J. Phycol. **42,** 1271–1288 (2006)

DOI: 10.1111/j.1529-8817.2006.00279.x

A REVISED CLASSIFICATION OF THE DICTYOTEAE (DICTYOTALES, PHAEOPHYCEAE) BASED ON *rbc*L AND 26S RIBOSOMAL DNA SEQUENCE ANALYSES[1]

Olivier De Clerck[2], *Frederik Leliaert, Heroen Verbruggen*

Research Group Phycology and Centre for Molecular Phylogenetics and Evolution, Biology Department, Ghent University, Krijgslaan 281 S8, 9000 Ghent, Belgium

Christopher E. Lane

Biochemistry and Molecular Biology, Dalhousie University, Halifax, Nova Scotia, Canada

Joel Campos De Paula

Departamento de Biologia Vegetal, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, Rio de Janeiro, CEP 20550-013, Brazil

Dioli Ann Payo, and Eric Coppejans

Research Group Phycology and Centre for Molecular Phylogenetics and Evolution, Biology Department, Ghent University, Krijgslaan 281 S8, 9000 Ghent, Belgium

***Dictyota* is a genus of tropical to warm temperate brown algae characterized by parenchymatous, flattened thalli that grow from a single, transversely oriented apical cell. *Dictyota* is currently distinguished from allied genera of the tribe Dictyoteae (*Dilophus*, *Glossophora*, *Glossophorella*, and *Pachydictyon*) by the structure of the cortical and medullary layers, as well as the relative abundance of surface proliferations. Even though the traditional classification of the Dictyoteae has repeatedly been criticized in the past, the absence of sound molecular data has so far discouraged any new taxonomic proposals apart from a merger of *Dilophus* with *Dictyota*, which has been accepted by only part of the phycological community. Phylogenetic analysis of *rbc*L gene, partial 26S rDNA sequence, and combined data sets, including four of five generitypes, demonstrates that the traditional classification does not accurately reflect the evolutionary history of the group. None of the genera are resolved as a monophyletic clade. Hence, a merger of *Glossophora*, *Glossophorella*, and *Pachydictyon* in *Dictyota* is proposed. Two new genera, *Canistrocarpus* (incorporating *D. cervicornis*, *D. crispata*, and *D. magneana*) and *Rugulopteryx* (accommodating *D. radicans*, *Dil. suhrii*, and *Dil. marginata*), are proposed. Both genera are supported by molecular indications and a combination of reproductive and vegetative characters. The position of *Dil. fastigiatus* as a clade sister to *Dictyota* s.l. and the absence of *Dil. gunnianus*, the generitype of *Dilophus*, from the analyses, prevented us from making a more definite statement on the status of the latter genus.**

Key index words: ***Canistrocarpus*; *Dictyota*; Dictyotales; molecular phylogeny; *rbc*L; *Rugulopteryx*; systematics; 26S rDNA**

Abbreviations: **BI, Bayesian inference; ML, maximum likelihood; MP, maximum parsimony; MPT, most parsimonious tree; PBS, partitioned Bremer support**

The Dictyotales represents one of the few brown algal orders whose members can form a conspicuous or even dominant component of tropical and temperate marine algal floras. The success of these macroalgae has often been linked to their ability to deter grazers in environments subject to severe grazing pressure, which makes them an important competitor of corals and other sessile benthic organisms for both space and light in many marine coastal ecosystems. From a systematic point of view, the order Dictyotales is welldefined, all members being characterized by apical growth, flattened parenchymatous thalli, and hairs aggregated in small tufts on the thallus surface. The life cycle is diplohaplontic and isomorphic. Sexual reproduction is always oogamous, and the male gametes are generally uniflagellate, except in some *Zonaria* species, which are characterized by biflagellate spermatozoids (van den Hoek et al. 1995, Phillips 1997). The diploid sporophyte typically produces unilocular sporangia with four nonflagellate meiospores (tetraspores), but a few genera produce eight aplanospores per sporangium (e.g. *Lobophora* and *Zonaria*) or flagellate spores (e.g. *Exallosorus*, Phillips 1997), features that are considered primitive.

The order Dictyotales consists of the large family Dictyotaceae, in which some 20 genera are currently recognized, plus two little-known monospecific genera,

[1]Received 27 July 2005. Accepted 3 July 2006.
[2]Author for correspondence: e-mail: olivier.declerck@ugent.be.

TABLE 1. Genera of the Dictyoteae with indication of the respective generitypes, defining characters, and number of species.

Genus	Type species	Defining characters	Currently recognized species
Dictyota	*D. dichotoma* (Hudson) Lamouroux	Medullary layers 1, cortical layers 1	~ 46
Dilophus	*Dil. gunnianus* J. Agardh	Medullary layers >1, cortical layers 1	16
Glossophora	*G. kunthii* (C. Agardh) J. Agardh	Surface proliferations, medullary and cortical layers 1 to variable	3
Glossophorella	*G. dhofarensis* Nizamuddin and Campbell	Surface proliferations, medullary and cortical layers >1 near the base	1(–2)
Pachydictyon	*P. furcellatum* J. Agardh [= *P. polycladum* (Kützing) Womersley]	Medullary layers 1, cortical layers >1	4

Dictyotopsis and *Scoresbyella*, that are each provisionally assigned to a separate family, the Dictyotopsidaceae (Allender 1980) and Scoresbyellaceae (Womersley 1987), respectively. The family Dictyotaceae is subdivided into the two tribes Dictyoteae and Zonarieae on the basis of the number of meristematic cells at the frond apices. In contrast the Zonarieae have a row or a small group of such cells, members of the Dictyoteae are characterized by a single, transversely oriented, lenticular apical cell. Recent molecular phylogenies have largely confirmed this traditional tribal classification (Lee and Bae 2002, Hoshina et al. 2004, Kraft et al. 2004). There is much less consensus, however, about genus delineations within the tribe Dictyoteae. J. Agardh (1882, 1894) originally recognized four genera (*Dictyota*, *Dilophus*, *Glossophora*, and *Pachydictyon*) that were distinguished by the relative number of cortical and medullary layers and by the presence or absence of surface proliferations (Table 1, Fig. 1). In Agardh's system, *Dictyota* comprised species with a unilayered cortex and medulla, whereas those with a multilayered medulla, in at least some part of the thallus, were assigned to *Dilophus*. Species with a unilayered medulla but a cortex that is at least locally composed of several layers were placed in *Pachydictyon*. *Glossophora*, a genus comprising only three species restricted to Australia, New Zealand, the Pacific coast of South America, and the Galapagos Archipelago, was chiefly characterized by the presence of multiple surface proliferations that even occasionally may bear reproductive structures. *Glossophora* is only to a lesser extent defined on the number of cortical and medullary layers, which are reported to be variable even within the respective species (Womersley 1987). Surface proliferations also characterize several *Dictyota* and *Dilophus* species, but they are always less abundant than in *Glossophora* and never serve as sporophylls. Recently a fifth genus, *Glossophorella*, was added to the Dictyoteae. It is characterized by multiple cortical layers, duplication of medullary cells near the margins, and the presence of surface proliferations (Nizamuddin and Campbell 1995).

The distinction among these four or five genera has been the subject of considerable debate, as some species are particularly hard to assign to one or another genus (Setchell and Gardner 1925, Taylor 1945, Dawson 1950). Hörnig et al. (1992a,b) demonstrated experimentally that the number of medullary layers can be altered in many species depending on the

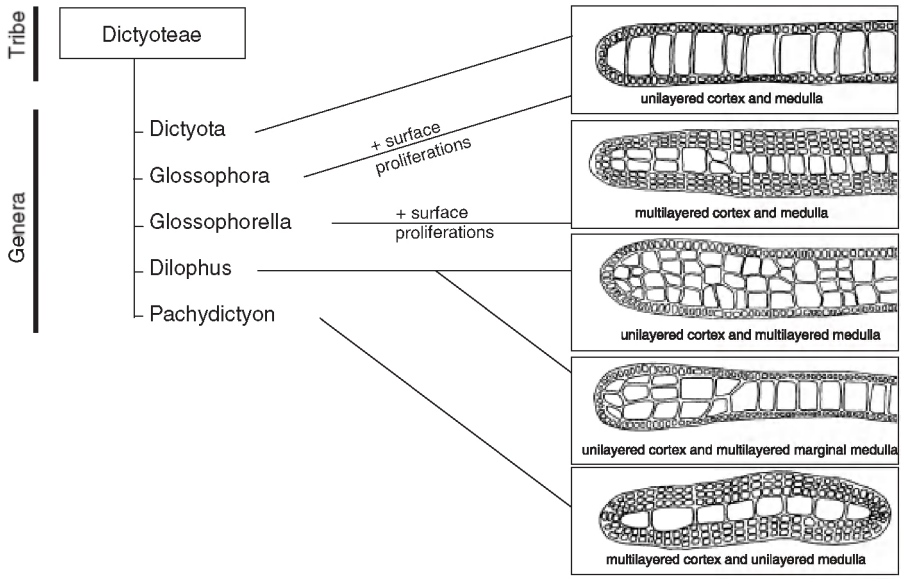

FIG. 1. Schematic representation of the traditional defining characters of genera in the tribe Dictyoteae.

culture conditions. They concluded that *Dilophus* did not warrant recognition at the generic level and hence proposed a merger of *Dilophus* with *Dictyota*. Although several authors have accepted the merger, others continue to recognize *Dilophus* as a separate genus (Phillips 1992, Huisman 2000). Moreover, recently published molecular phylogenies (Lee and Bae 2002, Hoshina et al. 2004, Kraft et al. 2004) indicate that the separation of *Dilophus* and *Dictyota* is justified, but taxon sampling in these studies was on the low side for drawing sound taxonomic conclusions. The status of *Pachydictyon*, *Glossophora*, and *Glossophorella* has received much less attention. The morphological data presented on *Dictyota naevosa* (Suhr) Montagne and *D. radicans* Harvey by De Clerck and Coppejans (2003) show that generic boundaries between *Dictyota* and the above-mentioned genera are equally fuzzy, indicating that these genera also need to be considered in a global evaluation of generic concepts in the Dictyoteae. Additionally, Hwang et al. (2004) showed that at least one species of *Pachydictyon*, *P coriaceum* (Holmes) Okamura, is resolved within the genus *Dictyota* using a combination of three different chloroplast-encoded genes (*rbc*L, *psa*A, and *psb*A).

