	*Hypoglossum*, *Zellera*, *Branchioglossum*, *Pseudogranchioglossum*, *Frikkiella*, *Yoshidaphycus*, *Tsengiella*, *Duckerella*, *Bartoniella*, *Phitymophora*, *Phitycolax*, *Chauviniella*	*Hypoglossum*, *Zellera*, *Bartoniella*, *Branchioglossum*
Membranoptera Gruppe	Membranoptereae	(Delesserieae)
Membranoptera, *Pantoneura*, *Cyclospora*, *Microrhinus*, *Holmesia*	*Membranoptera*, *Pantoneura*, *Holmesia*, *Neoholmesia*, *Austrofolium*	
Delesseria Gruppe	Delesserieae	Delesserieae
Delesseria, *Pseudolaingia*	*Delesseria*, *Apoglossum*, *Odontolaingia*, *Pseudolaingia*, *Phycodrina*, *Microrhinus*, *Heteroglossum*, *Marionella*, *Laingia*, *Patulophycus*, *Pseudogrinnellia*, *Apoglossocolax*	*Delesseria*, *Membranoptera*
	Congregatocarpeae	
	Congregatocarpus, *Tokidadendron*, *Neohypophyllum*	
	Zinovaeeae	
	Zinovaea, *Kurogia*	
	Botryocarpeae	(Hemineureae)
	Botryocarpa	
	Sympodophylleae	
	Sympodophyllum	
	Cumathamnieae	
	Cumathamnion	
Grinnellia Gruppe	Grinnellieae	Grinnellieae
Grinnellia	*Grinnellia*	*Grinnellia*
Nitophylleae	Nitophylloideae	Phycodryoideae
Pseudophycodrys Gruppe	Pseudophycodryeae	(Hemineureae)
Pseudophycodrys	*Pseudophycodrys*, *Pseudonitophylla*	
Phycodrys Gruppe	Phycodryeae	Phycodryeae
Phycodrys, *Haraldia*, *Erythroglossum*, *Calloseris*, *Sorella*, *Rhizoglossum*, *Polyneura*, *Polyneurella*, *Halicnide*, *Heterodoxia*, *Anisocladella*, *Cladodonta*, *Nienburgia*, *Pachyglossum*, *Chondrophyllum*	*Phycodrys*, *Haraldia*, *Calloseris*, *Halicnide*, *Heterodoxia*, *Anisocladella*, *Sorella*, *Erythroglossum*, *Polyneura*, *Mikamiella*, *Yendonia*, *Cladodonta*, *Nienburgia*, *Nienburgella*, *Womersleya*, *Crassilingua*, *Asterocolax*, *Sorellocolax*	*Phycodrys*, *Polyneura*, *Cladodonta*, *Nienburgia*, *Heterodoxia*, *Womersleya*
Yendonia Gruppe		
Yendonia, *Hypophyllum*		
Myriogramme Gruppe	Myriogrammeae	Myriogrammeae
Myriogramme, *Abroteia*, *Schizoseris*, *Platyclinia*, *Neuroglossum*, *Gonimocolax*, *Polycoryne*	*Myriogramme*, *Haraldiophyllum*, *Hideophyllum*, *Platyclinia*, *Gonimocolax*	*Myriogramme*, *Haraldiophyllum*
	Schizoserideae	Schizoserideae
	Schizoseris, *Drachiella*, *Neuroglossum*, *Abroteia*, *Polycoryne*	*Schizoseris*, *Neuroglossum*, *Drachiella*, *Abroteia*
Cryptopleura Gruppe	Cryptopleureae	Cryptopleureae
Cryptopleura, *Acrosorium*, *Hymenena*, *Botryoglossum*, *Gonimophyllum*, *Rhodoseris*	*Cryptopleura*, *Acrosorium*, *Hymenena*, *Botryoglossum*, *Gonimophyllum*	*Cryptopleura*, *Acrosorium*, *Hymenena*, *Botryoglossum*

(continued)

Table 1. Continued

Kylin (1956)	Wynne (2001)	This article
		Nitophylloideae
Nitophyllum Gruppe *Nitophyllum*	Nitophylleae *Nitophyllum*, *Arachnophyllum*	Nitophylleae *Nitophyllum*, *Polyneuropsis*, *Calonitophyllum*, *Valeriemaya*
Papenfussia Gruppe *Papenfussia*	Papenfussieae *Papenfussia*	
	Valeriemayaeae *Valeriemaya*, *Polyneuropsis*, *Polyneurella*, *Calonitophyllum*, *Radicilingua*	(Nitophylleae)
Martensia Gruppe *Martensia*, *Opephyllum*	Martensieae *Martensia*, *Opephyllum*, *Neomartensia*	Martensieae *Martensia*, *Opephyllum*

ing five trees at each step), STEEPEST DESCENT, and nearest neighbor interchange branch swapping trees leading to most parsimonious solution (Maddison 1991). Trees found in these initial searches were then used as starting points for further searches with MULPARS, STEEPEST DESCENT, and tree bisection reconnection algorithm until final swapping was complete. The searches were done on each data set under the criterion of equal weights for all substitutions; from previous experience with character weighting, unequal weighting of nucleotide characters and different transition/transversion ratios did not significantly alter tree topology. Consistency and retention indices (Farris 1989, Kluge and Farris 1989) were calculated excluding uninformative characters. Support for nodes in the neighbor-joining trees was determined by calculating bootstrap proportion values (Felsenstein 1985) based on 1000 resamplings of neighbor-joining searches done with Kimura 2-parameter distances. Support for nodes of parsimony trees was assessed by calculating 200 bootstrap resamplings of the heuristic searches based on random stepwise additions, MULPARS, and tree bisection reconnection. Constraint analyses (Swofford 2000, Maddison 1991) were performed to force the topology of the *rbc*L data set to match the topology of the LSU rDNA data set.

The range of *rbc*L and LSU rDNA divergence values (%) for species within and among clades of Figs. 2 and 3 have been calculated. Mutational saturation of third codon positions in *rbc*L was examined by plotting all pairwise substitutions uncorrected for multiple substitutions against those corrected for multiple substitutions ("uncorrected p" and Kimura-2-parameter model; options available in PAUP* v.4, Swofford 2000) according to the procedure in Daugbjerg and Andersen (1997). For all pairwise combinations, values corrected and uncorrected for multiple substitutions were calculated for first/second positions only and third codon positions only.

RESULTS

LSU rDNA and *rbc*L sequences were generated from 72 taxa in the red algal family Delesseriaceae, and 7 taxa in the order Ceramiales was selected in the global LSU rDNA and *rbc*L analyses using the Ceramiaceae as the outgroup (Figs. 1–3). Additionally, two restricted data sets comprising 13 additional taxa were analyzed based on *rbc*L data, one containing 13 species of Delesserioideae and one containing 24 species of Phycodryoideae with two species of *Nitophyllum* serving as outgroup taxa (Figs. 4 and 5).

The LSU rDNA alignment included 1742 sites. A large number of insertions/deletions (indels) were required in the data set to align the 5′ and 3′ ends of these sequences, and due to questionable homology of sites in these areas they were not included in analyses. Additionally, sites where two large indels are required for alignment of interior portions of the sequences were excluded so that the final data matrix included 1267 total and 622 parsimony informative sites (49%). The *rbc*L alignment consisted of 1467 sites, but because information was missing for the 5′ ends of many sequences the first 84 sites were excluded from the analyses. The analyzed data matrix included 1383 total and 567 parsimony informative sites (41%). The almost linear relationship for first and second codon *rbc*L positions suggests that these positions are not mutationally saturated, whereas the nonlinear relationship (curves slightly to the right) for third codon positions strongly suggests that multiple substitutions occur at the site. Combining the LSU rDNA and *rbc*L alignments produced a third data set. Following the same exclusion criteria as used in the separate data sets below, this matrix included 2650 total and 1189 parsimony informative sites (45%). Tree lengths of 100,000 randomly generated trees from all data sets had a skewed distribution (g_1 at least less than -0.3733, $P < 0.01$, for all data sets) indicating the presence of nonrandom structure (Hillis and Huelsenbeck 1992).

Parsimony analyses obtained from heuristic searches of 1) the combined LSU rDNA + *rbc*L, 2) LSU rDNA, and 3) *rbc*L alignments are presented in three phylogenetic trees (Figs. 1–3). Parsimony analyses of the combined LSU rDNA + *rbc*L data set resulted in two equally minimal length trees, one of which is shown in Figure 1. Parsimony analyses of the LSU rDNA data set resulted in 42 equally minimal length trees, one of which is shown in Figure 2. Parsimony analyses of the *rbc*L data set resulted in a single-most parsimonious tree (Fig. 3). Constraining the *rbc*L topology to fit that of the LSU rDNA analysis required 23 additional steps (<0.5%). These results are discussed together, listing bootstrap values from analyses of the three trees in the sequences LSU rDNA + *rbc*L (Fig. 1)/LSU rDNA (Fig. 2)/*rbc*L (Fig. 3). Although distance trees are not presented, they were congruent with the parsimony trees. Distance bootstrap values have been included on the parsimony trees.

A group containing the morphologically more complex families of the Ceramiales, namely, Rhodomelaceae, Dasyaceae, and Delesseriaceae received strong support (100/100/83) in searches in which selected species of Ceramiaceae were chosen as outgroup taxa. Spe-

TABLE 2. List of species, their collection information, and the *rbc*L† and LSU rDNA‡ GenBank accession numbers followed by the fraction (in %) sequenced

Species	Collection information	Accession number
Ceramiaceae		
Centroceras clavulatum (C. Agardh) Montagne	Redfish Bay, Port Aransas, Texas, USA; coll. S. Fredericq and F. Gurgel, 18.v.98.	†AF259490, 97% ‡AF259414, 100%
Ceramium brevizonatum v. *caraibicum* H. Petersen and Børgesen in Børgesen	Yucatan, Mexico; coll. F. Gurgel, 13.ii.98.	†AF259490, 97%; ‡AF259415, 82%
Euptilota formosissima (Montagne) Kützing	Mataikora, Wairarape, New Zealand; coll. W. Nelson, 25.iii.94.	†AF259490, 99%; ‡AF259428, 100%
Dasyaceae		
Dasya baillouviana (S. Gmelin) Montagne	North Carolina, USA; coll. W. Freshwater; 4.ii.93.	†AF259493, 76%; ‡AF259424, 83%
Heterosiphonia plumosa (Ellis) Batters	Penmarch, Brittany, France; coll. M. Hommersand, 20.vi.93.	†AF259494, 93% ‡AF259432, 100%
Rhodomelaceae		
Bostrychia radicans (Montagne) Montagne	St. Louis Bay, Mississippi, USA; coll. F. Gurgel, 11.ii.98.	†AF259497, 90%; ‡AF259407, 99%
Cladhymenia lyalli Harvey	Lyall Bay, New Zealand; coll. W. Nelson, 21.iv.94.	†AF259496, 75%; ‡AF259417, 88%
Delesseriaceae		
Abroteia orbicularis J. Agardh	Kaikoura, New Zealand; coll. W. Nelson, 18.x.97.	†AF254149, 98%; ‡AF259402, 100%
Abroteia sp.	Kaikoura, New Zealand; coll. W. Nelson, 18.x.97.	†AF254150, 97%; ‡AF259403, 100%
Acrosorium decumbens (J Agardh) Kylin	Ringaringa, Stewart Island, New Zealand; coll. W. Nelson, 9.x.98.	†AF254151, 94%; ‡AF259404, 100%
Acrosorium venulosum (Zanardini) Kylin	Martin's Haven, Wales, United Kingdom; coll. K. Lock and S. Gilbert, 23.vii.97.	†AF254156, 95%; ‡AF259405, 100%
Apoglossum ruscifolium (Turner) J. Agardh	Receira das Ilhas near Ericeira, Distr. Lisboa, Portugal; coll. F. and M. Hommersand, 7.iv.2000.	†AF312310, 98%; ‡AF312312, 87%
Bartoniella crenata (J Agardh ex Mazza) Kylin	Ker Mouth, South Africa; coll. O. De Clerck, 23.x.99.	†AF254158, 93%; ‡AF259406, 88%
Botryocarpa prolifera Greville	Llondudno, South Africa; coll. O. De Clerck, xi.99.	†AF254159, 94%
Botryoglossum platycarpum (Turner) Kützing	Yzerfontein, South Africa; coll. O. De Clerck, 24.xi.99.	†AF254160, 98% ‡AF259408, 100%
Branchioglossum woodii (J Agardh) Kylin	Culture collection, Mexico; coll. J. West	†AF254161, 98%; ‡AF259409, 67%
Caloglossa becarrii (Zanardini) De Toni	Pédro Miquel Locks, Pédro Miquel city, #00421, Panama; coll. B. Wysor, 12.v.99.	†AF254162, 91%; ‡AF259410, 100%
Caloglossa leprieurii (Montagne) G. Martens	Culture coll., Carolina Biological Supply Co., Georgia, USA	†AF254164, 98%; ‡AF259412, 100%
Caloglossa stipitata Post	Fort Rodman, Panama, Panama Bay, Pacific side, #01002, Panama; coll. B. Wysor, 12.ix.99.	†AF254165, 91%; ‡AF259411, 80%
Calonitophyllum medium (Hoyt) Aregood	Radio Island, Bogue sound, Carteret Co., North Carolina, USA; coll. M. Deals, 24.iv.94.	†AF254167, 97%; ‡AF259413, 100%
Cladodonta lyallii (Hooker f. et Harvey) Skottsberg	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S.-M. Lin and S. Fredericq, 4.i.98.	†AF257169, 94%
Claudea batanensis Tanaka	Dapdake, Bulusan, Luzon, Philippines; coll. S.-M. Lin, 22.iv.98.	†AF254171, 90%; ‡AF259418, 81%
Cryptopleura callophylloides (J Agardh) Wynne	8 miles of Swakopmund, Namibia; coll. F. and M. Hommersand, 7.vii.93.	†AF254172, 96%; ‡AF259419, 59%
Cryptopleura ramosa (Hudson) Kylin and Newton	West Angle Bay, Pembrokeshire, Wales, United Kingdom; coll. F. and M. Hommersand, 22.vii.97.	†AF254175, 96%; ‡AF259420, 100%
Cryptopleura lobulifera (J Agardh) Kylin	Punta Santo Tomas (below Ensenada), Baja California, Mexico; coll. F. and M. Hommersand, 2.vii.96.	†AF254176, 99%; ‡AF259421, 82%
Cryptopleura ruprechtiana (J Agardh) Kylin	Cattle Point, San Juan Island, Friday Harbor, Washington, USA; coll. B. Wysor, 20.vi.98.	†AF254179, 98%; ‡AF259422, 100%
Delesseria decipiens J. Agardh	Sunset Bay, Cape Arago, Charleston, Oregon, USA; coll. B. Wysor, 12.vi.98.	†AF254181, 94%; ‡AF259425, 82%
Delesseria sanguinea (Hudson) Lamouroux	Newcastle, Co. Down, N. Ireland, United Kingdom; coll. C. Maggs, 15.iii.99.	†AF254182, 86%; ‡AF259426, 68%
"*Delesseria*" *crassinervia* Montagne	Ringaringa, South Island, New Zealand; coll. W. Nelson, 6.x.94.	†AF257409, 98%; ‡AF259462, 99%
"*Delesseria*" *epiglossum* J. Agardh	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 4.i.98.	†AF257410, 99%; ‡AF259464, 100%
"*Delesseria*" *fuegiensis* Skottsberg	Sealion Island, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 8.i.98.	†AF257412, 99%; ‡AF259466, 100%
"*Delesseria*" *lancifolia* (J.D. Jooker) J. Agardh	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. M. Hommersand, 28.xii.97.	†AF257413, 98%; ‡AF259465, 100%

(continued)

TABLE 2. CONTINUED

Species	Collection information	Accession number
"*Delesseria*" sp.	Punta Peñon, Bahia Fildes, King George I., S. Shetland Isls., Antarctic Peninsula; coll. S. Fredericq and J. Rodríguez, 9.ii.94.	†AF257418, 98%; ‡AF259467, 100%
Drachiella spectabilis Ernst and Feldmann	Martin's Haven, Wales, United Kingdom; coll. K. Lock and S. Gilbert, 23.vii.97.	†AF254183, 93%; ‡AF259427, 100%
Drachiella sp.	Little Santa Cruz Is., Zamboanga City, Philippines; coll. S.-M. Lin, 28.iv.98.	†AF257448, 98%; ‡AF259480, 92%
Grinnellia americana Martens	Jetty, Radio I. Carteret Co., North Carolina, USA; coll. M. Deals, 23.iv.94.	†AF254184, 92%; ‡AF259429, 100%
Haraldiophyllum sp.	La Herradura, Coquimbo, Chile; coll. S. Fredericq, 19.i.95.	†AF254188, 96%; ‡AF259430, 100%
Haraldiophyllum bonnemaisonii (Kylin) Zinova	Near Fanad Head, Co. Donegal, United Kingdom; coll. C. Maggs. 21.v.2000.	†AF312311, 98%; ‡AF312313, 93%
Haraldiophyllum mirabile (Kylin) Zinova	Canove Island, San Juan Islands, Washington, USA; coll. B. Wysor, 29.vi.98.	†AF254185, 84%; ‡AF312314, 90%
"*Hemineura*" *cruenta* Harvey	D1, Vailavae, New Zealand; coll. W. Nelson, 24.xi.94.	†AF257453, 98%; ‡AF259486, 100%
Hemineura frondosa (Hooker et Harvey) Harvey	W. Port MacDonnell, Victoria, Australia; coll. F. and M. Hommersand, 28.viii.95.	†AF254189, 93%; ‡AF259431, 81%
Heterodoxia denticulata (Kuntze) J. Agardh	Warrnambool, Victoria, Australia; coll. F. and M. Hommersand 12.xi.95.	†AF254190, 89%
Hymenena curdieana (Harvey) Kylin	Warrnambool, Victoria, Australia; coll. F. and M. Hommersand 13.vii.95.	†AF254425, 98%; ‡AF259434, 100%
Hymenana falklandica Kylin	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 5.i.98.	†AF254426, 98%; ‡AF259435, 100%
Hymenena flabelligera (J. Agardh) Kylin	Goose Is., NE of Cattle Point, San Juan I., Friday Habor, Washington, USA; coll. B. Wysor, 25.vi.98.	†AF254431, 98%; ‡AF259437, 100%
Hymenena venosa (Linnaeus) Krauss	Llandudmo, South Africa; coll. O. De Clerck, xi.99.	†AF257365, 98%; ‡AF259438, 100%
Hypoglossum hypoglossoides (Stackhouse) Collins and Hervey	Wemeldinge, Zeeland, The Netherlands; coll. F. and M. Hommersand, 7.viii.97.	†AF257368, 99%; ‡AF259439, 69%
Hypoglossum sp.	West Angle Bay, Pembrokeshire, Wales, United Kingdom; coll. F. and M. Hommersand, 22.vii.97.	†AF257369, 94%; ‡AF259440, 70%
Laingia hookeri (Lyall ex Harvey) Kylin	Aramoana, Otago, New Zealand; coll. W. Nelson, 29.iii.94.	†AF257371, 94%; ‡AF259441, 100%
Marionella prolifera (Kylin) Wagner	Whaririki Beach, Northwest Nelson, South I., New Zealand; coll. W. Nelson, 28.ix.96.	†AF257373, 55%
Martensia australis Harvey.	Little Santa Cruz Is., Zamboanga City, Philippines; coll. S.-M. Lin, 28.iv.98.	†AF257374, 94%; ‡AF259446, 100%
Martensia elegans Hering	Palm Beach, Natal Province, South Africa; coll. F. and M. Hommersand, 23.vii.93.	†AF257375, 98%; ‡AF259447, 100%
Martensia fragilis Harvey	Yu-liu, Taipei Co., Taiwan; coll. S. Fredericq and S.-M. Lin, 7.vii.94.	†AF257378, 81%; ‡AF259449, 99%
Martensia fragilis Harvey	Chiraman's Hat, Kameohe' Bay, Oahu, Hawaii, USA; coll. K. Cole, 29.v.98.	†AF257377, 85%; ‡AF259448, 99%
Martensia pavonia (C. Agardh) J. Agardh	Cayos Zapatilla, Bocas del Toro, Caribbean Sea, Panama; coll. B. Wysor, 21.x.99.	†AF257379, 91%; ‡AF259451, 77%
Martensia sp. 1.	Tambuli, Cebu, Philippines; coll. S.-M. Lin, 18.iv.98.	†AF257380, 80%; ‡AF259445, 99%
Martensia sp. 2.	Little Santa Cruz Is., Zamboanga City, Philippines; coll. S.-M. Lin, 28.iv.98.	†AF257382, 99%; ‡AF259452, 100%
Membranoptera tenuis Kylin	Auke Bay, Alaska, USA; coll. S. Linstrom, 4.iv.98.	†AF257383, 94%; ‡AF259453, 88%
Membranoptera weeksiae Setchell et Gardner in Gardner	Boiler Bay, Oregon, USA; coll. S. Fredericq, 17.vi.99.	†AF257384, 99%; ‡AF259454, 90%
Myriogramme livida (Hooker et Harvey) Kylin	Sealion Island, Falkland Islands; coll. S. Fredericq and S.-M. Lin, 7.i.98.	†AF257391, 95%; ‡AF259443, 100%
Myriogramme manginii (Gain) Skottsberg	Bahia Elefante, Base Frei, King George I., S. Shetland Isls., Antarctic Peninsula; coll. S. Fredericq and M. Ramírez, 5.ii.94.	†AF257392, 93%; ‡AF259455, 100%
"*Myriogramme*" *multinervis* (Hooker et Harvey) Kylin	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 5.i.98.	†AF257451, 98%; ‡AF259483, 100%
"*Neomartensia*" *flabelliformis* (Harvey ex J. Agardh) Yoshida et Mikami	Wan Li Dong, Kenting National Park, Pingtung Co., Taiwan; coll. S.-M. Lin and M.-L. Qiu, 23.xii.96.	†AF257376, 80%; ‡AF259450, 60%
Neuroglossum binderianum Kützing	Grossbucht, Luderitz, Namibia; coll. F. and M. Hommersand, 9.vii.93.	†AF257394, 98%; ‡AF259456, 100%
Nienburgia andersoniana (J. Agardh) Kylin	Horseshoe Cove, Bodega Bay, CA, USA; coll. F. and M. Hommersand, 19.i.93.	†AF254396, 97%

(continued)