In recent times, authors have attempted to find more stable and pylogenetically informative reproductive characters to separate genera. Phillips (1992) showed that marked differences exist in the arrangement and structure of sporangia among the Australian *Dilophus* species, several of which (*Dil. fastigiatus*, *Dil. robustus*, and *Dil. marginatus*) are characterized by sporangia subtended by two stalk cells rather than one as is the rule in the other *Dilophus* species and throughout the Dictyoteae generally. Coppejans et al. (2001) and De Clerck (2003) observed that male reproductive structures (antheridia) in *D. crispata* Lamouroux and *D. magneana* De Clerck et Coppejans are not surrounded by hyaline, unicellular paraphyses but by densely pigmented multicellular filaments. De Paula et al. (2001) highlighted the aberrant nature of the *D. crispata–cervicornis–magneana* group in respect to bioactive secondary metabolites, as these show unique diterpene signatures that are markedly different from those of the remaining *Dictyota* and *Dilophus* species examined. In the absence of reliable support from gene-sequence data, the transfer of the *D. crispata–cervicornis–magneana* group to a separate genus has been suggested but not effected (see De Clerck 2003).

This study aims to: (1) assess the status of the genera currently placed in the Dictyoteae based on sequence data of the plastid encoded large subunit RUBISCO gene (*rbc*L) and nuclear encoded large subunit rDNA (26S, partial); (2) evaluate the taxonomic utility of traditional morphological characters at the generic level; (3) assess the concordance of recently introduced anatomical characters with the molecular phylogenetic results; and (4) interpret the molecular phylogeny in a morphological context and propose a revised classification of the tribe Dictyoteae. For clarity reasons, names of taxa follow the traditional classification recognizing all five genera of the Dictyoteae.

MATERIALS AND METHODS

Taxon sampling and laboratory protocols. Broad taxon sampling was carried out to ensure as complete a representation as possible of the Dictyoteae (Table 2). This sampling included generitypes of all but one genus, as well as several species that are questionably placed in their present genera based on morphological inconsistencies. Sequences of the Dictyoteae were supplemented by a wide selection of taxa spanning the entire phylogenetic spectrum of the Zonarieae. The latter were defined as out-group. The sole representative of the family Scoresbyellaceae, *S. profunda*, was also included.

Following Chase and Hillis (1991), DNA was extracted from samples desiccated in the field in silica gel, and vouchers were deposited in GENT. Total genomic DNA was extracted using a standard CTAB-extraction method and subsequent purification with a Wizard® DNA Clean-Up System (Promega Inc., Madison, WI, USA) following the manufacturer's protocol. The *rbc*L gene was amplified as a single or as two overlapping products. In order to amplify the *rbc*L gene in a single stretch, the *rbc*L68F primer (Draisma et al. 2001) was combined with the reverse primer S3R (Siemer et al. 1998). If two separate products were needed, *rbc*L68F was combined with *rbc*L1380R and *rbc*L496F with S3R (all primer sequences listed in Draisma et al. 2001). The 5′-end of the 26S rDNA [approximately 1200 base pairs (bp)] was amplified as a single product using primers AB28 (Draisma et al. 2001) and T13N (Harper and Saunders 2001). The PCR conditions of all primer combinations consisted of an initial denaturation at 94° C for 3 min, followed by 94° C for 1 min, annealing at 46° C for 1 min, extension at 72° C for 2 min for 28 cycles, followed by a final extension of 10 min at 72° C. Excess primer and dNTP were removed with ExoSAP-IT® (USB Corp., Cleveland, OH, USA) for 15 min at 37° C, followed by 15 min at 80° C to inactivate the enzymes. The resulting products were used for cycle sequencing with the primers of the initial PCR reactions using an ABI Prism Dye Terminator Cycle Sequencing Ready Reaction kit following the manufacturer's instructions. Sequencing products were analyzed with an ABI 3100 Prism Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA). Sequences were edited and assembled with Autoassembler version 1.4.0. The *rbc*L gene, lacking indels, was aligned by eye in BioEdit 7.0.4.1 (Hall 1999). Owing to missing data at the 5′ and 3′ termini of the *rbc*L sequences, a 1207 bp fragment was selected for analysis excluding the first 105 and last 155 bp of the 1467 bp gene.

The 26S sequences were aligned on the basis of secondary structure information with DCSE v. 2.60 (De Rijk and De Wachter 1993). The rationale for using secondary-structure models for aligning rRNA sequences is based on the fact that the conservation of secondary structures exceeds that of nucleotides (Kjer 1995). The 26S sequence of *Scytosiphon lomentaria* (Lyngbye) Link, the only representative of the Phaeophyceae incorporated in the European Ribosomal RNA data base (http://www.psb.ugent.be/rRNA/, Wuyts et al. 2004), was used as a model for building our alignment. The alignment of the variable B13-1, B14, B15, D5, and D5-1 helices and the highly variable region enclosed by the C1 helix (see De Rijk et al. 1999 for nomenclature) was aided by folding the sequences of each sample using the Mfold software (http://www.bioinfo.rpi.edu/, Zuker 2003). Foldings were conducted at 37° C using a search within 5% of thermodynamic suboptimality. The different optimal and suboptimal secondary structures were screened for common motifs. The aligned partial rDNA sequences were 1363 sites in total. The region enclosed

TABLE 2. Taxa used in this study in the phylogenetic analysis.

Taxa	Collecting data	Accession number	
		*rbc*L	26S
Dictyota acutiloba J. Agardh	Ala Moana, Honolulu, Oahu, Hawaii (O. De Clerck, 25.iv.2003, ODC888)	DQ472056	DQ472111
Dictyota alternifida J. Agardh	Australia (W. J. Lee et al., unpublished)	AY422662	
Dictyota bartayresii var. *plectens* Allender and Kraft	Ned's Beach, Lord Howe Island (G. W. Saunders, 11.iii.2001, GWS1029)	DQ472052	DQ472106
Dictyota bartayresii var. *plectens* Allender and Kraft	Keppel Bay, Yeppoon, Queensland, Australia (T. Cowling, 18.viii.2005, TC2)	DQ472085	
Dictyota canaliculata De Clerck and Coppejans	SW Cabilao Island, Philippines (H. Verbruggen, 29.i.2004, HV678)	DQ472062	DQ472117
Dictyota cervicornis Kützing	Apale, Isabel, Leyte (D. A. Payo, 17.vii.2003, DAP021)	DQ472073	
Dictyota cervicornis Kützing	Maribago, Mactan Island, Philippines (H. Verbruggen, 24.i.2004, HV619)	DQ472049	
Dictyota cervicornis Kützing	SE of Olango Island, Philippines (H. Verbruggen, 25.i.2004, HV631)	DQ472048	DQ472103
Dictyota cervicornis Kützing	SW Panglao Island, Philippines (H. Verbruggen, 1.ii.2004, HV711)	DQ472047	DQ472102
Dictyota ceylanica Kützing	Faaa, Tahiti, French Polynesia (H. Verbruggen, 21.v.2002, HV214a)	DQ472067	DQ472122
Dictyota ciliolata Sonder ex Kützing	SE Olango Island, Philippines (H. Verbruggen, 25.i.2004, HV632)	DQ472053	DQ472107
Dictyota ciliolata Sonder ex Kützing	Balicasag Island, Bohol, Philippines (D. A. Payo, 26.vii.2003, DAP029)	DQ472071	DQ472125
Dictyota crispata Lamouroux	Hinakpan, Manicani, Guiuan, Eastern Samar, Philippines (D. A. Payo, 5.viii.2003, DAP048)	DQ472070	DQ472124
Dictyota crispata Lamouroux	Bantayan Beach, Dumaguete, Philippines (D. A. Payo, 5.viii.2003, DAP039)	DQ472069	
Dictyota dichotoma (Hudson) Lamouroux	Point du Nid de Corbet, Audresselles, France (O. De Clerck, 16.x.2004, ODC1027)	DQ472051	DQ472105
Dictyota dichotoma (Hudson) Lamouroux	Le Troc, Banyuls sur Mer, France (O. De Clerck, 24.v.2005, ODC1055)	DQ472080	
Dictyota "dichotoma" (Hudson) Lamouroux	Japan (R. Hoshina et al., unpublished)	AB096882	
Dictyota friabilis Setchell	Arue, Tahiti, French Polynesia (H. Verbruggen & M. Zubia, 16.v.2002, HV153)	DQ472064	DQ472119
Dictyota friabilis Setchell	Lanikai, Oahu, Hawaii (O. De Clerck, 25.iv.2003, ODC 898)	DQ472065	DQ472120
Dictyota hamifera Setchell	Afaahiti, Tahiti, French Polynesia (H. Verbruggen and A. N'Yeurt, 23.v.2002, HV222)	DQ472055	DQ472110
Dictyota jamaicensis Taylor	Drax Hall, East of St. Ann's Bay, St. Ann Parish, Jamaica (H. Verbruggen, 15.viii.2004, HV926)	DQ472061	DQ472116
Dictyota "koreana"	Korea (Lee et al., unpublished)	AY422668	
Dictyota mertensii (Martius) Kützing	Drax Hall, East of St. Ann's Bay, St. Ann Parish, Jamaica (H. Verbruggen, 15.viii.2004, HV923)	DQ472060	DQ472115
Dictyota naevosa (Suhr) Montagne	Mission Rocks, Kwazulu-Natal, South Africa (O. De Clerck and F. Leliaert, 13.vi.2003, KZN2241)	DQ472084	DQ472108
Dictyota pulchella Hörnig & Schnetter	East side of airport causeway, St. George, Bermuda (C. E. Lane, and C. W. Schneider, 2.iv.2003, CL030101)	DQ472058	DQ472113
Dictyota radicans Harvey	Figure of Eight Island, Esperance Bay, South Australia (N. Goldberg, 2.xi.2002, D98)	DQ472045	DQ472100
Dictyota sandvicensis Sonder ex Kützing	Lanikai, Oahu, Hawaii (O. De Clerck, 25.iv.2003, ODC896)	DQ472063	DQ472118
Dictyota sp.	Isipingo, Kwazulu-Natal, South Africa (O. De Clerck and F. Leliaert, 16.vi.2003, KZN2305)	DQ472066	DQ472121
Dilophus alternans J. Agardh	Priory Bay, St. Ann Parish, Jamaica (H. Verbruggen, 12.viii.2004, HV902)	DQ472059	DQ472114
Dilophus fasciola (Roth) Howe	Ile de Frioul, Marseille, France (O. De Clerck, 23.ix.2004, ODC1029)	DQ472074	DQ472126
Dilophus fasciola (Roth) Howe	Les Paulilles, Port Vendres, France (O. De Clerck, 23.v.2005, ODC1049)	DQ472078	
Dilophus fastigiatus Sonder	Woody Island, Esperance Bay, South Australia (N. Goldberg, 3.iv.2003, D96)	DQ472068	DQ472123
Dilophus intermedius (Zanardini) Allender and Kraft	Keppel Bay, Yeppoon, Queensland, Australia (T. Cowling, 18.viii.2005, TC1)	DQ472086	
Dilophus intermedius (Zanardini) Allender and Kraft	Lord Howe Island, Australia (G. W Saunders, 11.iii.2001, GWS1020)	DQ472075	
Dilophus marginatus J. Agardh	Victoria, Australia (G. W Saunders, GWS0111)	DQ472043	DQ472098
Dilophus spiralis (Montagne) Hamel	Le Troc, Banyuls sur Mer, France (O. De Clerck, 24.v.2005, ODC1053)	DQ472079	
Dilophus spiralis (Montagne) Hamel	Le Troc, Banyuls sur Mer, France (O. De Clerck, 24.v.2005, ODC1057)	DQ472081	

TABLE 2 (Continued)

Taxa	Collecting data	Accession number	
		*rbc*L	26S
Dilophus stoloniferus (Dawson) Schnetter & Bula-Meyer	Dancalan, N of Bulusan, SW Luzon, Philippines (H. Verbruggen, 11.ii.2004, HV819)	DQ472072	
Dilophus suhrii (Kützing) Papenfuss	Palm Beach, Kwazulu-Natal, South Africa (O. De Clerck et al., 11.xi.2003, KZN-b 2346)	DQ472044	DQ472099
Glossophora kunthii (C. Agardh) J. Agardh	Pan de Azucar, Chile (S. Faugeron, viii.2004, Chile-M1)	DQ472057	DQ472112
Glossophora kunthii (C. Agardh) J. Agardh	Cape Palliser, Wairarapa, New Zealand (G. Zuccarello, 12.ii.2005, NZ-D122)	DQ472076	
Glossophora nigricans (J. Agardh) Womersley	South of Pinguin Island, Perth, Western Australia (J. Huismans, 8.ii.2004, D92)	DQ472077	
Glossophorella dhofarensis Nizamuddin and Campbell	Sidah, Dhofar, Oman (T. Schils, 26.ix.2003, DHO163)	DQ472083	DQ472127
Pachydictyon coriaceum (Holmes) Okamura	Japan (Hoshina et al., unpublished)	AB096890	
Pachydictyon coriaceum (Holmes) Okamura	Dana Point, Orange County, California, USA (S. Murray, 23.xi.2004, CSUF003)	DQ472054	DQ472109
Pachydictyon paniculatum (J. Agardh) J. Agardh	Frederick Island, Esperance Bay, South Australia (N. Goldberg, 22.x.2002, D97)	DQ472082	
Pachydictyon polycladum (Kützing) Womersley	Flinders Jetty, Victoria, Australia (G. W. Saunders, 23.iv.1993, GWS0139)	DQ472050	DQ472104
Scoresbyella profunda Womersley	Geographe Bay, Western Australia (J. M. Huisman, x. 2003, DIC44)	DQ472046	DQ472101
Dictyopteris polypodioides (de Candolle) Lamouroux	Ile de Frioul, Marseille, France (O. De Clerck, 23.ix.2004, ODC1031)	DQ472042	DQ472097
Distromium didymothrix Allender and Kraft	Roach Is. Admiralty Group, Lord Howe Island (G. W. Saunders, 12.iii.2001, GWS1041)	DQ472035	DQ472091
Padina boergesenii Allender and Kraft	Ala Moana, Honolulu, Oahu, Hawaii (O. De Clerck, 25.iv.2003, ODC890)	DQ472037	DQ472093
Padina crassa Yamada	Ned's Beach, Lord Howe Island, Australia (G. W. Saunders, 11.iii.2001, GWS1033)	DQ472038	
Padina sanctae-crucis Børgesen	Whale Bone Bay, St. George's Island, Bermuda (C. E. Lane & C. W. Schneider, 28.iii.2003, CL 030305)	DQ472036	DQ472092
Homoeostrichus sinclairii (J. D. Hooker and Harvey) J. Agardh	Figure of Eight Island, Esperance Bay, South Australia (N. Goldberg, 2.xi.2002, D95)	DQ472034	DQ472090
Stypopodium hawaiiensis (Doty and Newhouse) Abbott	Lanikai, Oahu, Hawaii (O. De Clerck, 25.iv.2003, ODC900)	DQ472040	DQ472095
Stypopodium flabelliforme Weber-van Bosse	NW side of Cabilao Island, Philippines (H. Verbruggen, 28.i.2004, HV661)	DQ472039	DQ472094
Taonia atomaria (Woodward) J. Agardh	Cap Creus, Spain (H. Verbruggen, v.2004, HV887)	DQ472041	DQ472096
Zonaria spiralis (J. Agardh) Papenfuss	Black Island, Esperance Bay, South Australia (N. Goldberg, 14.x.2002, D99)	DQ472031	DQ472087
Zonaria diesingiana J. Agardh	Manley Beach, Sydney, Australia (G. W. Saunders 10.iii.2001, GWS1015)	DQ472033	DQ472089
Zonaria subarticulata (Lamouroux) Papenfuss	Protea Banks, Kwazulu-Natal, South Africa (O. De Clerck and F. Leliaert, 9.vi.2003, KZN 2221)	DQ472032	DQ472088

TABLE 3. Tree statistics for combined and partitioned data sets using maximum parsimony.

	Base pairs (total /inform/ uninform)[a]	CI/RI	Length shortest tree (steps)	PBS[b]	Length if constrained to *rbc*L–26S tree (steps)[c]	No. of shortest trees	No. of resolved nodes[d]
*rbc*L + 26S combined	2419/585/162	0.439/0.580	2440	317.3	NA	13	38
26S	1212/246/79	0.680/0.786	678	196.7	694 (2.4%)	125	33
*rbc*L – all characters	1207/339/83	0.355/0.504	1718	120.6	1734 (0.9%)	10	21
*rbc*L – pos1,2	805/67/38	0.464/0.564	248	26.1	269 (8.5%)	>10.000	9
*rbc*L – pos3	402/272/45	0.343/0.510	1440	94.5	1458 (1.3%)	6	32

[a]Number of base pairs in partitions and number of potentially informative character changes.
[b]Total partitioned Bremer support (PBS) of each partition from combined analysis of all data.
[c]Minimum length of a tree when constrained to the topology of the combined analysis, with the percentage increase in parentheses.
[d]Number of resolved nodes in a strict consensus tree of all shortest trees.
NA, not available.

by the C1 helix could not be aligned between in-group and out-group taxa. A modified block-coding approach was applied to circumvent this difficulty (Geiger 2002, Verbruggen et al. 2006). Additionally, 276 positions with ambivalent alignment, situated in the loop regions of the variable helices, were removed before phylogenetic analysis.

Data exploration, homoplasy, and phylogenetic information. In order to examine the extent to which homoplasy influenced the resulting phylogeny, several approaches were taken. Given the higher mutation rates of third codon positions relative to first and second codon positions in protein-encoding genes, the *rbc*L data were tested for substitutional saturation by plotting the observed number of substitutions against corrected distances estimated from maximum likelihood (ML) using a GTR + I + Γ model with parameters estimated in PAUP. The number of transversions and transitions was also plotted against uncorrected distances for the first and second codon position and the third position, respectively. To examine the contribution of each gene, tree searches were performed under maximum parsimony (MP; settings as below, but without Goloboff fit) using varying subsets of the combined data set (*rbc*L all positions, *rbc*L non-third codon positions, *rbc*L third codon position, 26S). Partitioned Bremer Support (PBS, Baker and DeSalle 1997) was computed for each data partition after producing constraint tree files in TreeRot (Sorenson 1999). Likewise, the added tree length for each partition was calculated by constraining it against the tree resulting from the complete data set.

Phylogenetic analysis. MP and ML analyses of the *rbc*L, containing 60 sequences belonging to 47 different species, were performed using PAUP 4.0b10 (Swofford 2002). MrBayes 3.0 (Huelsenbeck and Ronquist 2001) was used for Bayesian phylogenetic inference (BI). MP analyses consisted of heuristic searches with 1000 random sequence addition replicates and Tree bisection reconnection (TBR) with the option MULTREES and the Goloboff fit criterion ($K = 2$, Goloboff 1993) in effect. The optimal models of nucleotide substitution for ML were determined in Modeltest 3.6 according to the Akaike Information Criterion (Posada and Crandall 1998, Posada and Buckley 2004). ML analyses were performed under the same heuristic search settings as MP, but with the number of random sequence addition replicates limited to 100. Bootstrap analyses consisted of 1000 replications of full heuristic searches under MP and 100 replications with the number of rearrangements limited to 10.000 (or 3600 s) for each replicate under ML using a neighbor-joining tree as the starting tree. BI analyses were performed using a GTR + I + Γ model in accordance with the recommendations of Huelsenbeck and Ranalla (2004), who demonstrated that the most complex models offer the highest probability of estimating the correct tree topology even if the matrix can be summarized in a more simple model. Posterior probabilities were calculated using a Metropolis-coupled Markov chain Monte Carlo approach with sampling according to the Metropolis–Hastings algorithm. The analysis used four chains, one cold and three incrementally heated. Each run consisted of 1 million generations and was sampled every 100th generation. In order to determine the burn-in value, the likelihood values were plotted against generation numbers.

A more restricted data set, containing *rbc*L and 26S sequences of 38 taxa, was also analyzed in combination, following an incongruence length difference test (ILD test, Farris et al. 1995) performed in PAUP 4.0b10 (1500 replications of simple sequence addition and TBR), which suggested no significant topological incongruence between 26S and *rbc*L data sets ($P = 0.01$), following recommendations of Cunningham (1997) on critical α values. MP and ML analyses were performed as for the *rbc*L data set. The BI settings allowed for different substitution models between both genes.

The likelihood of alternative topologies was tested against the optimal ML topology using Shimodaira–Hasegawa tests (SH tests) as implemented in PAUP 4.0b10 using RELL optimization and 1000 bootstrap replicates (Shimodaira and Hasegawa 1999, Goldmann et al. 2000). The SH tests were performed on a pruned data set (*rbc*L and 26S) containing only the in-group taxa and *Scoresbyella profunda* as out-group, which did not affect the topology of the in-group. This data set (in-group taxa + *Scoresbyella*) was used to map various morphological and anatomical characters in MacClade 4.0 (Maddison and Maddison 2000).