TABLE 2. CONTINUED

Species	Collection information	Accession number
Nienburgia borealis (Kylin) Kylin	Mosquito Bay, between Harvey Is. and San Juan Is., Washington, WA, USA; coll. B. Wysor, 2.vii.98.	†AF254398, 48%
Nitophyllum delicatum Millar	Jervis Bay, New South Wales, Australia; coll. A. Millar and D. Hardin, 24.x.95.	†AF257400, 97%; ‡AF259457, 94%
Nitophyllum punctatum (Stackhouse) Greville	Asturias, Spain; coll. C. Maggs, 5.iii.99.	†AF257402, 97%; ‡AF259459, 95%
Nitophyllum sp. 1.	Galeta (STRI-research station), Colon, Caribbean Sea, Panama; coll. B. Wysor, 2.ix.99.	†AF257405, 97%; ‡AF259460, 59%
Nitophyllum sp.2.	Wan Li Dong, Kenting National Park, Pingtung co., Taiwan; coll. S.-M. Lin and M.-L. Qiu, 23.xii.96.	†AF257401, 54%; ‡AF259458, 100%
Opephyllum martensii Schmitx In Schmitz and Hauptfleisch	La Vista Del Mar, Upper Calarian, Zamboanga, Philippines; coll. S.-M. Lin, 1.v.98.	†AF257407, 93%; ‡AF259461, 100%
Patulophycus eclipes Millar et Mynne	The Docks, Jervis Bay, New South Wales, Australia; coll. A. Millar and D. Hardin, 25.x.95.	†AF257419, 93%
Phycodrys quercifolia (Bory) Skottsberg	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 4.i.98.	†AF257424, 98%; ‡AF259469, 100%
Phycodrys quercifolia (Bory) Skottsberg	South Bay, Kaikoura, New Zealand; coll. w. Nelson, 18.x.97.	†AF257426, 49%
Phycodrys ovifolia (Kützing) Wynne	Isla Mancerra, Bahia coral, Prov. Valdivia, Chile; coll. F. and M. Hommersand, 11.i.95.	†AF257423, 94%
Phycodrys radicosa (Okamura) Yamada et Inagaki in Yamada	Gingdao, Shuntung Peninsula, China; coll. F. and M. Hommersand, 23.vi.94.	†AF257427, 98%
Phycodrys rubens (Linnaeus) Batters	West Angle Bay, Pembrokeshire, United Kingdom; coll. F. and M. Hommersand, 22.vii.97.	†AF257429, 95%; ‡AF259470, 100%
Phycodrys rubens (Linnaeus) Batters	Mouth of the Hvammsfiord, west Iceland, Iceland; coll. A. Coleman, 23.viii.99.	†AF257428, 92%
Phycodrys riggii Gardner	Kittilngook Bay, St. Lawrence Island, Alaska, USA; coll. S. Lindstrom, 5.viii.96.	†AF257430, 94%; ‡AF259471, 86%
Platyclinia taylorii Levring	1 km N or Pta Chabunco, Chile; coll. M. Hommersand, 27.xii.97.	†AF257432, 98%; ‡AF259474, 100%
Polyneura latissima (Harvey) Kylin	Seal Rock, Oregon, USA; coll. S. Fredericq, 16.v.99.	†AF257438, 98%; ‡AF259475, 100%
Polyneura bonnemaisonii (C. Agardh) Maggs et Hommersand	Ile Verte, Roscoff, Brittany, France; coll. F. and M. Hommersand, 22.vi.93.	†AF257437, 98%
Polyneuropsis stolonifera Wynne, McBride et West	North Jenner Beach, Sonoma Co., California, USA; coll. C. Kjeldsen, 14.viii.90.	†AF257439, 93%; ‡AF259476, 55%
Pseudophycodrys phyllophora (J. Agardh) Skottsberg	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 5.i.98.	†AF257441, 98%; ‡AF259477, 68%
Pseudophycodrys pulcherrima Baardseth	Bahia Collins, Bahia Fildes, King George I., S. Shetland Is., Antarctic Peninsula; coll. S. Fredericq and J. Rodríguez, 10.ii.94.	†AF257442, 99%; ‡AF259478, 65%
Sarcomenia delesserioidea Sonder	Warrambool, Victoria, Australia; coll. G. Kraft, 13.vii.97.	†AF257443, 96%; ‡AF259479, 75%
Schizoseris condensata (Reinsch) Ricker	Rookery Bay, Stanley, E. Falkland I., Falkland Islands; coll. S. Fredericq and S.-M. Lin, 4.i.98.	†AF257444, 94%; ‡AF259484, 100%
Schizoseris-like sp.	S. Princes Is. chain, Three Kings Is., New Zealand; coll. W. Nelson, 25.xi.98.	†AF257452, 94%; ‡AF259485, 92%
Vanvoorstia spectabilis Harvey	La Vista Del mar, Upper Calarian, Zamboanga, Philippines; coll. F. and M. Hommersand, 28.iv.98.	†AF257456, 93%; ‡AF259487, 72%
Womersleya monanthos (J. Agardh) Papenfuss	Pt. Lansdale, Victoria, Australia; coll. F. and M. Hommersand, 30.vii.95.	†AF257457, 98%
Zellera tawallina Martens	Bulusan, Luzon, Philippines; coll. S.-M. Lin, 22.iv.98.	†AF257458, 97%; ‡AF259488, 85%

cies of Rhodomelaceae always formed a cluster, sometimes with strong support (100/100/<50), whereas the Dasyaceae (*Dasya* + *Heterosiphonia*) was supported in the LSU rDNA (97) analysis (Fig. 2) and was dispersed among the Delesseriaceae in *rbc*L analyses (Figs. 1 and 3). Inclusion of additional species of *Dasya*, *Eupogodon*, and *Heterosiphonia* did not change this result. The topological position of the genus *Sarcomenia* was unresolved in this study, being associated with the Rhodomelaceae in the LSU rDNA + *rbc*L tree (Fig. 1) and with different groups of Delesseriaceae in the LSU rDNA and *rbc*L trees (Figs. 2 and 3).

The remaining Delesseriaceae formed a single assemblage without bootstrap support composed of three large groups, treated here as the subfamilies Delesserioideae, Phycodryoideae, and Nitophylloideae. The first of these contained three assemblages composed of six tribes and the genus *Vanvoorstia* that consistently formed a cluster but without bootstrap support. These were 1) the Caloglosseae (99/94/56) with *Caloglossa*, 2) the Apoglosseae (90/88/<50) composed of *Apoglossum* and a cluster of southern hemisphere species of *Delesseria*, referable to *Paraglossum*, and 3) an assemblage consisting of *Vanvoorstia* and the tribes Hemi-

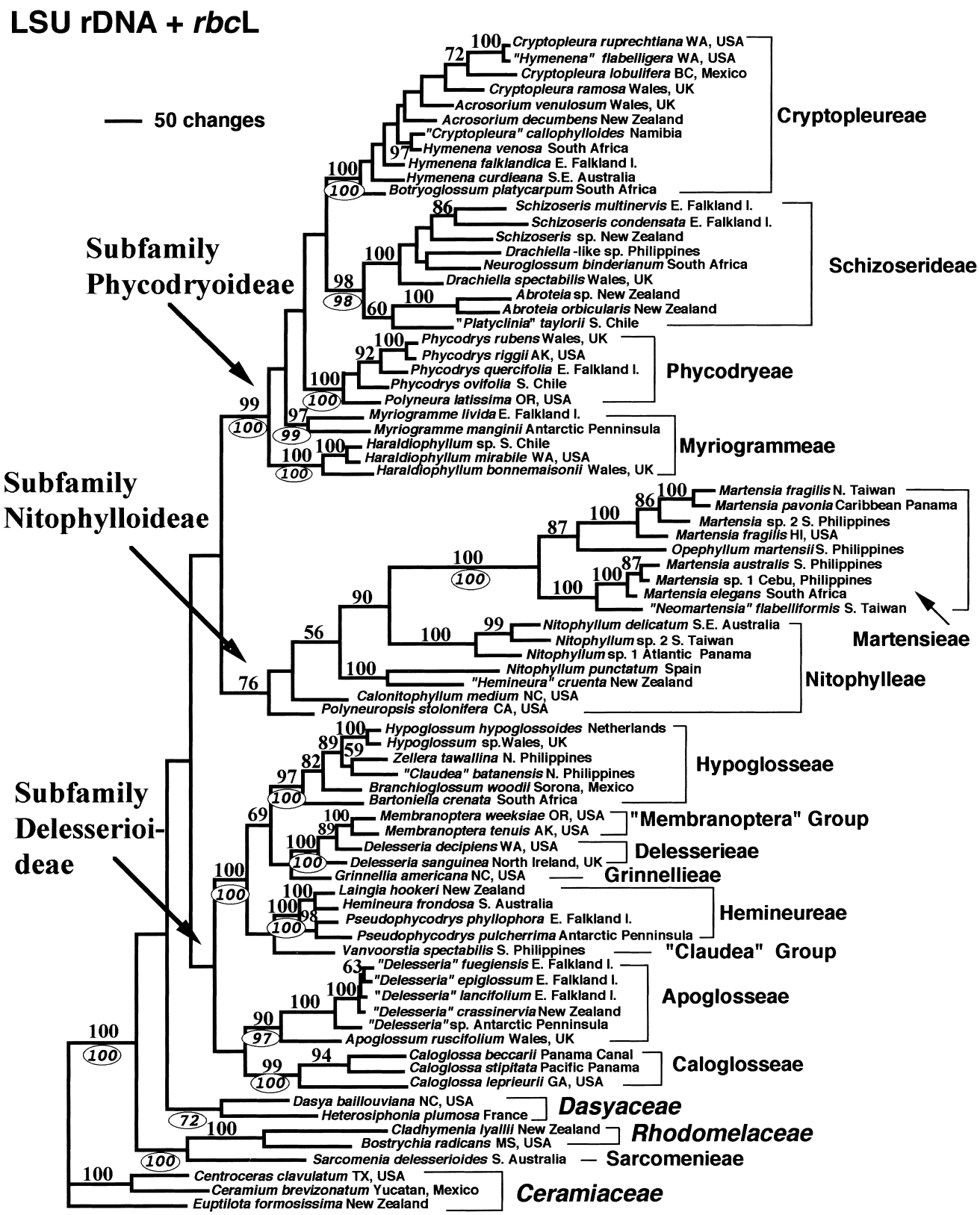

FIG. 1. One of two equally most parsimonious trees inferred from combined LSU rDNA + *rbc*L sequence analysis showing inter- and intratribal relationships within the Delesseriaceae. Tree length = 8754 steps, consistency index = 0.29, retention index = 0.61, informative characters =1189 out of 2660 included sites. Bootstrap proportion values (200 replicates, >50%) derived from parsimony and neighbor-joining analyses are shown above and below the nodes. Branch lengths are proportional to the amount of sequence change.

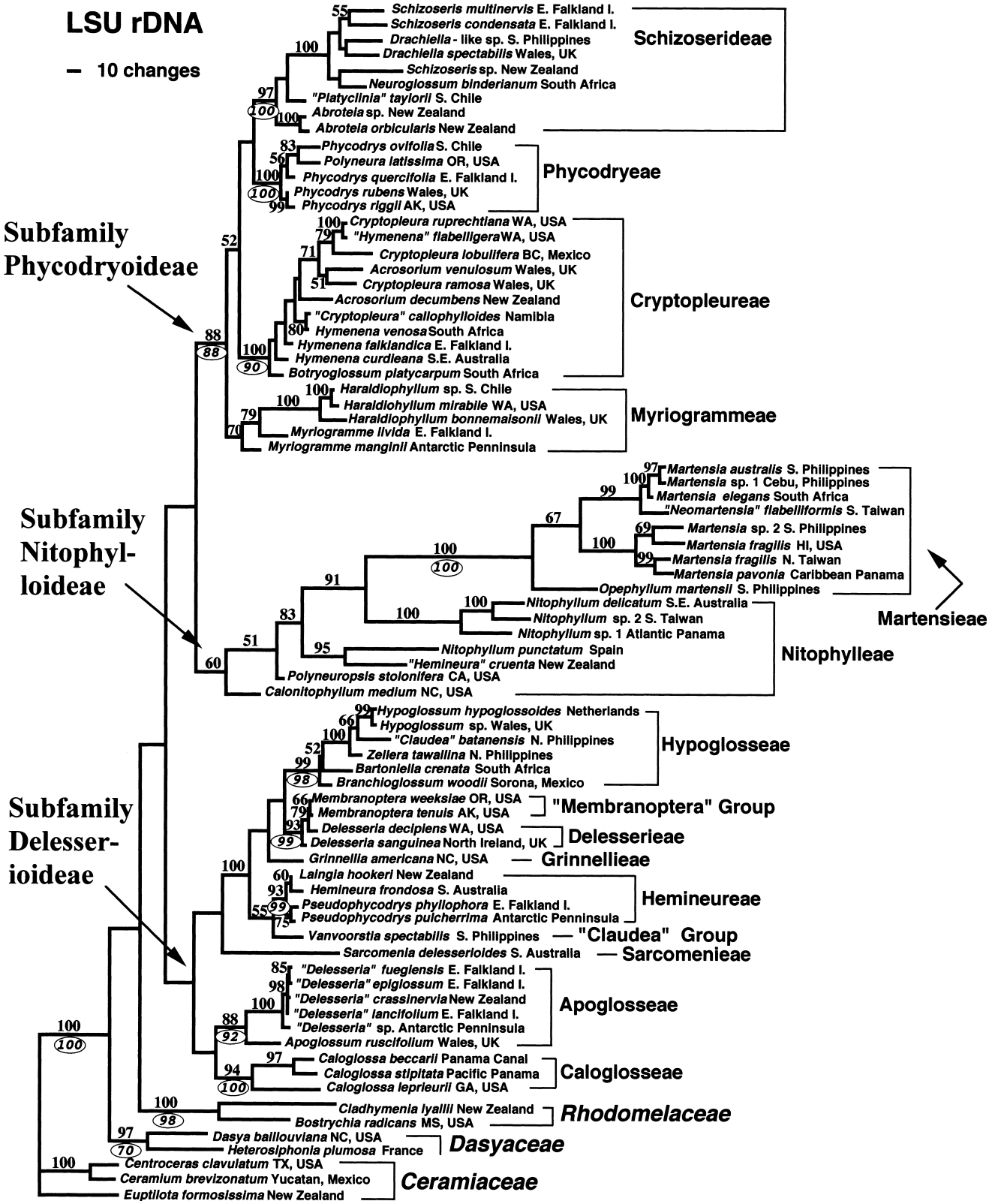

FIG. 2. One of 42 equally most parsimonious trees inferred from LSU rDNA sequence analysis showing inter- and intratribal relationships within the Delesseriaceae. Tree length = 3925 steps, consistency index = 0.37, retention index = 0.68, informative characters = 622 out of 1267 included sites. Bootstrap proportion values (200 replicates, >50%) derived from parsimony and neighbor-joining analyses are shown above and below the nodes. Branch lengths are proportional to the amount of sequence change.

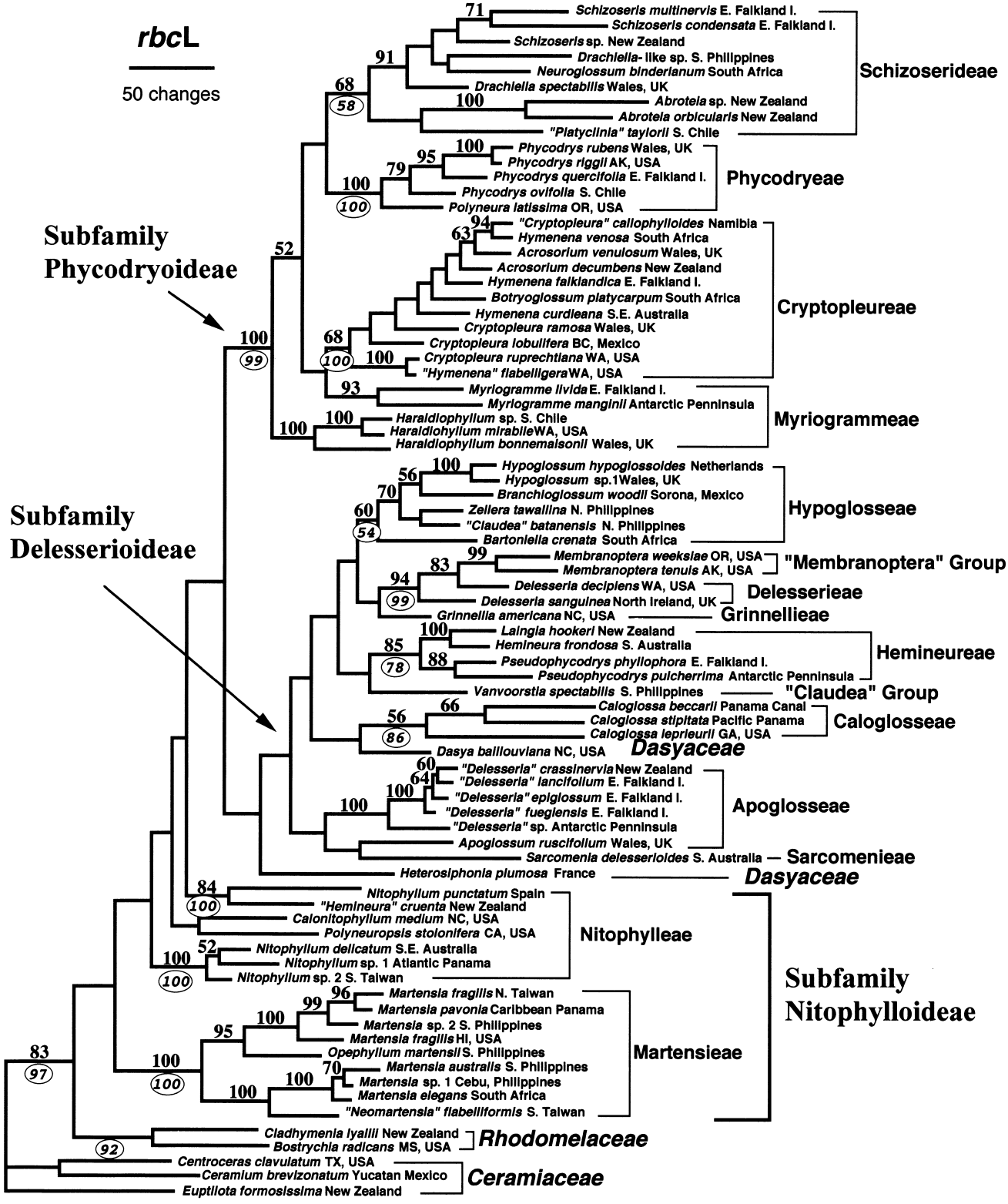

FIG. 3. Single tree inferred from *rbc*L sequence analysis showing inter- and intratribal relationships within the Delesseriaceae. Tree length = 4710 steps, consistency index = 0.2155, retention index = 0.5413, informative characters = 567 out of 1383 included sites. Bootstrap proportion values (200 replicates, >50%) derived from parsimony and neighbor-joining analyses are shown above and below the nodes. Branch lengths are proportional to the amount of sequence change.

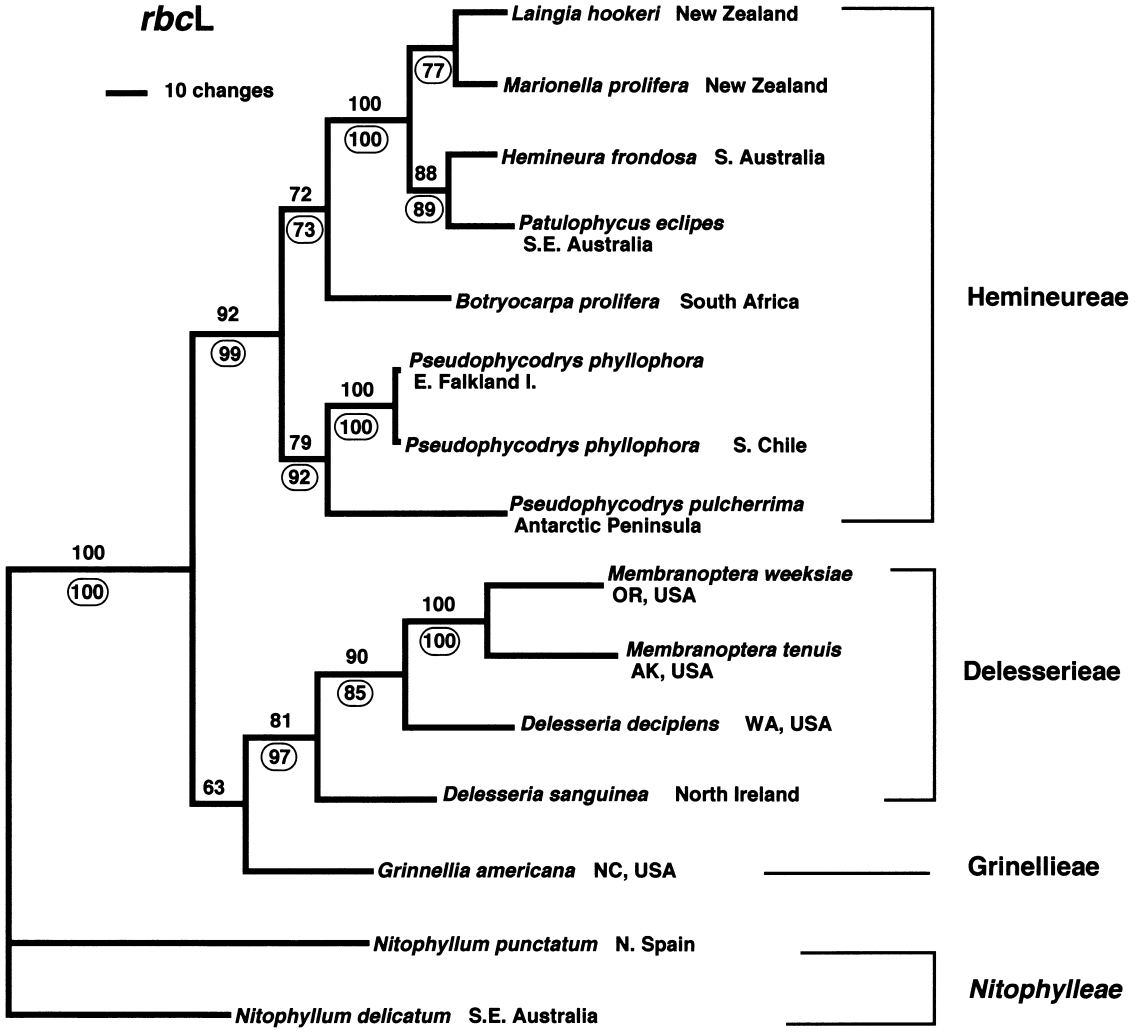

FIG. 4. One of two equally most parsimonious trees inferred from *rbc*L sequence analysis showing inter- and intrageneric relationships of the Hemineureae, Delesserieae, and Grinnellieae in the subfamily Delesserioideae. Tree length = 723 steps, consistency index = 0.5174, retention index = 0.5674, informative characters = 230 out of 1383 included sites. Bootstrap proportion values (200 replicates, >50%) derived from parsimony and neighbor-joining analyses are shown above and below the nodes. Branch lengths are proportional to the amount of sequence change.

neureae, Ginnellieae, Delesserieae, and Hypoglosseae. The third assemblage received strong bootstrap support (100/100) in LSU rDNA + *rbc*L and LSU rDNA trees (Figs. 1 and 2) but was unsupported in *rbc*L trees (Fig. 3). The position of *Vanvoorstia*, a genus currently placed in the Claudeeae, was unsupported. The Hemineureae (100/93/85) with *Hemineura, Laingia*, and *Pseudophycodrys*; the Delesserieae (100/93/94), with *Delesseria* and *Membranoptera*; and the Hypoglosseae (97/99/60) with *Hypoglossum*, *Zellera*, *Branchioglossum*, and *Bartoniella*, were all well supported; however, the position of the Grinnellieae with one genus, *Grinnellia*, was unsupported. Divergence values among clades in the Delesserioideae range from 3.4% to 16.1% for LSU rDNA and from 5.6% to 15.9% for *rbc*L.