RESULTS

Data exploration, homoplasy, and phylogenetic information. Tree searches under MP of the combined *rbc*L and 26S character matrix resulted in 13 shortest trees of 2440 steps. The trees based on the two gene regions analyzed separately were highly congruent in overall topology (Treebase study accession number S1523). This is also reflected in the low added tree length (0.9%–2.4%) when the partitioned data sets are constrained against the shortest tree resulting from the combined analysis (Table 3). The total number of sites of 26S and *rbc*L was roughly similar after exclusion of ambiguously aligned regions, but the number of potentially parsimony-informative sites was slightly higher for the *rbc*L data (28%) than for the 26S data (20%). The number of steps in the

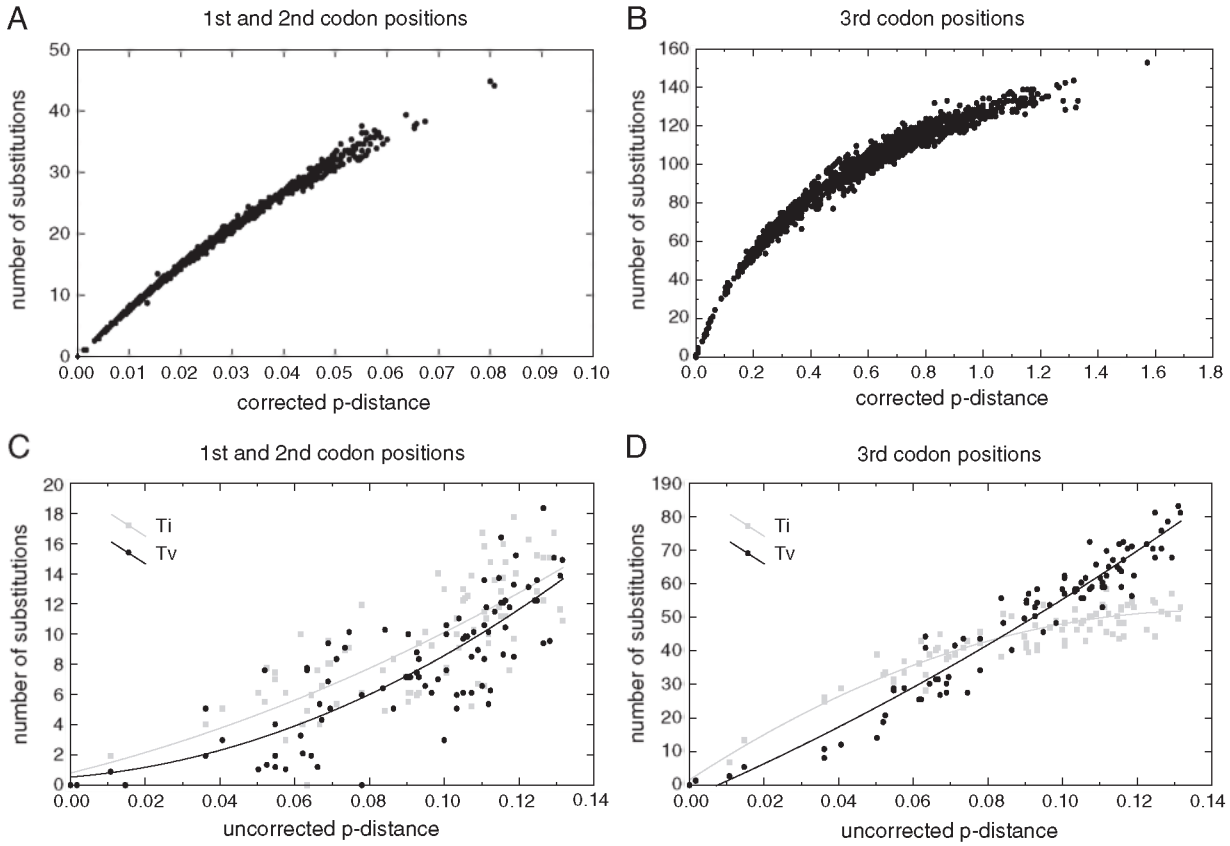

FIG. 2. Analysis of saturation of character variation of the *rbc*L gene. Corrected *p*-distances are calculated using a GTR + *I* + Γ model with parameters estimated in PAUP for each specific data partition. Panels at the top (A, B) show corrected *p*-distances versus observed substitutions for the first and second codon position (A) and the third codon position (B). Panels at the bottom (C, D) show the observed transitions and transversions of the same data partitions.

parsimony analysis, however, was lowest in the 26S data, which is also translated in the highest internal consistency and a higher number of resolved nodes compared with the *rbc*L data set (Table 3). From the PBS values, it is also clear that the 26S data have a higher contribution to branch support in the combined analysis than do the *rbc*L data. Despite a higher internal consistency, 26S data produced more most-parsimonious trees (125 MPTs vs. 10 MPTs for the *rbc*L data). Possible indications of substitutional saturation of the *rbc*L gene in the Dictyotales are confirmed when the corrected pairwise distances are plotted against the number of observed substitutions (Fig. 2). Whereas the first and second codon positions show a near-linear correlation (Fig. 2A), the plot for the third codon position levels off with increasing genetic distance (Fig. 2B). When subdivided into transitions and transversions it is evident that third codon saturation can largely be ascribed to transitions (Fig. 2, C and D), which are known to occur more often than transversions. Additional MP analyses of the *rbc*L data partitioned according to codon position resulted in trees that differed greatly in topology and resolution, but more importantly showed that the vast majority of the phylogenetic information is situated in the third codon position (272 potentially informative characters vs. 67 for the first and second positions combined). An MP analysis based on the non-third codon position only, being apparently unmarred by saturation, resulted in over 10,000 trees, the strict consensus tree of which had few resolved nodes. MP analysis of third codon positions yielded higher resolution, with 32 nodes resolved.

Phylogenetic analyses. The *rbc*L data set (60 sequences, 47 different taxa) consists of 1207 characters, 364 of them being potentially parsimony informative. Parsimony analysis with Goloboff's implied weighting resulted in a single MPT (CI = 0.336, RI = 0.664, Goloboff fit = −200.55). Modeltest found the general time reversible model with substitution rates across sites following a gamma distribution (shape $\alpha = 0.5603$) and a proportion of invariable sites of 0.8116 to yield the best fit to the *rbc*L character matrix (GTR + *I* + Γ) according to the AIC. The substitution rate matrix estimated by PAUP was A–C = 1.5920, A–G = 3.7321, A–T = 1.7970, C–G = 0.7122, C–T = 7.4388. The various phylogenetic analyses of the *rbc*L data matrix were highly congruent, differing only in the relative placement of clades that received little to no support

(Fig. 3). The relationships between the *Padina* clade; the clade containing *Zonaria*, *Distromium*, and *Homoeostrichus*; and the remaining taxa were unresolved under ML and BI. *Padina* was resolved to be sister to *Dictyopteris*, *Stypopodium*, and *Taonia* under MP. *Zonaria*, *Homoeostrichus*, and *Distromium* formed a monophyletic yet unsupported clade under ML and MP. Bayesian inference resolved *Homoeostrichus* and *Distromium* as sister to *Dictyopteris*, *Taonia*, *Stypopodium*, *Scoresbyella*, and the Dictyoteae. Results also indicate a sister-group relationship of *Stypopodium*, *Taonia*, and *Dictyopteris* to *Scoresbyella* and the rest of Dictyoteae. In general, support for relationships among genera belonging to the Zonarieae was very low, regardless of the type of analysis. The Dictyoteae was consistently resolved as a monophyletic clade, but support again was lacking. *S. profunda*, which is currently assigned to its own family, was interestingly resolved as the nearest relative of the monophyletic Dictyoteae. The latter was composed of four major, well-supported clades: (1) a lineage composed of *D. radicans*, *Dil. suhrii*, and *Dil. marginatus*; (2) a lineage containing *D. cervicornis* and *D. crispata*; (3) a lineage consisting of *Dil. fastigiatus*; and (4) a large clade containing the remaining representatives of the *Dictyota*, *Dilophus*, *Pachydictyon*, *Glossophora*, and *Glossophorella* (Fig. 3). The relationships among these four clades were generally only supported by posterior probabilities and lack bootstrap support. Within the fourth lineage, most of the currently recognized genera are polyphyletic (*Dilophus*, *Pachydictyon*) or paraphyletic (*Dictyota*). *Glossophorella dhofarensis* forms a well-supported sister species to *D. canaliculata*. Only *Glossophora*, represented by three specimens attributed to two different species, forms a monophyletic clade without BP or PP support. Although some terminal and a few subterminal clades usually receive moderate to good support, relationships between the various species are generally poorly resolved.

The combined *rbc*L and 26S data set (41 sequences, 38 different species) includes 2419 characters, of which 585 were potentially parsimony informative. MP, with Goloboff weighting implied, resulted in a single tree (CI = 0.326, RI = 0.581, Goloboff fit = − 192.91). The Akaike information criterion implemented in Modeltest suggested a GTR + I + Γ model with shape parameter $\alpha = 0.7767$ and a proportion of invariable sites of 0.5603 fit the data best. The substitution rate matrix was defined as A–C = 1.0845, A–G = 3.2515, A–T = 3.3118, C–G = 1.2115, C–T = 7.2703. A single ML tree was recovered with log-likelihood = − 15,526.35. The log-likelihood of trees hit in the MCMCMC chains reached stationarity after 7000 generations. The three inference methods resulted in well-resolved trees that differed very little in overall topology. Only the ML tree is shown (Fig. 4); MP and BI trees are available from Treebase (accession number: S1523). The topologies of the respective trees did not differ substantially from the analyses based only on the *rbc*L data. The major difference is an overall enhancement of the resolution at the generic level. Although the position of *Padina* relative to the other taxa remains unresolved, there is good support for most relationships especially under ML or BI. *Dictyopteris*, *Taonia*, and *Stypopodium* form a well-supported clade sister to *Scoresbyella* and the Dictyoteae. Relationships in the larger *Dictyota–Dilophus–Glossophora–Glossophorella–Pachydictyon* clade remain rather poorly supported, especially by bootstrap percentages. SH tests conducted on a subset of the data, the Dictyoteae as in-group and *Scoresbyella* as out-group, unequivocally rejected topologies enforcing monophyly of *Dictyota*, *Dilophus*, and *Pachydictyon*, the genera represented by more than a one species in the combined data set (Fig. 5). Similarly, sister relationships of *Glossophora* and *Glossophorella*, both represented by a single sequence, with respect to the remaining Dictyoteae were likewise rejected.