The relationship of the tribes Hemineureae and Delesserieae was further analyzed in an *rbc*L data set that included three additional taxa belonging to *Marionella*, *Patulophycus*, and *Botryocarpa* and the Delesserieae and Grinnellieae with two species of *Nitophyllum* selected as the outgroup taxa (Fig. 4). Bootstrap support for the Hemineureae remained high in both parsimony and neighbor-joining analyses (92, 99). A terminal clade that included *Laingia*, *Marionella*, *Hemineura*, and *Patulophycus* was well supported (100, 100) as distinct from *Botryocarpa* and *Pseudophycodrys* (Fig. 4).

A second clade, treated here as the subfamily Phycodryoideae, subfam. nov., contained three well-supported tribes, the Phycodryeae (100/100/100), the Schizoserideae (98/97/68), and the Cryptopleureae (100/100/68), and one unresolved group, the Myriogrammeae, with two genera *Myriogramme* and *Haraldiophyllum* that were weakly associated (70) in the LSU rDNA tree (Fig. 2) and variably associated with other taxa in the LSU rDNA + *rbc*L and *rbc*L trees (Figs. 1 and 3). Divergence values among clades in the Phyco-

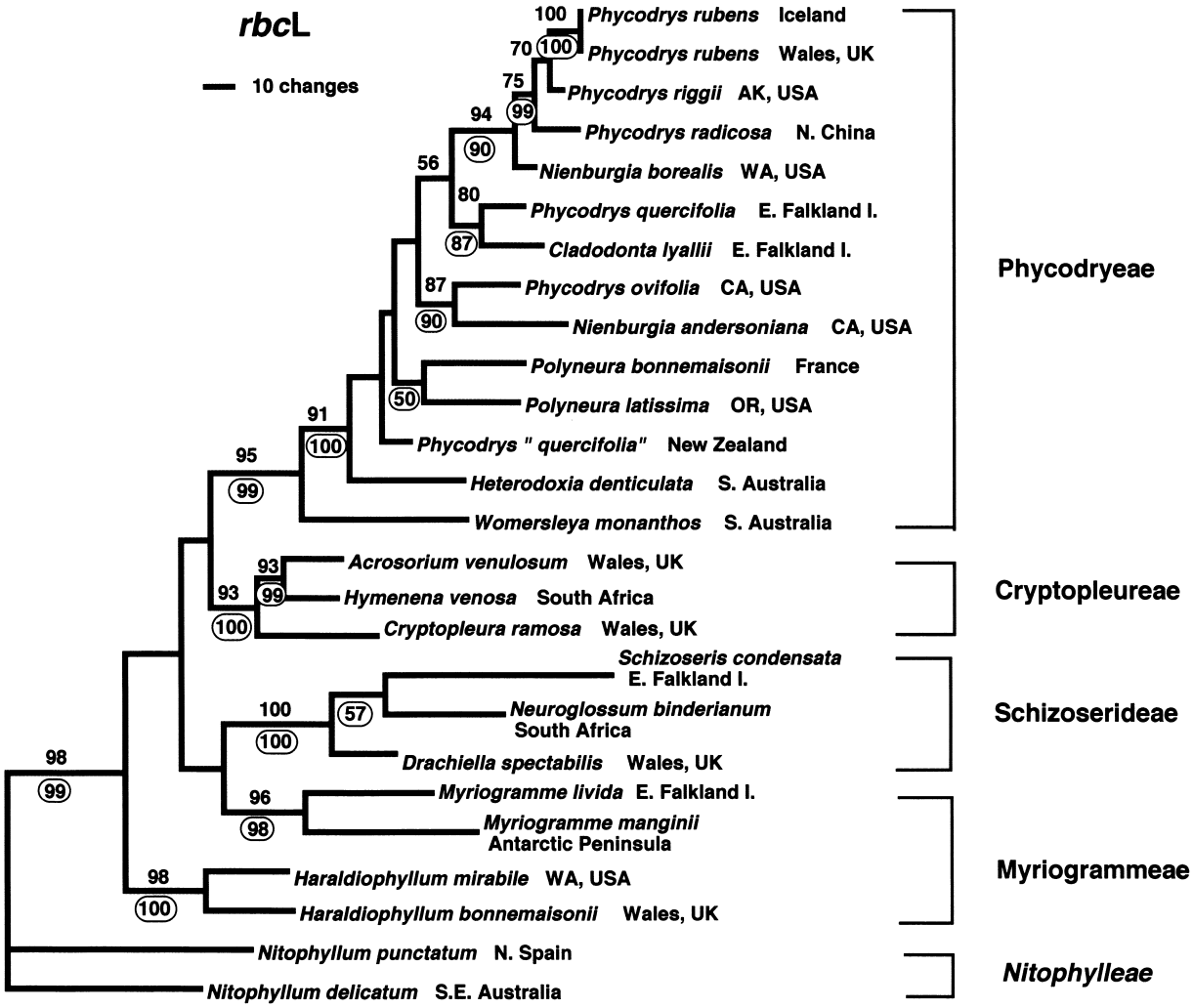

FIG. 5. One of seven equally most parsimonious trees showing inter- and intrageneric relationships of the Phycodryeae in the subfamily Phycodryoideae. Tree length = 4710 steps, consistency index = 0.4817, retention index = 0.5165, informative characters = 345 out of 1383 included sites. Bootstrap proportion values (200 replicates, >50%) derived from parsimony and neighbor-joining analyses are shown above and below the nodes. Branch lengths are proportional to the amount of sequence change.

dryoideae range from 5.3% to 15.4% for LSU rDNA and from 7.5% to 14.8% for *rbc*L.

The addition of nine taxa belonging to *Womersleya*, *Heterodoxia*, *Cladodonta*, *Polyneura*, *Nienburgia* (2), and *Phycodrys* (3) to the Phycodryeae reduced bootstrap support for the tribe Phycodryeae only slightly in parsimony and neighbor-joining analyses from (100, 100) to (95, 99) in an *rbc*L analysis that included representative members of the other three tribes and used the same two species of *Nitophyllum* used previously as outgroup taxa (Fig. 5).

A third group comprised the emended subfamily Nitophylloideae containing two tribes: Nitophylleae and Martensieae. The Nitophylleae formed a grade consisting of *Polyneuropsis*, *Calonitophyllum*, and two clusters of species attributed to *Nitophyllum*. The type species of *Nitophyllum*, *N. punctatum*, clustered with a taxon from New Zealand belonging to *Valeriemaya* (A. J. K. Millar, Sydney Botanical Garden and W. A. Nelson, Museum of New Zealand, personal communication) presently known as *Hemineura cruenta* Harvey (100/95/84). Three species from Australia, Taiwan, and Panama formed a second strongly supported group (100/100/100). The Martensieae comprised a strongly supported clade (100/100/100), including the genus *Opephyllum* and two well-supported clusters of species placed in *Martensia*: an Indo-Pacific group that includes the type species, *M. elegans*, and *Neomartensia* (100/99/100), and a group containing both Indo-Pacific and Atlantic species (100/100/100). The position of *Opephyllum* was variable in the three analyses. Divergence values among clades in the Nitophylloideae range from 20.4% to 30.4% for LSU rDNA and from 11.8% to 14.9% for *rbc*L.

The number of taxa analyzed was insufficient to test the validity of generic concepts in the Delesseri-

aceae; however, the present circumscription of many of them is called into question and will be addressed in forthcoming papers.

DISCUSSION

Since its establishment by Oltmanns (1904), the Ceramiales has been regarded as a natural order characterized by a uniform procarp and a generative auxiliary cell that is typically cut off after fertilization. A monophyletic Ceramiales received support from molecular sequences of the nuclear small subunit rRNA gene (SSU rDNA) (Saunders et al. 1996). Kylin (1956) recognized four families in the Ceramiales: Ceramiaceae, Delesseriaceae, Dasyaceae, and Rhodomelaceae. The opinion of Papenfuss (1944) that the latter three so-called higher or morphologically more complex families are derived from a common ancestor was supported by Saunders et al. (1996). The strong bootstrap support (100/100/83) of a clade containing the latter three ceramialean families seen here should be viewed with caution in light of the small sample size of the outgroup family Ceramiaceae. In molecular studies based on sequences of SSU rDNA that included representatives of nine tribes, the Rhodomelaceae emerged as a strongly supported monophyletic family (Phillips 2000). Treated as the tribe Dasyeae in the Rhodomelaceae by Falkenberg (1901), the Dasyaceae was elevated to family rank by Rosenberg (1933) and characterized by a sympodial (cellulosympodial) rather than monopodial pattern of vegetative growth and the production of pigmented pseudolaterals on which the spermatangial branches and tetrasporangial "stichidia" are born. Both Rosenberg (1933) and Papenfuss (1944) regarded the Dasyaceae as being more closely related to the Delesseriaceae than to the Rhodomelaceae. The Dasyaceae contains two assemblages: one spirally branched, with periaxial cells cut off in a circle in fertile female segments, procarps lacking pericarp initials, and postsporangial cover cells in the tetrasporangial stichidia, as in *Dasya*, and a second dorsiventral, with periaxial cells cut off in an alternating (rhodomelacean) sequence in fertile female segments, pericarp initials present in the procarps, and presporangial cover cells in the tetrasporangial stichidia, as in *Heterosiphonia* (Parsons 1975). The two groups comprise a single clade in the molecular studies of De Jong et al. (1998). They form a single cluster in LSU rDNA (Fig. 2) trees but are scattered among the delesseriacean taxa in LSU rDNA + *rbc*L (Fig. 1) and *rbc*L (Fig. 3) trees here. Further studies are required to establish the status and taxonomic composition of the Dasyaceae.

The family Delesseriaceae Nägeli 1847 was divided by Schmitz (1889) and Schmitz and Hauptfleisch (1897) into three tribes, Nitophylleae, Delesserieae, and Sarcomenieae, with the Delesserieae and Nitophylleae formally established at the tribal level by Schmitz (1892, p. 113). Kylin (1923, 1924) recognized two subfamilies: Delesserioideae (as Delesserieae, including the Sarcomenieae), in which procarps always occur along the thallus midrib, and the Nitophylloideae (as Nitophylleae), in which the procarps are distributed over the surface of fertile parts. Womersley and Shepley (1959) demonstrated that the periaxial cells are cut off in a rhodomelacean sequence in members of the Sarcomenieae with the first abaxial, the next two lateral, and the fourth adaxial. In female plants the procarps are restricted to the fourth adaxial periaxial cell. They established the Sarcomenioideae, which they treated as a subfamily equivalent to the Rhodomeloideae in the family Rhodomelaceae. Most workers have followed Papenfuss (1961) in placing the Sarcomenia group in the Delesseriaceae (see Wynne 1996, 2001). Only the type species *Sarcomenia delesserioides* was investigated here and its position was ambiguous, being associated with the Rhodomelaceae in the LSU rDNA + *rbc*L tree (Fig. 1) and with the Delesseriaceae in the LSU rDNA and *rbc*L trees (Figs. 2 and 3). Its status and taxonomic position remains problematic.

Removing the Dasyaceae and *Sarcomenia* from the analysis does not significantly change the overall topology of the *rbc*L tree or the bootstrap values. If the Sarcomenieae is removed, the remaining Delesseriaceae appears to form a natural group characterized by a bladelike thallus. In species that possess a central axis, the axial cells first cut off two laterals followed by two transverse periaxial cells, with the lateral periaxial cells forming the blade. Alternatively, a central axis is absent and the thallus grows by a marginal meristem and is either monostromatic or polystromatic, composed of a central cellular layer bearing cortical filaments on both sides.

Three subfamilies are identified in our molecular trees (Figs. 1–3). One corresponds to the Delesserioideae of Kylin (1924), except that the *Pseudophycodrys* group belongs here rather than in the Nitophylloideae. Skottsberg (1923) placed *Pseudophycodrys* near *Delesseria*, partly because internal rhizoids are present in the midrib and larger veins and because procarps and cystocarps are formed close to the veins. Kylin (1924), however, incorporated *Pseudophycodrys* into the Nitophylloideae because of the presence of intercalary divisions in the primary cell rows of major axes. Procarps are close to the midribs and macroscopic veins in *P. phyllophora* (Skottsberg 1923), the type species from the Falkland Islands, and are scattered in *P. pulcherrima* (Baardseth 1941) from Tristan da Cunha. Our molecular studies place *Pseudophycodrys* firmly in the Delesserioideae, in agreement with Skottsberg.

As reinterpreted here, the Nitophylloideae of Kylin (1924, 1956) comprises two subfamilies, an emended Nitophylloideae containing *Nitophyllum*, *Polyneuropsis*, *Calonitophyllum*, *Valeriemaya*, *Papenfussia*, *Martensia*, and *Opephyllum* and a new subfamily, the Phycodryoideae, containing the remainder of taxa placed in the Nitophylloideae by Kylin. The composition of subfamilies, tribes or groups, and genera of Delesseriaceae published by Kylin (1956) and Wynne (2001) are listed in Table 1 in comparison with the taxa treated here.

Of the three subfamilies recognized in this article, the Phycodryoideae received strong bootstrap support

(99, 88, 100) and the emended Nitophylloideae is weakly supported in the LSU rDNA + *rbc*L and LSU rDNA trees (Figs. 1 and 2) and is unsupported in the *rbc*L tree (Fig. 3). The Delesserioideae consists of three supported groups that comprise an unsupported clade. We believe that the Delesserioideae (including *Pseudophycodrys*) should be recognized based on a common set of vegetative and reproductive characters pending further study of the included taxa. The topological position of the three subfamilies is unsupported by bootstrap replication analyses, and no assumptions are made as to which morphologies are ancestral and which advanced based on the molecular evidence. It was possible to set up an analysis of a data set that included only positions 1 and 2 and eliminated position 3 that showed monophyly for the Nitophylloideae in the *rbc*L trees. We believe that the data for the Dasyaceae and Sarcomenieae are partly responsible for the discordance in the *rbc*L tree and the absence of monophyly for the Nitophylloideae.

Delesserioideae Kylin (1923, p. 113, "Delesserieae")

Vegetative growth primarily by transversely dividing, dome-shaped apical cells, intercalary cell divisions absent or present in first; second- or higher order cells rows; midribs present, usually with associated rhizoids; procarps restricted to first-order cell rows (except *Pseudophycodrys*), with one carpogonial branch and two sterile groups, rarely with two carpogonial branches and one or two sterile groups; cover cells absent; fusion cell prominent, multinucleate, formed through incorporation of neighboring gametophytic and inner gonimoblast cells; carpospores in clusters or chains, sometimes appearing terminal.

The Caloglosseae is widely assumed to be ancestral among the Delesseriaceae based on its simple blade with the formation of exogenous apical initials bearing branches or hairs, all second- and third-order initials reaching the thallus margin, the absence of intercalary divisions in primary cell rows, and by the presence of a connecting cell linking the carpogonium to the auxiliary cell after fertilization (Papenfuss 1961). This latter distinction is invalidated by the discovery of connecting cells in other Delesseriaceae (Hommersand and Fredericq 1997a,b, Lin et al. 2001). The tribe forms a distinct clade having strong bootstrap support in LSU rDNA + *rbc*L and LSU rDNA trees (99/94). Its further characterization must await molecular studies of *Taenioma*, the other genus presently placed in the Caloglosseae.

The Apoglosseae is a new tribe that will be established formally in a separate article. It is based on *Apoglossum*, a genus currently included in the Delesseria group, and contains a cluster of southern hemisphere species placed in *Delesseria* that correctly belong in *Paraglossum* J. Agardh 1898 (type species *Paraglossum lancifolium* [J. Agardh] J. Agardh). It is distinguished from the Delesserieae and related tribes by the position of the second sterile group (basal rather than laterobasal), a small fusion cell incorporating few gonimoblast cells, and gonimoblasts basal, not suspended in the cystocarp cavity by elongated gametophytic cells. The Apoglosseae received strong bootstrap support (90/88) in LSU rDNA + *rbc*L and LSU rDNA trees but is unsupported in *rbc*L trees.

The core assemblage in the Delesserioideae contains the genus *Vanvoorstia*, the Hemineureae, the Grinnellieae, the Delesserieae, and the Hypoglosseae. This clade is strongly supported (100/100) in LSU rDNA + *rbc*L and LSU rDNA trees but is unsupported in the *rbc*L tree. *Vanvoorstia* is presently placed along with *Claudea*. The branches typically interconnect to form nets and alternate segments cut off a fifth branch-bearing periaxial cell that is ventral in *Claudea* and dorsal in *Vanvoorstia* (Wynne 1996). Because this study did not include the type species *Claudea elegans*, we cannot speculate about the position and affinities of *Vanvoorstia*. The other four tribes share some essential morphological traits. All are blade-like with a prominent central axis and second-order cell rows that typically reach the margins and branch abaxially to produce third-order cell rows. The cystocarps are prominent with thick pericarps, conspicuous fusion cells, and gonimoblasts bearing carposporangia in clusters or branched chains. The core assemblage studied here contains only genera in which intercalary cell divisions are absent in the primary cell rows that form the central axis. Other tribes of monopodially branched genera (Congregatocarpeae) and ramisympodially branched genera (Zinovaeeae, Cumathamnieae, and Sympodophylleae) share some of the essential features of this assemblage and may belong here. In the traditional classification (Kylin 1924, 1956), groups having the most regular thallus organization were regarded as primitive. Thus, the Hypoglossum group, in which all third-order cell rows reach the thallus margin, and the Membranoptera group, which lacks intercalary cell divisions in second- and third-order cell rows, were treated as basal groups. Our molecular studies suggest the opposite. There is strong bootstrap support (89/93/83) for the basal position of *Delesseria sanguinea* in the Delesserieae in which intercalary cell divisions are present in second- and third-order cell rows and appear to have been lost in taxa leading to *Membranoptera*. The molecular data also suggest that the heavily corticated genus *Bartoniella* is basal (82/69/70) in the Hypoglosseae compared with the uncorticated taxa.

The tribe Hemineureae as circumscribed here, including *Hemineura*, *Patulophycus*, *Marionella*, *Laingia*, *Botryocarpa*, and *Pseudophycodrys*, received strong bootstrap support (100/93/85) in the overall analyses (Figs. 1–3) and also in the *rbc*L analysis (92, 99) that contained three additional taxa (Fig. 4). The tribe is problematic when one considers the range in morphologies of the included genera, with *Hemineura* having been placed in the Hemineura group; *Patulophycus*, *Marionella*, and *Laingia* in the Delesseria group; *Botryocarpa* in the Botryocarpa group; and *Pseudophycodrys* in the Pseudophycodrys group (Kylin 1956, Wynne 2001). The procarps in *Hemineura* contain two carpogonial

branches and two sterile groups (Lin et al. 2001), whereas the other genera appear to have typical procarps with one carpogonial branch and two sterile groups as in *Delesseria* (Fig. 6B) (Wagner 1954, Edding 1982, Millar and Wynne 1992). Branching is exceedingly variable among the genera of Hemineureae, tak-