DISCUSSION

Homoplasy and phylogenetic information. Evolutionary biologists are united in their opinion that homoplasy is a confounding factor in recovering phylogenies. In its most common sense, *homoplasy* equates to an error in homology assessment, a factor that needs to be identified and understood before interpretation of the outcome of a phylogenetic analysis. As a direct consequence of this problem, numerous measures or indices of homoplasy have been developed over the past 25 years to effectively analyze the phenomenon and to predict its bearing on the inference of natural relationships (Sanderson and Hufford 1996). Fast-evolving sites are commonly regarded as a likely source of homoplasy and become particularly problematic when inferences about deeper relationships are needed. As a consequence, the use of fast-evolving sites in phylogenetic analysis has been extensively debated, with calls made for down-weighting or excluding potentially homoplastic variation (Swofford et al. 1996, Pisani 2004, Vogler et al. 2005) or, on the other hand, serious pleas made to appreciate the phylogenetic signal emanating from those sites (Börklund 1999, Källersjö et al. 1999). A particular case of fast-evolving sites is represented by third codon positions in protein-coding genes. As opposed to first and second codon positions, mutations at the third position are often silent, leading to increased variability and rapid saturation (Swofford et al. 1996). The data in our study confirm the widely held belief that third codon positions are often saturated. This is obvious from the scatterplots of the corrected pairwise distances against the number of observed substitutions (Fig. 2). Non-third codon positions show a near-linear correlation, whereas the curve of the third codon position levels off considerably, indicating saturation. In depth exploration reveals that these indications of saturation are primarily the result of transitions rather than transversions. The homoplastic variation in the *rbc*L data set is mirrored in lower consistency and retention indices

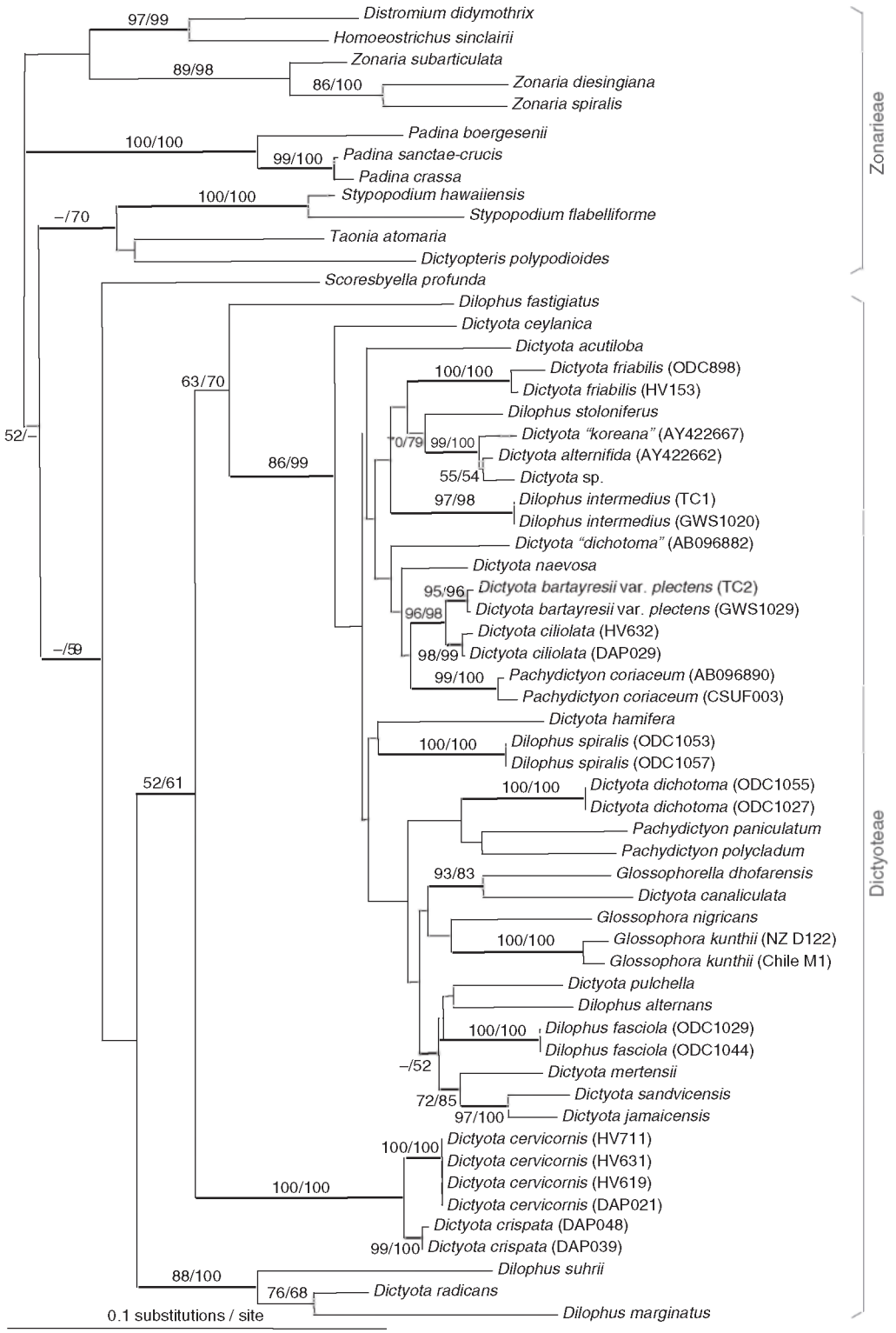

FIG. 3. Phylogram of the single maximum likelihood (ML) tree ($-\ln L = 10{,}992.93$) based on *rbc*L gene sequences (1207 bp) using a GTR + I + Γ model. The bootstrap values of both ML and maximum parsimony (MP) analyses supporting the corresponding branches are indicated if higher than 50 (MP/ML). Thick branches represent nodes receiving Bayesian posterior probabilities higher than 0.95.

of the obtained topologies as compared to the values obtained from the 26S data. Although the more rapidly evolving sites are highly homoplastic, the third codon position contains the bulk of the phylogenetic data. Removal of this position from the data set does not result in any improvement of phylogenetic reso-

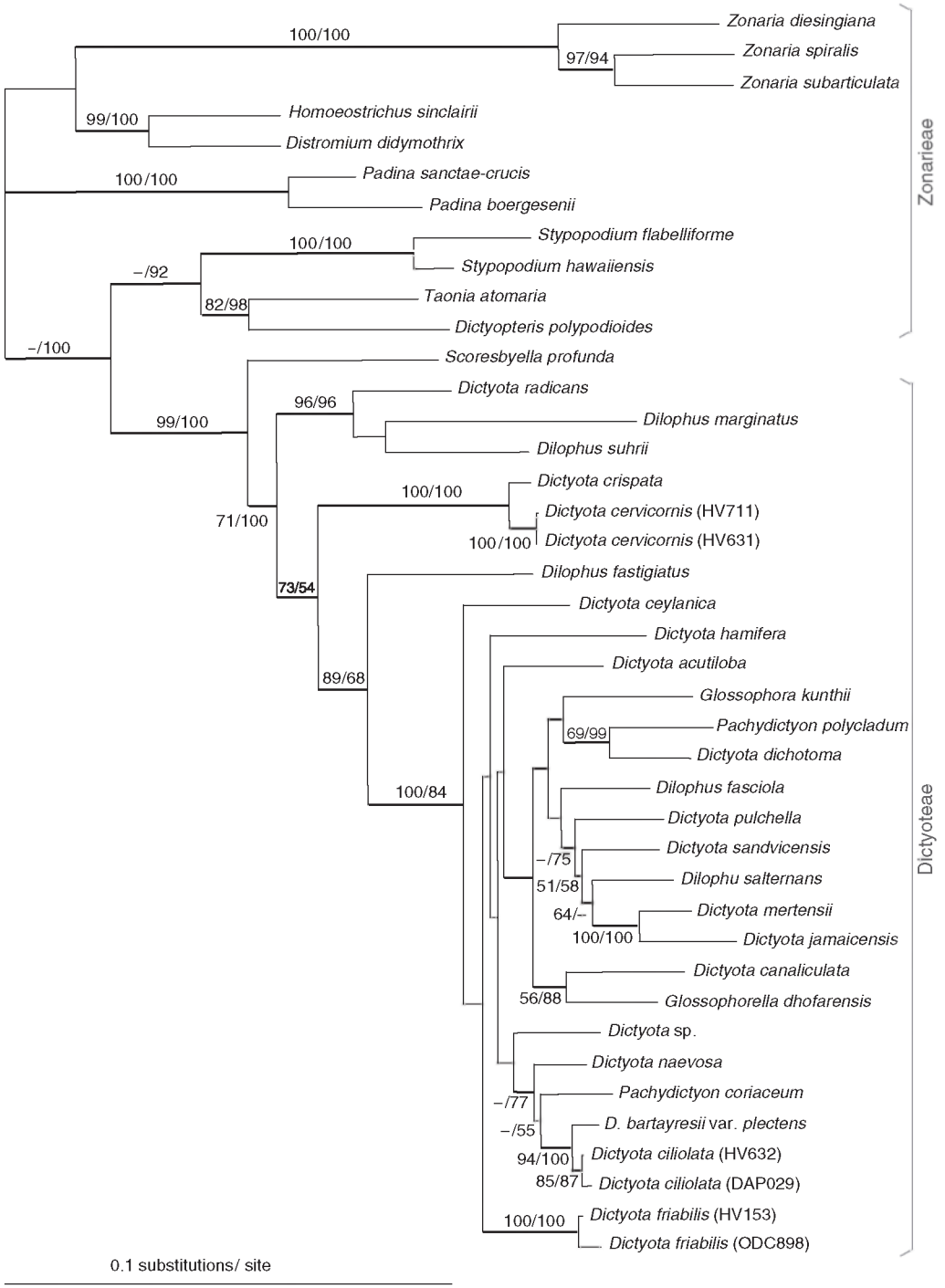

FIG. 4. Phylogram of the single maximum likelihood (ML) tree ($-\ln L = 15{,}526.35$) based on combined *rbc*L and 26S sequences using a GTR + I + Γ model. The bootstrap values of both ML and maximum parsimony (MP) analyses supporting the corresponding branches are indicated if higher than 50 (MP/ML). Thick branches represent nodes receiving Bayesian posterior probabilities higher than 0.95.

lution. On the contrary, analyses limited to the first and second position of the *rbc*L data, comprising a meager 67 potentially parsimony-informative characters, resulted in thousands of equally most parsimonious trees, the strict consensus tree of which had only nine resolved nodes (Table 3). Surprisingly, a data set including just the third codon position resulted in only six trees that, if constrained against the definite tree resulting from the combined 26S–*rbc*L data set, was only 1.3% longer. Furthermore, the topology of those trees was in relatively good agreement with the final tree. These results support the inclusion of fast-evolving sites in the Dictyotales data set, even though they are homoplastic. Earlier,

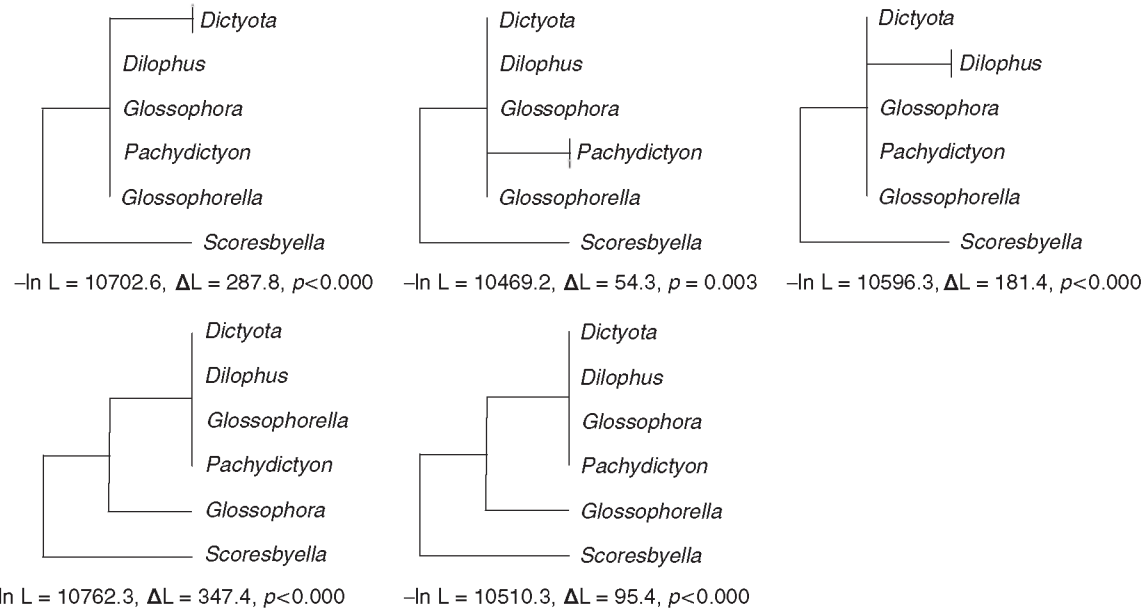

FIG. 5. Results of the Shimodaira–Hasegawa tests for assessing the likelihood of alternative topologies using various constraint trees.

Siemer et al. (1998) and Draisma et al. (2001) arrived at similar conclusions regarding saturation of the third codon position of the *rbc*L gene in brown algal phylogenies. The analyses and the conclusions presented in this study should, however, not form a safeguard toward any future study, and we would advocate the necessity to analyze the signal-to-noise ratio in data sets carefully case by case.

Classification of the Dictyotales. Members of the Dictyoteae, all of which are characterized by a single, horizontally oriented apical cell, are derived from a paraphyletic Zonarieae in our analyses. These observations, despite meager support, are in agreement with Lee and Bae (2002) and Hoshina et al. (2004), who resolved *Spatoglossum*, *Dictyopteris*, and *Stypopodium* as being sister taxa to the Dictyoteae. It should be pointed out, however, that tribal relationships in the Dictyotales can only be fully understood if non-dictyotalean out-group taxa are incorporated in the analyses.

Interestingly, *S. profunda*, a species not included in previous studies and the sole representative of the Scoresbyellaceae, is resolved as being the closest relative of the Dictyoteae. Womersley (1987) placed *S. profunda* in its own family because of the lengthwise orientation of the apical cell, although he did comment on the similarities *Scoresbyella* otherwise seemed to have with many Dictyoteae. The male reproductive structures, the only reproductive structures known to date, are essentially identical to those encountered in the Dictyoteae in which the antheridia form scattered to confluent sori surrounded by three to four rows of elongate, unicellular paraphyses. This would indicate that the presence of a group or row of apical cells is ancestral in this order and that the transition toward a single apical cell has occurred only once. The orientation and mode of cell division in *Scoresbyella* is highly reminiscent of *Dictyotopsis propagulifera*, an enigmatic monostromatic alga of mangrove habitats in the tropical western Pacific Ocean, which is likewise placed in its own family within the Dictyotales (Allender 1980). In both species, the apical cell is wedge-shaped or lenticular and cuts off cells laterally from two faces rather than a single convex surface. Further segmentation of the derivative cells in *Scoresbyella* is similar to that process throughout the Dictyoteae, resulting in differentiation between a cortex and a medulla. Such tangential cell divisions do not occur in *Dictyotopsis*, making it the only monostromatic representative of the Dictyotales. The phylogenetic position of *Dictyotopsis* could not be assessed during the present study due to a lack of specimens suitable for DNA analysis.

At present, generic delineation within the Dictyoteae, although repeatedly questioned in the past, is still almost exclusively based on vegetative anatomical characters involving medullary and cortical structures. This traditional classification, however, is completely irreconcilable with our molecular phylogenies. Previous studies (Lee and Bae 2002, Hoshina et al. 2004, Kraft et al. 2004, Hwang et al. 2005) initially lent support to the traditional classification, but this was clearly the result of limited taxon sampling. These studies invariably included between three and five different species, covering only three of five genera. *Glossophora* and *Glossophorella* were not included in these analyses. Increased inter- and intrageneric taxon sampling in the Dictyoteae leads to the completely different insight that none of the current genera are monophyletic. SH tests, likelihood-based topology tests, were used to check whether or not topologies in which monophyly of the current genera was enforced fitted the data equally well as the tree obtained from ML analysis. All

topologies with enforced monophyly of one of the genera turned out to be significantly worse than the obtained ML tree (Fig. 5). The highly homoplastic nature of vegetative characters becomes even more evident when mapped on the molecular phylogeny that incorporates only the Dictyoteae with *Scoresbyella* as out-group (Fig. 6). A multilayered medullary structure, the defining character of the genus *Dilophus*, is seen to have evolved independently on several occasions. Nevertheless, a broad tendency for members of the tribe to display a multilayered medulla in the basal clades and to move toward a unilayered medulla in the more derived taxa can be observed. Medullary thickness is shown to be heterogeneous and thus not to be useful as a diagnostic character of genera delineation. Some species are characterized by a medulla comprised of several layers over the entire width in the middle and proximal parts of the thallus but with a unilayered or only marginally multilayered medulla above (e.g. *Dil. fastigiatus*, *Dil. gunnianus*, *Dil. robustus*, *Dil. spiralis*, *Dil. suhrii*; Hamel 1939, Phillips 1992, De Clerck 2003). In other species, duplications of the medullary layer are effectively restricted to the margins over the entire length of the thallus, except perhaps at the extreme basal parts (e.g. *Dil. alternans*, Hörnig et al. 1992a, b). In *Dil. fasciola* and *Dil. crenulatus* the medulla is uniformly unilayered except for the lowermost basal portion, where it becomes two to three layers thick (Feldmann 1937, Nizamuddin and Gerloff 1979).

Duplications of medullary cells often coincide with the means of attachment, as several of such species are attached by terete stoloniferous holdfasts, whereas those with monostromatic medullas are anchored by basal discs or scattered rhizoids. Transverse sections of stoloniferous holdfasts always seem to reveal a multilayered medulla (De Clerck 2003, p. 137, Fig. 51E). A closer look at the structure of the transition zone between tendrils and the expanded fronds above, however, reveals that the traditional distinction between medullary and cortical cells is not as obvious as has been assumed. The parenchymatous nature of the stoloniferous holdfast is the result of divisions in both the cortical and medullary layers (De Clerck and Coppejans 2003). Apart from those structural duplications, an occasional two-layered medulla is commonly observed in many species. Actually, just about any species seems capable of locally producing a two-layered medulla in the expanded fronds. Moreover, the number of medullary layers seems at least to some degree influenced by external conditions, as culture experiments have shown that this feature depends on the culture medium in several species (Hörnig et al. 1992a).

Similarly, the structure of the cortex in members of the Dictyoteae is highly homoplasious. Even within the long-standing genus *Pachydictyon*, the term "multilayered cortex" encompasses a wide variety of cortical structures, ranging from species characterized by a cortex that is essentially unilayered but with the odd cortical cell duplication in the basal parts of the thallus (e.g. *P. aegerrime*, Allender and Kraft 1983) to species characterized by a cortex 10–12 cells thick (*P. coriaceum*, Okamura 1899). Occasional duplication of cortical cells, especially along the thallus margins, is a fairly common phenomenon among the more robust *Dictyota* or *Dilophus* species and has generally been given little or no attention, with the noteworthy exception of Dawson's (1950) study of Mexican Pacific Dictyoteae. Phillips (1992) illustrated duplicated cortex cells in several *Dilophus* species, but did not further remark on the character. An interesting example of cortical variability is *D. naevosa*, in which the cortex may become up to two to six cells thick in the proximal parts (Womersley 1987). Why it should have remained in *Dictyota* in light of this classically determinative feature, however, has never been discussed.

Surface proliferations are restricted to a few species, but they are distributed among all of the established genera of the Dictyoteae. However, the high density of surface proliferations observed in *Glossophora* and *Glossophorella* is usually not encountered in the other genera. Comparably high densities have, however, been observed in *Dil. intermedius* (Allender and Kraft 1983), but in this species these proliferations never bear reproductive structures as is occasionally observed in *Glossophora* (Womersley 1987). In *D. crispata*, *D. cervicornis*, and *D. mertensii*, surface proliferation density varies greatly. One should differentiate between surface proliferations as outgrowths from the vegetative tissue and those that are the result of the *in situ* germination of sporangia. The latter condition has been discussed in detail for *Dil. fasciola* by Feldmann (1937), who ascribed it to and apomeiotic development of spore mother cells. In fact, *in situ* germination of sporangia is a widespread phenomenon recorded for many species, among them *D. dichotoma*, the generitype of *Dictyota* (Hwang et al. 2005).