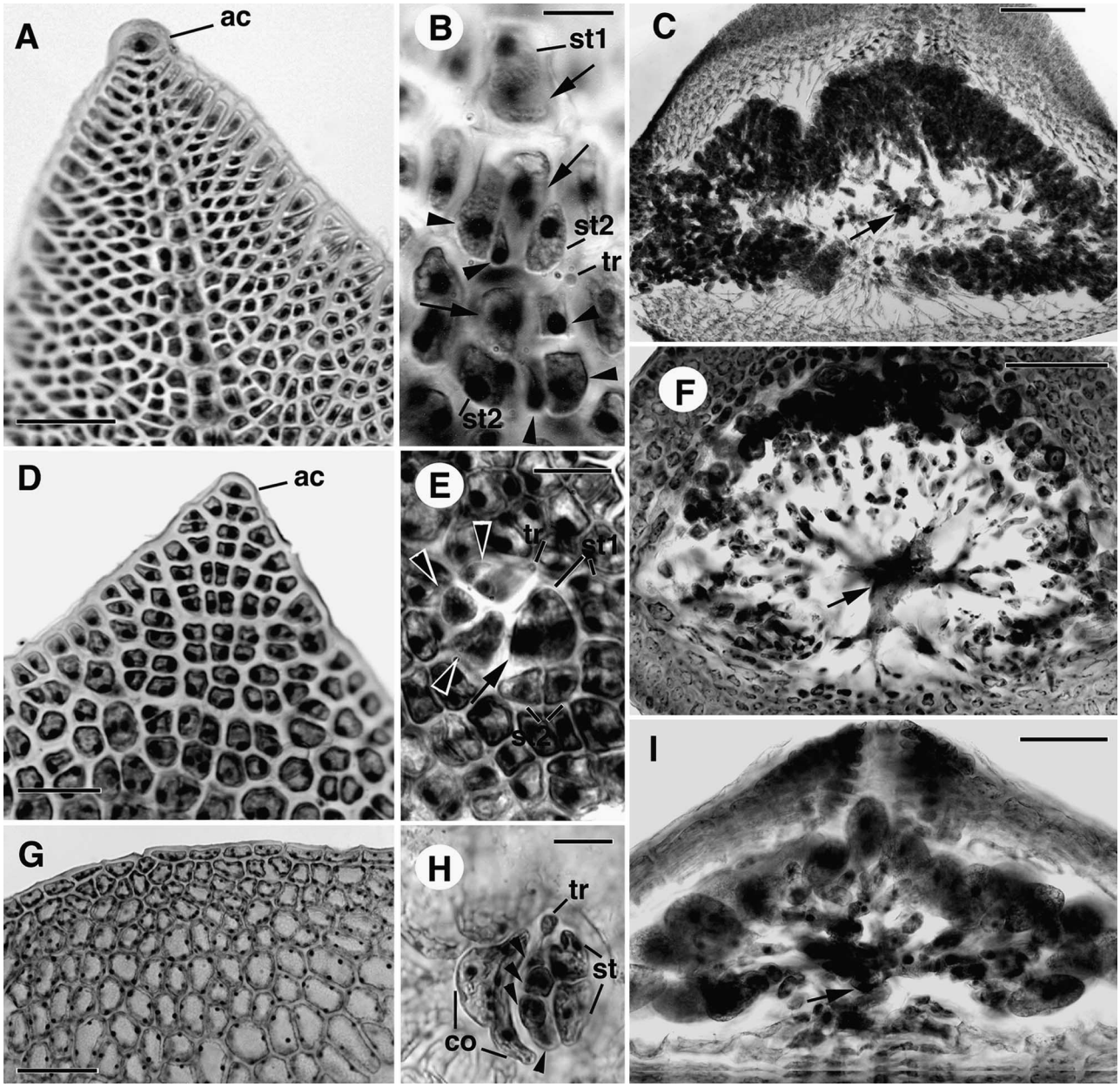

FIG. 6. Illustrations of principal characters for separating the subfamilies Delesserioideae (A–C), Phycodryoideae (D–F), and Nitophylloideae (G–I). (A) *Delesseria sanguinea* (Oysterhaven, Ireland). Apex showing apical cell (ac) and branching of first-, second-, and third-order cell rows. Scale bar, 100 μm. (B) *Delesseria sanguinea* (Oysterhaven, Ireland). Procarp showing supporting cell (arrow) bearing carpogonial branch (arrowheads) with trichogyne (tr), sterile group one (st_1), and sterile group two (st_2). Scale bar, 25 μm. (C) *Delesseria sanguinea* (Isle of Man, UK). Cross-section of mature cystocarp suspended by elongated gametophytic filaments showing central fusion cell (arrow) and gonimoblasts bearing carpospores. Scale bar, 250 μm. (D) *Phycodrys rubens* (Point Lepreau, New Brunswick, Canada). Apex showing apical cell (ac) and growth pattern. Scale bar, 100 μm. (E) *Phycodrys rubens* (North Kattegate, Denmark). Procarp showing supporting cell (arrow) bearing carpogonial branch (arrowheads) with trichogyne (tr), sterile group one (st_1), and sterile group two (st_2). Scale bar, 25 μm. (F) *Phycodrys rubens* (Tommy's Beach, Nova Scotia, Canada). Mature carposporophyte showing large multinucleate central fusion cell (arrow) and clusters of carposporangia. Scale bar, 250 μm. (G) *Nitophyllum punctatum* (St. Denis tip, Île d'Orelon, France). Young blade showing marginal and intercalary meristems. Scale bar, 100 μm. (H) *Nitophyllum punctatum* (St. Denis tip, Île d'Orelon, France). Mature procarp showing supporting cell flanked by cover cells (co) and bearing straight carpogonial branch (arrowheads) with trichogyne (tr) and lateral sterile group (st). Scale bar, 25 μm. (I) *Nitophyllum punctatum* (St. Denis tip, Île d'Orelon, France). Mature carposporophyte with uninucleate basal cell (arrow) and terminal carposporangia. Scale bar, 200 μm.

ing place from the midrib, macroscopic nerves, margins or surfaces of the blades; however, the blades are polystromatic except at the margin in all of the species. The cortex is well developed, but midribs contain weakly developed rhizoids. All have prominent cystocarps with conspicuous fusion cells and thick pericarps, and unlike members of the Delesserieae, the carposporophyte is attached at the floor of the cystocarp rather than being suspended by elongated gametophytic cells. So far, all are known only from the Southern Hemisphere.

The Delesserieae received strong bootstrap support (100/93/94) based on a limited sampling of species of *Delesseria* and *Membranoptera*. In contrast with the Hemineureae, the blades are monostromatic with polystromatic midribs with well-developed internal rhizoids, third-order cell rows may or may not reach the margin (Fig. 6A), procarps are borne in series on primary cell rows (Fig. 6B), and young and mature carposporophytes are suspended in the cystocarp cavity by elongated gametophytic cells (Fig. 6C). These traits are shared by the sympodially branched genus *Cumathamnion* (Wynne and Daniels 1966), tribe Cumathamnieae (Wynne 2001).

The Hypoglosseae is distinct in that all third-order cell rows typically reach the margin, although there are exceptions, and intercalary cell divisions are absent. Blades may be monostromatic or polystromatic. The carposporophyte is suspended in the cystocarp cavity by elongated gametophytic cells in *Hypoglossum hypoglossoides* (Maggs and Hommersand 1993, p. 196) (Fig. 6F), as in members of the Delesserieae. The tribe is a well-supported (97/99/60) sister to the Delesserieae and Grinnellieae in our analyses (Figs. 1–3).

The monotypic tribe Grinnellieae from the western North Atlantic Ocean resembles the Delesserieae in most respects. Procarps are produced in minute bladelets from small islets of cells immersed in the plane of the vegetative blade. The Grinnellieae clusters with the Delesserieae in our analyses but without bootstrap support.

Phycodryoideae Lin, Fredericq et Hommersand, subfam. nov.

Type: Phycodrys Group Kylin 1924, p. 27 (=Phycodryeae M.J. Wynne 2001)

Type genus: *Phycodrys* Kützing (1843, p. 444)

Incrementum per cellulas apicales transversales aut oblique dividentes marginales; secundae-ordines series cellulares producentes tertias-ordines series cellulares abaxialiter aut adaxialiter; divisiones intercalares in seriebus cellularibus omnino ordinibus; costae aut veni nonconsociati cum rhizoideis; procarpia dispersa secus marginem juvenium laminarum utrinque thalli, typice unico filo carpogoniali turmibus sterilibusque, subinde duo filis carpogonialibus turma sterilique; cellulae obtectae absentes, aut si praesentes nunc anticae; carpopsporophytum non suspensum cavitate cystocarpii per cellulas elongatas gametophyticas aut filamenta; cellula fusionalis ampla, multinucleata, incorporans vicinas cellulas gametophyticas internas cellulis gonimoblasti, fusiones cellulosae typice circa synapses; carposporangia maturescentia sequentia catenataque, interdum terminalia.

Growth by means of transversely dividing apical cells or obliquely dividing marginal cells; second-order cell rows producing third-order cell rows abaxially or adaxially; intercalary divisions in cell rows of all orders; midribs or veins not associated with rhizoids; procarps scattered along the margin of young blades on both sides of the thallus, typically with one carpogonial branch and two sterile groups, occasionally with two carpogonial branches and one sterile group; cover cells absent, or if present anterior; carposporophyte not suspended in the cystocarp cavity by elongated gametophytic cells or filaments; fusion cell large, multinucleate, incorporating neighboring gametophytic and inner gonimoblast cells, with cell fusions typically around the pit connections; carposporangia maturing sequentially and forming chains, sometimes terminal.

The subfamily Phycodryoideae consists of four tribes: Phycodryeae, Cryptopleureae, Myriogrammeae, and Schizoserideae. All four are well-defined based on morphological characters, and all but the Myriogrammeae are well supported in bootstrap replication analyses.

The Phycodryeae are characterized by branching mainly from the margins; growth is primarily by means of transversely dividing apical cells, second-order cell rows producing third-order cell rows abaxially (Fig. 6D); blades monostromatic or polystromatic; midribs or nerves present or absent; microscopic veins absent; procarps lacking cover cells, consisting of a carpogonial branch and two sterile groups or two carpogonial branches and one sterile group (Fig. 6E); fusion cells large with most unincorporated gonimoblast cells transformed into carposporangia (Fig. 6F). The tribe received strong bootstrap support (100/100/100) in the general analyses (Figs. 1–3), partly due to the inclusion of only two genera, *Phycodrys* and *Polyneura*, but bootstrap support remained high upon the addition of nine taxa in an *rbc*L analysis (95, 99) that included species placed in *Phycodrys*, *Nienburgia*, *Cladodonta*, *Heterodoxia*, and *Womersleya* (Fig. 5). It should be noted that *Heterodoxia* and *Womersleya* from Australia occupy a basal position in the *rbc*L tree with strong bootstrap support (91, 100; 95, 99).

The Cryptopleureae are distinguished by having membranous thalli that are either monostromatic or polystromatic; growth marginal, initiated by three-sided apical cells with two cutting faces and continued by marginal and intercalary meristems; macroscopic nerves present or absent, microscopic veins usually present; procarps compact, consisting of a supporting cell and a one- to two- (three-) celled sterile group-1, a curved four-celled carpogonial branch; and a one- to two-celled sterile group-2, usually dividing once and remaining distinct after fertilization; gonimoblasts repeatedly subdichotomously branched with carposporangia terminal, maturing in basipetal succession. Bootstrap support for the Cryptopleureae was strong (100/100/100) in all three analyses (Figs. 1–3).

The Myriogrammeae have thalli that are membranous and monostromatic or tristromatic becoming polystromatic toward the base; microscopic veins absent; growth diffuse by means of marginal and intercalary meristems; procarps associated with anterior cover cells, and consisting of a supporting cell, a one- to two-celled lateral sterile group, a four-celled carpogonial branch, and a one-celled basal sterile group; sterile groups enlarging but not dividing after fertilization; gonimoblasts initially branching pseudodichotomously and bearing carposporangia in chains or clusters (*Myriogramme*) or terminally associated with sympodial branching (*Haraldiophyllum*); tetrasporangia originating primarily from central cells. It is somewhat surprising that the association of *Myriogramme* and *Haraldiophyllum* does not receive bootstrap support, in as much as the two genera are difficult to tell apart and both possess a unique character, namely, the presence of a cover cell initial cut off anteriorly from the fertile periaxial cell prior to initiation of the procarp (Hommersand and Fredericq 1997a).

The Schizoserideae possess thalli that are monostromatic except at the base or become polystromatic, often with prominent nerves or macroscopic veins; microscopic veins absent; growth by marginal and intercalary meristems; plastids discoid in young cells, fusing to form a single dissected parietal plate or convoluted ribbon-like plastid in older cells; procarps formed on one or both sides of the thallus, consisting of a one-celled sterile group-1, a strongly curved four-celled carpogonial branch and a one-celled sterile group-2; cover cells absent; fusion cell large, usually branched through incorporation of inner gonimoblast filaments; carposporangia formed in branched chains. Bootstrap support for the Schizoserideae was strong (98/97/68) with *Abroteia* from New Zealand and "*Platyclinia*" from Chile well separated from the cluster that included *Drachiella, Neuroglossum* and *Schizoseris* (100/100/91), three genera that are weakly differentiated.

Nitophylloideae Kylin (1923, p. 114, as "Nitophylleae"), subfam. emend. Lin, Fredericq *et* Hommersand

Thalli thin, membranous, solid or partly net-like; vegetative growth either by means of transversely dividing apical cells or by marginal and intercalary meristems; intercalary cell divisions present in cell rows of any order; second-order cell rows producing third-order cell rows adaxially; midribs not associated with rhizoids; procarps often diagonally opposite on both sides of the blade, consisting of a group of lateral cover cells, one lateral sterile group, and a straight four-celled carpogonial branch between the cover cells and sterile group, second sterile group absent, cover cells absent in *Papenfussia*; basal gonimoblast cell small and uninucleate; pit connections broadening between the gonimoblast initial, supporting cell, the fertile central cell and associated vegetative cells without any fusions; carposporangia maturing sequentially, usually appearing terminal but sometimes forming chains.

Recognition of an emended Nitophylloideae that excludes all but a few select genera formerly placed in this subfamily requires special explanation. The chief distinguishing morphological character of the emended subfamily is the presence of a unique procarp in which the supporting cell first cuts off a cover cell initial laterally, followed by a sterile group initial on the opposite side and a four celled carpogonial branch between the two as illustrated by Kylin (1924, Fig. 55) (also see Fig. 6H). An identical procarp structure was seen in *Martensia* (personal observation). Some genera, such as *Polyneuropsis*, *Calonitophyllum*, and *Valeriemaya* (represented here by *"Hemineura" cruenta*) possess apical cells. Others, such as *Nitophyllum* and *Martensia*, grow by means of marginal meristems and intercalary cell divisions (Fig. 6G) and possess apical cells only in juvenile thalli, if at all. All are thin and membranous and have cystocarps with thin pericarps and small fusion cells (Fig. 6I). Bootstrap support for the Nitophylloideae was only moderate (76/60) in LSU rDNA + *rbc*L and LSU rDNA trees (Figs. 1 and 2) and was absent in *rbc*L trees (Fig. 3), and justification for recognizing the emended subfamily rests in part on the morphological evidence.