As opposed to the apparent limited taxonomic utility of the aforementioned vegetative characters, mapping of additional characters on the molecular tree (Fig. 6) does result in clear-cut patterns that can form the basis of a new classification. The presence of aberrant antheridial paraphyses was first reported for *D. magneana* (Coppejans et al. 2001) and later for *D. crispata* (De Clerck 2003). Paraphyses associated with antheridia are a common feature in the Dictyotales, and the different types are considered to be important diagnostic characters at the genus level (Phillips 1997, Phillips and Clayton 1997). In all Dictyoteae for which male reproductive structures are known, the antheridia are surrounded by three to six rows of unicellular, elongated cortical cells devoid of chloroplasts. The inner row of paraphyses (i.e. the paraphyses bordering the antheridia) is of the same height as the antheridia. The paraphyses observed in *D. crispata* and *D. magneana* differ not only in being multicellular and pigmented, but also in overtopping the peripheral antheridia. Other differences include the fact that the antheridial sori in *Dictyota* are gener-

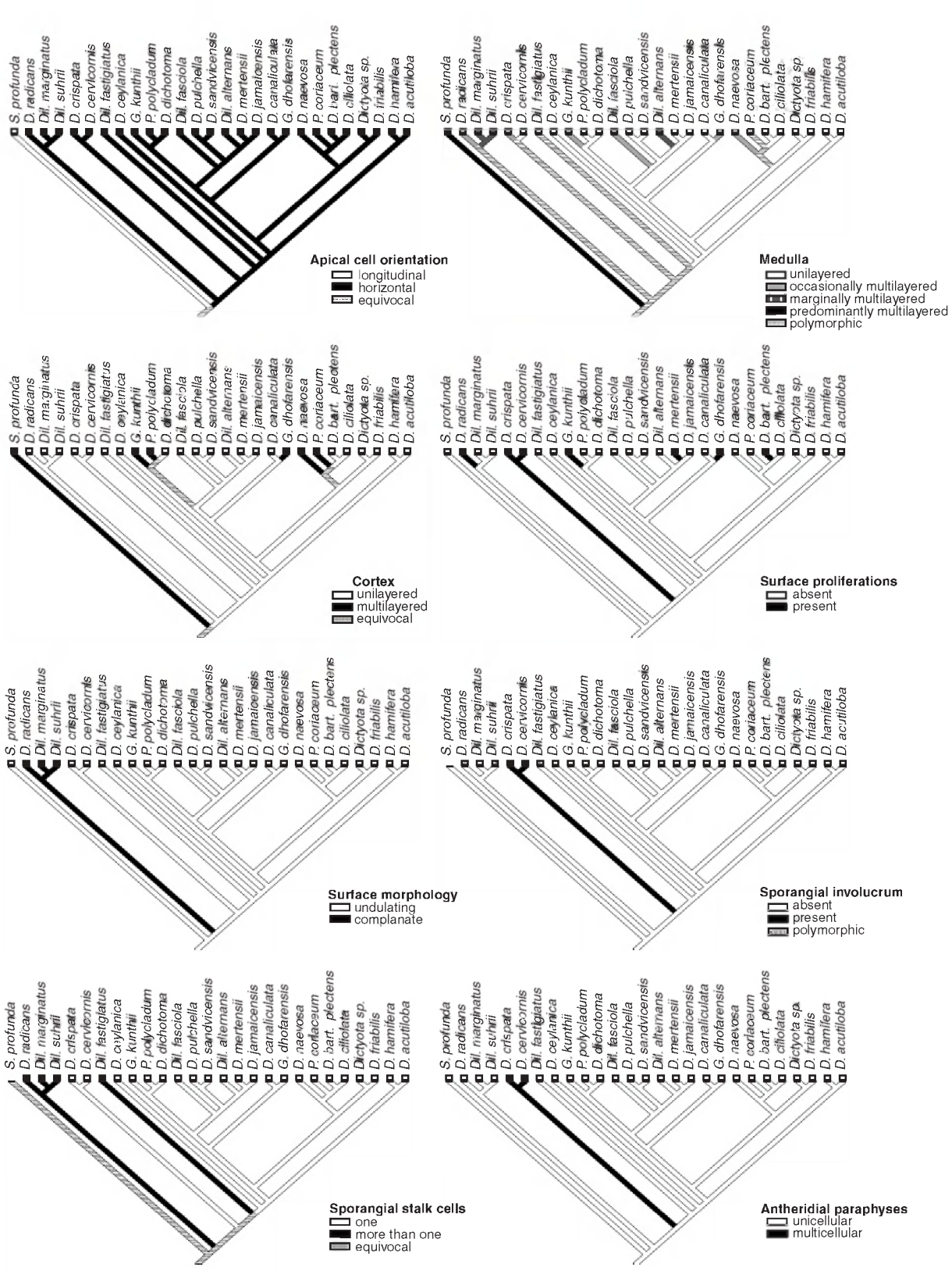

FIG. 6. Mapping of eight vegetative and reproductive characters onto a maximum likelihood tree, containing only the in-group taxa (Dictyoteae) and *Scoresbyella* as out-group.

ally larger than 200 μm in diameter and often spread to become confluent with neighboring sori, whereas they are smaller than 200 μm and remain discrete in *D. crispata* and *D. magneana* (De Clerck 2003).

Male reproductive structures have not been observed with certainty in *D. cervicornis*. Abbott and Huisman (2004) reported multicellular paraphyses for *D. acutiloba* J. Agardh from the Hawaiian Islands and commented on the similarity of that species with *D. cervicornis*, stating that both species "share all major characteristics." Conspecificity of these taxa is, however, negated by our molecular phylogeny in which both species are positioned in completely different clades. A possible explanation could be that the male plant depicted by Abbott and Huisman is in fact representative of *D. cervicornis*, the presence of which has gone unnoticed in Hawaii due to its striking habit resemblance to *D. acutiloba*. The *D. cervicornis–crispata* clade is further characterized by the presence of a conspicuous involucrum surrounding the sporangia. Such an involucrum consists of a collar of inflated and radially elongated cortical cells and was first noticed by Jaasund (1970). In transverse section, this results in a well-developed cup surrounding the basal part of the sporangium. Although the involucrum may go unnoticed in mature sporangia when viewed from the thallus surface, once the spores have been released a clear collar of involucral cells becomes evident (Coppejans et al. 2001: pl. 1F–H). In *D. radicans* and *D. suhrii* (De Clerck 2003), as well as in some species of *Dilophus* studied by Phillips (1992, e.g. *Dil. fastigiatus* and *Dil. robustus*), the cortical cells in the immediate vicinity of the sporangium may elongate somewhat, but the resulting involucrum always remains inconspicuous.

The species possessing inconspicuous involucres are perhaps better characterized by the number of stalk cells subtending their sporangia. A sporangial stalk cell is formed in most Dictyotales apart from *Lobophora* and *Zonaria* (Phillips and Clayton 1997). Ontogenetically, a stalk cell is formed in the early stages of sporogenesis by a mitotic division of an enlarged cortical cell that results in a basal stalk cell and a distal tetraspore mother cell (Williams 1904, Kumagae et al. 1960). Phillips (1992) was the first to appreciate the taxonomic significance of sporangia subtended by multicellular stalks, which were initially reported for *Dil. fastigiatus*, *Dil. marginatus*, and *Dil. robustus*. Later, the presence of two-celled stalks was also reported for *D. radicans* and *Dil. suhrii* (De Clerck 2003). Based on the molecular phylogeny, it seems most likely that this character evolved independently on two occasions in the Dictyoteae, once in *Dil. fastigiatus* and once in the *D. radicans*, *Dil. marginatus*, and *Dil. suhrii* clade. In combination with involucral morphology, however, this points to a clear anatomical discrimination of the *D. radicans–Dil. marginatus–Dil. suhrii* clade on the one hand versus *Dil. fastigiatus* on the other. In the first clade, all species are also morphologically characterized by undulating thalli, whereas the fronds of *Dil. fastigiatus* are complanate and smooth. The rugose thallus surface of *Dil. robustus*, also characterized by two sporangial stalk cells but due to lack of suitable material not included in the analyses, could possibly be interpreted as derived from an undulating thallus.

Taxonomic conclusions. The molecular and morphological results presented leave little doubt that the current generic classification of the Dictyoteae does not reflect the evolutionary history of the tribe. This incongruence between the molecular phylogeny and the current classification could form the impetus for a very broad interpretation of the genus *Dictyota* that would include all species characterized by a single transversely oriented apical cell regardless of differences related to vegetative or reproductive structures. On the other hand, one may argue that three or four separate genera are warranted. Based on the facts that the molecular phylogeny is well resolved (and alternative topologies strongly rejected) and that diagnostic vegetative and reproductive criteria are available, we opt for a somewhat less than totally inclusive definition of *Dictyota* and the description of two new genera (described below) based on molecular and morphological data. The taxonomic position of the genus *Dilophus* is left undecided at this stage, because material of *Dil. gunnianus* (the generitype of *Dilophus*) suitable for DNA extraction was not available and also because of the phylogenetic position of *Dil. fastigiatus*. The latter occupies a position sister to the large *Dictyota–Dilophus–Glossophora–Glossophorella–Pachydictyon* clade and is differentiated from the larger clade by the presence of two rather than one stalk cells. *Dil. gunnianus* and *Dil. fastigiatus* are morphologically similar to such an extent that less typical growth forms are hard to assign to one species or the other. The number of sporangial stalk cells does, however, differentiate both species unequivocally, *Dil. gunnianus* being characterized by a single stalk cell (Phillips 1992). Extrapolating from the morphological observations, one would expect *Dil. gunnianus* to be resolved within the *Dictyota–Dilophus–Glossophora–Glossophorella–Pachydictyon* clade. In the absence of sequence data for the type species however, one cannot rule out a close relationship between *Dil. fastigiatus*, *Dil. gunnianus*, and *Dil. robustus*, and hence the taxonomic conservatism that we adopt for the moment still regards *Dilophus* as a valid genus.

The emended description of *Dictyota* and diagnoses of the new genera *Canistrocarpus* and *Rugulopteryx* are as follows:

Dictyota Lamouroux, J. Bot. (Desvaux) 2: 38 (1809) nom. cons.

Thallus flattened, ribbon-like, erect or prostrate, with smooth, dentate, crenulate or ciliate margins; attachment by basal rhizoids or marginal rhizoidal processes scattered along the edges of the thallus or restricted to the base, stoloniferous holdfasts present or absent; branching dichotomous, anisotomous or alternate, rarely falcate; apices obtuse, rounded, apiculate or acute; phaeophycean hairs and superficial

proliferations present or absent; thallus differentiated into a cortex and a medulla, the relative number of layers variable. Sporangia isolated, grouped in sori or surrounding a central hair tuft, lacking a conspicuous involucrum of sterile cells, subtended by a single stalk cell. Antheridia subtended by a single stalk cell, arranged in sori, surrounded by hyaline, unicellular paraphyses. Oogonia subtended by a stalk cell, arranged in sori.