The Nitophylleae includes plants with midribs or macroscopic veins present, or ribs and veins absent, microscopic veins present or absent, and perforations or a latticework absent. The tribe forms a grade basal to the Martensieae. The genus *Nitophyllum* falls into two groups, one that includes the type species *N. punctatum* and *Valeriemaya* (as *"Hemineura" cruenta*) (bootstrap support = 100/95/84) and the other that includes a range of *Nitophyllum* species and possibly *Papenfussia* (bootstrap support =100/100/100) and an unsupported group containing *Polyneuropsis* and *Calonitophyllum* that is basal in LSU rDNA + *rbc*L and LSU rDNA trees (Figs. 1 and 2).

The Martensieae have thalli without nerves or veins that are either perforated with small regular holes or form a marginal latticework; cystocarps distributed along the perforations or along the lattice with the ostioles emerging on one side, and tetrasporangia in small round sori distributed over the thallus surface or within the lattice work. The Martensieae forms a strongly supported clade (100/100/100) that contains the nonreticulate genus *Opephyllum* and two clades referable to *Martensia*, one of which contains the type species *M. elegans* from South Africa and the questionable genus *Neomartensia* (Figs. 1–3). A revision of *Martensia* is called for.

CONCLUSIONS

The molecular studies reported here based on DNA sequence analysis of two genes, LSU rDNA and *rbc*L, and observations of the comparative vegetative and reproductive morphology identify three subfamilies in the Delesseriaceae: the Delesserioideae, in which the procarps are borne on primary axes (except in *Pseudophycodrys*); the Phycodryoideae, subfam. nov., in which the procarps are scattered over the

thallus surface and a large fusion cell is established by the progressive incorporation of neighboring gametophytic and inner gonimoblast cells around the pit connections; and the Nitophylloideae, in which the procarps are scattered and in which a fusion cell is lacking and the pit connections between gonimoblast cells broaden. The chief distinguishing morphological character of the emended subfamily Nitophylloideae is the presence of a unique procarp in which the supporting cell first cuts off a cover cell initial laterally followed by a sterile group initial on the opposite side and a four celled carpogonial branch between the two. The present phylogeny calls for a revision in the tribal position of many delesseriacean genera. Only about 40% of the reported genera have been sequenced, and further molecular and morphological studies are needed.

Deeper branches in trees for the Delesseriaceae that reflect relationships at subfamily and tribal levels are resolved more robustly by the LSU rDNA and combined LSU rDNA and *rbc*L data sets than by the *rbc*L data set alone. Tests on the utility of LSU rDNA data are in agreement with the conclusion of Freshwater et al. (1999) that LSU rDNA data resolve relationships at higher taxonomic levels in the red algae more robustly than *rbc*L.

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Agardh, J. 1898. *Species Genera et Ordines Algarum*. Vol. 3, Part 3. Gleerup, Lund, [VI] + 239 pp.

Baardseth, E. 1941. *The Marine Algae of Tristan da Cunha*. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938, No 9. Oslo, 173 pp.

Daugbjerg, N. & Andersen, R. A. 1997. A molecular phylogeny of the heterokont algae based on analyses of chloroplast-encoded *rbc*L sequence data. *J. Phycol.* 33:1031–41.

De Jong, Y. S. D., Van der Wurff, A. W. G., Stam, W. T. & Olsen, J. L. 1998. Studies on Dasyaceae. 3. Towards a phylogeny of the Dasyaceae (Ceramiales, Rhodophyta), based on comparative *rbc*L gene sequence and morphology. *Eur. J. Phycol.* 33:187–201.

Edding, M. 1982. *Morphology and Taxonomy of* Pseudophycodrys *Skottsberg, 1923*. M.S. thesis. Duke University, North Carolina, vii 1 101 pp.

Falkenberg, P. 1901. Die Rhodomelaceen des Golfes von Neapel. *Fauna Flora Golfes Neapels. Monogr.* 26:1–754.

Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417–9.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–91.

Freshwater, D. W. & Rueness, J. 1994. Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbc*L nucleotide sequence analysis. *Phycologia* 33:187–94.

Freshwater, D. W., Fredericq, S., Butler, B. S., Hommersand, M. H. & Chase, M. W. 1994. A gene phylogeny of the red algae (Rhodophyta) based on plastid *rbc*L. *Proc. Natl. Acad. Sci. USA* 91:7281–5.

Freshwater, D. W., Fredericq, S. & Bailey, J. C. 1999. Characteristics and utility of nuclear-encoded large-subunit ribosomal gene sequences in phylogenetic studies of red algae. *Phycol. Res.* 47:33–8.

Hillis, D. M. & Huelsenbeck, J. P. 1992. Signal noise, and reliability in molecular phylogenetic signal. *J. Hered.* 83:189–95.

Hillis, D. M., Mable, B. K., Larson A., Davis, S. K. & Zimmer, E. A. 1996. Nucleic acids IV: sequencing and cloning. *In* Hillis, M. N., Moritz, C. & Mable, B. K. [Eds.] *Molecular Systematics*, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, pp. 321–81.

Holmgren, P. K., Holmgren N. H. & Barnett, L.C. 1990. *Index Herbariorium. Part I. The Herbaria of the World*, 8th ed. International Association for Plant Taxonomy, New York Botanical Garden, New York, 693 pp.

Hommersand, M. H. & Fredericq, S. 1997a. Characterization of *Myriogramme livida*, Myriogrammeae trib. nov. (Delesseriaceae, Rhodophyta). *J. Phycol.* 33:106–21.

Hommersand, M. H. & Fredericq, S. 1997b. Characterization of *Schizoseris condensata*, Schizoserideae trib. nov. (Delesseriaceae, Rhodophyta). *J. Phycol.* 33:475–90.

Hommersand, M. H., Fredericq, S. & Freshwater, D. W. 1994. Phylogenetic systematics and biogeography of the Gigartinaceae (Gigartinales, Rhodophyta) based on sequence analysis of *rbc*L. *Bot. Mar.* 37:193–203.

Hughey, J. R. & Hommersand, M. H. 1999. Isolation of PCR amplifiable DNA from old and formalin-fixed red algal herbarium specimens. *J. Phycol.* 35(Suppl.):15.

Kluge, A. G. & Farris, J. S. 1989. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18:1–32.

Kylin, H. 1923. Studien über die Entwicklungsgeschichte der Florideen. *K. Svensk Vetensk.-Akad. Handl.* 63:1–139.

Kylin, H. 1924. Studien über die Delesseriaceen. *Lunds Univ. Årsskr. N.F. Avd.* 2, 20:111 pp.

Kylin, H. 1956. *Die Gattungen Der Rhodophyceen*. Gleerup, Lund, 673 pp.

Kützing, F. T. 1843. *Phycologia generalis*. Leipzig, xvi + 1–144 + xvii-xxxii + 145–458 + [1] pp., 80 pls.

Lin, S.-M., Hommersand, M. H. & Kraft, G. T. 2001. The Characterization of *Hemineura frondosa*, Hemineureae trib. nov. (Delesseriaceae, Rhodophyta) from southern Australia. *Phycologia* 40: 135–46.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* 40:315–28.

Maggs, C. & Hommersand, M. H. 1993. *Seaweeds of the British Isles, vol. I. Rhodophyta: part 3A, Ceramiales*. The Natural History Museum, London, xv 1 444 pp.

Millar, A. J. K. & Huisman, J. M. 1996. *Dicroglossum crispatulum* gen. et comb. nov. from western Australia representing a new tribe within the Delesseriaceae (Rhodophyta). *J. Phycol.* 32:127–37.

Millar, A. J. K. & Wynne, M. J. 1992. *Valeriemaya* gen. nov. (Rhodophyta), with a discussion of apical organizations within the Delesseriaceae. *Br. Phycol. J.* 27:131–43.

Nägeli, C. 1847. Die neuern Algensysteme und Versuch zur Begründung eines eigenen Systems der Algen und Florideen. *Neue Denkschr. Allg. Schweizer. Gesellsch. Gesammten Naturwiss.* 9(2):1–275.

Oltmanns, F. 1904. *Morphologie und Biologie der Algen*. Vol. I. Gustav Fischer, Jena, VI + 733 pp.

Papenfuss, G. F. 1944. Structure and taxonomy of *Taenioma*, including a discussion on the phylogeny of the Ceramiales. *Madrono* 7:193–214.

Papenfuss, G. F. 1961. The structure and reproduction of *Caloglossa leprieurii*. *Phycologia* 1:8–31.

Parsons, M. J. 1975. Morphology and taxonomy of the Dasyaceae and Lophothalieae (Rhodomelaceae) of the Rhodophyta. *Aust. J. Bot.* 23:549–713.

Phillips, L. E. 2000. Taxonomy of the New Zealand-endemic genus *Pleurostichidium* (Rhodomelaceae, Rhodophyta). *J. Phycol.* 36: 773–86.

Rosenberg, T. 1933. Studien über Rhodomelaceen und Dasyaceen. *Akad. Abh. Lund*, 1–87 pp., Figs. 1–25.

Saunders, G. W., Strachan, I. M., West, J. A. & Kraft, G. T. 1996. Nuclear small-subunit ribosomal RNA gene sequenced from representative Ceramiaceae (Ceramiales, Rhodophyta). *Eur. J. Phycol.* 31:23–9.

Schmitz, F. 1889. Systematische übersicht der bisher bekannten Gattungen der Florideen. *Flora* 72:435–56.

Schmitz, F. 1892. Kleinere Beiträge zur Kenntnis der Florideen I. *Nuova Notarisia* 3:110–9.

Schmitz, F. & Hauptfleisch, P. 1897. Delesseriaceae. *In* Engler A. & Prantl K. [Eds.] *Die natürlichen Pflanzenfamilien ... I. Teil, Abt. 2.* Leipzig, pp 396–405, Figs. 233–6.

Skottsberg, C. 1923. Botanische Ergebnisse der schwedischen Expedition nach patagonien und dem Feuerlande 1907–1909. IX. Marine algae. 2. Rhodophyceae. *K. Svenska Ventens-Akad. Handl.* 63:1–70.

Stevens, R. B. 1981. *Mycology Guidebook.* University of Washington Press, Seattle, WA, 712 pp.

Swofford, D. L. 2000. *PAUP*: Phylogenetic Analysis Using Parsimony and Other Methods)*. Version 4.0b4a. Sinauer Associates, Sunderland, Massachusetts.

Wagner, F. S. 1954. Contributions to the morphology of the Delesseriaceae. *Univ. Calif. Publs. Bot.* 27:279–346.

Wittmann, W. 1965. Aceto-iron-haemotoxylin-chloral hydrate for chromosome staining. *Stain Technol.* 40:161–4.

Womersley, H. B. S. & Shepley, E. A. 1959. Studies of the Sarcomenia group of the Rhodophyta. *Austral. J. Bot.* 7:168–223.

Wynne, M. J. 1983. The current status of genera in the Delesseriaceae (Rhodophyta). *Bot. Mar.* 26:437–50.

Wynne, M. J. 1996. A revised key to genera of the red algal family Delesseriaceae. *Nova Hedwig.* 112:171–90.

Wynne, M. J. 2001. The recognition of tribes within the Delesseriaceae (Ceramiales, Rhodophyta). *Contr. Univ. Michigan Herb.* 23: 407–17.

Wynne, M. J. & Daniels, K. 1966. *Cumathamnion*, a new genus of the Delesseriaceae (Rhodophyta). *Phycologia* 6:13–28.