Type species: Dictyota dichotoma (Hudson) Lamouroux.

Synonyms: Bicrista Kuntze, 1898, *Dichophyllium*, Rev. Gen. pl. 3(3): 397; Kützing, Phycol. Gen. 337:14–16 (1843); *Glossophora* J. Agardh, Lunds Univ. Årsskr. 17, Afd. Math. Naturvetensk. 4:108 (1882); *Glossophorella* Nizamuddin et Campbell, Pak. J. Bot. 27:258 (1995); *Pachydictyon* J. Agardh, Lunds Univ. Årsskr. 29, Afd. Kongl. Fysiogr. Sällsk. Lund Handl. 9:81 (1894).

The nomenclatural history of *Dictyota* Lamouroux and the reasons for its conservation against *Padina* Adanson are explained in detail by Silva (1952). Nomenclatural changes resulting from the merger of *Glossophora*, *Glossophorella*, and *Pachydictyon* with *Dictyota* are listed here:

Dictyota aegerrime (Allender et Kraft) De Clerck, comb. nov.

Basionym: Pachydictyon aegerrime Allender et Kraft, Brunonia 6:116, figs. 116D, E and 124C, E (1983).

Dictyota coriacea (Holmes) I. K. Hwang, H. S. Kim W. J. Lee, 2004: 189.

Basionym: Glossophora coriacea Holmes (1896): 251.

Synonyms: Pachydictyon coriaceum (Holmes) Okamura, 1899: 39; *Glossophorella coriacea* (Holmes) Nizamuddin *in* Nizamuddin and Campbell (1995): 259.

Dictyota dhofarensis (Nizamuddin et Campbell) De Clerck, comb. nov.

Basionym: Glossophorella dhofarensis Nizamuddin et A.C. Campbell, Pak. J. Bot. 27:258, Figs. 1 and 2 (1995).

Dictyota paniculata J. Agardh (1841): 5.

Synonyms: Pachydictyon paniculatum (J. Agardh) J. Agardh (1894): 84; *Dictyota minor* Sonder (1845): 50; *Pachydictyon minus* (Sonder) J. Agardh (1894): 84.

Dictyota polyclada Sonder ex Kützing (1859): 10, pl. 23, Fig. 2.

Synonyms: Pachydictyon polycladum (Sonder ex Kützing) Womersley (1967): 216; *Dictyota furcellata* Sonder ex Kützing (1859): 11, pl. 24, Fig. 1, nom. illeg.; *Pachydictyon furcellatum* J. Agardh (1894): 83–84.

Dictyota kunthii (C. Agardh) Greville (1830): xliii.

Basionym: Zonaria kunthii C. Agardh (1821): pl. xv.

Synonyms: Glossophora kunthii (C. Agardh) J. Agardh (1882): 110; *Dichophyllium kunthii* (C. Agardh) Kützing (1843): 338; *Glossophora harveyi* J. Agardh (1882): 111.

Dictyota nigricans J. Agardh (1882): 94.

Synonyms: Glossophora nigricans (J. Agardh) Womersley (1967): 214; *Dictyota latifolia* J. Agardh (1894): 65, nom. illeg.; *Dictyota vittarioides* J. Agardh (1894): 65; *Spatoglossum grandifolium* J. Agardh (1894): 37.

Dictyota galapagensis (Farlow) De Clerck, comb. nov.

Basionym: Glossophora galapagensis Farlow, Proc. Amer. Acad. Arts Sci. 38: 90 (1902).

Canistrocarpus De Paula et De Clerck, gen. nov.

Thallus complanatus, fasciatus, erectus vel prostratus, margine laevigato, affixus rhizoideis basalibus aut terminalibus secus thallum distributis; dichotome et anisotome divisus, ramificationibus alternis vel cervicorneis, interdum ramulis recurvatis; apicibus rotundatis, apiculatis vel acutis; pili et prolificationes superficiales adsunt; cortex et medulla cellulis uno strato dispositis pro parte maxima, aliquando duplicatis basim; sporangia solitaria vel in soris aggregata, involucro cellulis sterilibus circumcincta, cellula basali singulari; antheridia pedicellata, in soris aggregata, paraphysibus multicellularibus et pigmentosis circumdatis; oogonia pedicellata, in soris aggregata.

Type species: *Canistrocarpus crispatus* (Lamouroux) De Paula et De Clerck, comb. nov. [Basionym: *Dictyota crispata* Lamouroux, J. Bot. (Desvaux) 2:44 (1809).]

Thallus flattened, ribbon-like, erect or prostrate, with smooth margins, attached by basal rhizoids or by marginal rhizoids scattered along the thallus; branching dichotomous to anisotomous or alternate or cervicorn or recurved; apices rounded, apiculate to acute; hairs and superficial proliferations present; cortex and medulla predominantly formed by a single layer of cells, one or both "tissues" occasionally duplicated in the basal proliferations; sporangia isolated or grouped in sori, borne on a one-celled stalk and surrounded by a well-developed involucrum of sterile cells; antheridia subtended by a stalk cell, in sori surrounded by pigmented multicellular paraphyses; oogonia subtended by a stalk cell, grouped in sori.

Type species: Canistrocarpus crispatus (Lamouroux) De Paula et De Clerck, comb. nov. [Basionym: *Dictyota crispata* Lamouroux, J. Bot. (Desvaux) 2:44 (1809).]

Etymology: From the Greek word *canistros*, meaning "basket," and *carpus*, or "fruit" or "seed," in reference to the involucrate sporangia.

Additional species: Canistrocarpus cervicornis (Kützing) De Paula et De Clerck, comb. nov.

Basionym: *Dictyota cervicornis* Kützing, Tab. Phycol. 9:11, pl. 24, Fig. 2 (1859).

Canistrocarpus magneanus (De Clerck et Coppejans) De Paula et De Clerck, comb. nov.

Note: See De Clerck (2003) for a complete list of synonyms.

Basionym: *Dictyota magneana* De Clerck et Coppejans *in* Coppejans et al., Crypt. Algol. 22:23 pl. 1A–L (2001).

Note: Although *C. magneanus* was not included in the molecular phylogenetic analysis, its relationship to *C. crispatus* and *D. cervicornis* is strongly indicated. The species differs only from *C. crispatus* by its completely prostrate habit, the distinctive blue-gray iridescence, and surface proliferations that are restricted to the marginal portions of the thallus.

Rugulopteryx De Clerck et Coppejans, gen. nov.

Thallus complanatus, fasciatus, erectus, margine laevigato, affixus rhizoideis basalibus; haptera stolonifera adsunt, restricta basim, emergentia pagina thalli vel apicibus deformatis; ramificationibus dichotome et anisotome; apicibus rotundatis; cellula apicali protrusa vel aliquantum emarginata; pili superficiales adsunt; prolificationes superficiales adsunt vel carentes; pagina undulata vel rugosa thallis adultis; cortex cellulis uno strato dispositis pro parte maxima, aliquando duplicatis basim; medulla cellulis uno strato dispositis praeter hapteris vel marginibus multistratosis; sporangia et gametangia limitata ad concavita paginarum; sporangia in pagina dispersa vel aggregata in soris, cellulis involucralibus inconspicuis circumcincta, cellula basali duplicata; antheridia pedicellata, aggregata in soris, paraphysibus unicellularibus et nonpigmentosis circumcinctis; oogonia pedicellata, aggregata in soris vel soris parvis dispersus.

Type species: *Rugulopteryx radicans* (Harvey) De Clerck et Coppejans, comb. nov. [Basionym: *Dictyota radicans* Harvey, Trans. Roy. Irish Acad. 22:536 (1855)].

Thallus flattened, ribbon-like, erect, with smooth margins; attached by rhizoids restricted to the basal parts of the thallus; stoloniferous holdfasts present, restricted to the base or emerging from the surface as well as from deformed apices; branching dichotomous to anisotomous; apices rounded; apical cell protruding to somewhat emarginate; phaeophycean hairs present; surface proliferations present or absent; surface undulating or rugose in mature thalli; cortex predominantly unilayered, with occasional duplications in the basal parts; medulla uniformly unilayered except for the stoloniferous holdfasts or multilayered near the margins; reproductive structures confined to concavities of the thallus surface; sporangia in small sori or in block-like patches, surrounded by an inconspicuous involucrum, with two stalk cells; antheridia subtended by a stalk cell, in sori surrounded by pigmented multicellular paraphyses; oogonia subtended by a stalk cell, grouped in sori or small-scattered groups.

Type species: Rugulopteryx radicans (Harvey) De Clerck et Coppejans, comb. nov. [Basionym: *Dictyota radicans* Harvey, Trans. Roy. Irish Acad. 22:536 (1855)].

Etymology: From the Latin word *rugulosus*, meaning "somewhat wrinkled," and *pteryx*, or "wing," in reference to the rugose surfaces of the thalli.

Additional species: Rugulopteryx suhrii (Kützing) De Clerck et Coppejans, comb. nov.

Basionym: *Stoechospermum suhrii* Kützing, Tab. Phycol. 9:17, pl. 41, Fig. 2 (1859).

Note: The basionym *S. suhrii* Kützing is a substitute name for *Zonaria marginata* Suhr (1834), the latter being a later homonym of *Z. marginata* C. Agardh (1824). See Silva et al. (1996) for a detailed account on the complicated nomenclatural history of this species and its taxonomic synonym *Dictyota suhrii* Murray.

Rugulopteryx marginata (J. Agardh) De Clerck et Coppejans, comb. nov.

Basionym: *Dilophus marginatus* J. Agardh, Lunds. Univ. Årsskr. 29, Afd. Kongl. Fysiogr. Sällsk. Lund Handl. 9:91 (1894).

Note: *Dictyota rugulosa* Lucas (1935) would be the correct name of this taxon were it to be referred to *Dictyota*.

The authors are indebted to the Fund for Scientific Research Flanders (Research Grant 3G002496 and postdoctoral fellowship to O. D. C.), the King Leopold III Fund for Nature Exploration and Conservation, and the Bijzonder Onderzoeksfonds (Ghent University) for a grant to H. V. and F. L. We thank Ellen Cocquyt and Caroline Vlaeminck for their assistance with the molecular work. Cathy De maire and Christelle VanKerckhove are acknowledged for caring over the GENT herbarium collection and for assistance with administration. We offer our sincere gratitude to Nisse Goldberg, Gary Saunders, Craig Schneider, John Huisman, Sylvain Faugeron, Tom Cowling, and Steve Murray, all of whom sent vouchers and silica dry samples from various locations. Last but not least we thank Paul Goetghebeur for correcting the Latin diagnoses.

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