Evolution and Diversification of the Hookeriales (Bryopsida) with emphasis on *Distichophyllum* (Daltoniaceae) and its allied genera.

Dissertation

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Meiner Familie

und meinen verstorbenen Großeltern gewidmet

Dedicated to my family

and late grandparents

献给我的家人

与已故祖父母

Contents:

General Introduction

The Hookeriales include ca. 650 species of predominantly tropical and Southern temperate pleurocarpous mosses that prefer humid forest habitats. Although, a small number of Hookerialean species occurs naturally in the northern temperate especially in Europe and North America, a few have been introduced through horticultural practice (e.g. *Calyptrochaeta apiculata* in United Kingdom). Hence, these mosses are often considered 'exotic looking' to bryologists from the north temperate countries. Nevertheless, for the last ca. 35 years, the circumscriptions and systematics of these mosses has become a challenging topic of debate. Putting emphasis on different morphological characters and thus proposing contradictory classifications, the genera have been rearranged in various ways by different authors. The different systematic concepts based on morphology range from two to nine families (e.g., Miller 1971, Crosby 1974), while the first molecular pilot phylogeny based on four-genes (Buck et al. 2005) put forward a seven-family classification and accepted 52 genera.

The Daltoniaceae has 14 genera occurring mainly in tropical Asia, Australasia and Southern South America, but less prominent in tropical America and Africa where members of the other Hookerialean families are more common. The family is among the most diverse in terms of habitat adaption from aquatic, to terrestrial (on soil or humus), to decaying wood, to epiphytes (including true epiphylls). About half the number of accepted species within the Daltoniaceae belongs to the genus *Distichophyllum*, the focus of the present research.

Although a molecular phylogeny is available for the Hookeriales, several relationships among the currently accepted families remain unclear (Buck et al., 2005). Thus the main task of Chapter 1 was to resolve the backbone relationship of the Hookeriales. This is essential prior to studies of the focus of this research project, i.e. the Daltoniaceae. To improve previous phylogeny to show relationships in the Hookeriales, efforts are made to improve taxon sampling by including the type species of each genus when possible, and increasing sampling of larger genera to better represent them in terms of biogeography and morphology. In addition, samples from several genera which were once associated with the orders or considered within the Hookeriales were also included to test or ascertain previous untested phylogenetic suggestions. Apart from the original four gene markers used in a previous study (Buck et al. 2005), a fast evolving non-coding region (nrITS I & 2) is added to improve resolution and statistical support. Past classifications and phylogenies based on different morphological concepts with biased emphasis on either generations of the life cycle of this group, these gametophytic and sporophytic characters were analyzed to detect convergent evolution and to test various phylogenetic concepts.

Such contrasting classifications are not unique within the Hookeriales but apply to many groups of mosses. Nevertheless, the controversial classification history and disagreement about whether gametophyte or sporophyte characters are providing more phylogenetic information would make the Hookeriales a perfect group to test this long-standing issue in systematic bryology. Moreover, the study could test and confirm the presence of reversibility in morphological characters and to determine its frequency of occurrences.

Chapter 2 of the dissertation focused on the relationships of the large genus *Distichophyllum* and its allied genera such as *Leskeodon* and *Distichophyllidium* which are much smaller in terms of species numbers. A genus of ca. 100 accepted species today, *Distichophyllum* has been generally subdivided into two sections. However, some authors such as Fleischer (1908) and Matteri (1975) have commented that the two traditional sections put forward by Brotherus (1907, 1925) have no standing. One of the objectives, thus, is to ascertain if the two proposed sections under *Distichophyllum* are reflected in the phylogenetic reconstruction. If not, what would be the best division of the large genus. On the other hand, several smaller genera recognized today were segregates from *Distichophyllum*. Peristome features, particularly the exostome ornamentation, was one of the criteria use for delimiting the genera. It is hypothesized that peristomial features, although not a good character to delimit families and higher ranks, is good for recognizing genera (Buck, 1991, 2007). This study will test the validity of using exostome ornamentation for generic delimitation within the Daltoniaceae.

A worldwide taxonomical monograph of *Distichophyllum* does not exist and thus often hampering accurate identification of this large and morphological diverse genus. Consequently, misidentifications of specimens are not uncommon. To avoid isolation of DNA from misidentified voucher specimens, all voucher used in DNA isolation are re-identified or re-confirmed. This also avoids different concepts of species delimitation in identifications by different persons whom have identified the specimens. This procedure has surprisingly accumulated several new and noteworthy country or island records. Some taxonomical knowledge is also accumulated while trying to accurately identify some challenging species. The new and noteworthy records, along with taxonomical clarifications of some of the lesser known species are presented in Chapter 3 of the dissertation.

As one of the common approach to start a project, the initial phase was spent collecting and reviewing literature. While doing so, it was found that the name *Distichophyllum* is an illegitimate name according to the International Code of Botanical Nomenclature (ICBN). A series of linked nomenclatural problems arises with this new but correct interpretation of the legitimacy of *Distichophyllum*. Hence, in order to keep the well-known name in current use and to avoid numerous new binomials to replace all the names under *Distichophyllum*, a proposal to conserve *Distichophyllum* should be summated for considerations by the nomenclature committee of the ICBN. A modified version of this proposal is presented in Chapter 4.

Chapter 1:

The gametophyte strikes back: testing opposing morphological concepts on the haploid and diploid generations in the moss order Hookeriales (Bryopsida)

To be submitted to “Molecular Phylogenetics and Evolution”

Contents

1.1. Introduction

Bryophytes (liverworts, mosses, hornworts), like all land plants, exhibit a heteromorphic haplodiplontic life cycle. However, in contrast to other groups, the haploid gametophytic phase is dominant in bryophytes. The unbranched diploid sporophytes are attached to the maternal gametophytes and nutritionally, at least partially, dependent on them. The sporophyte consists of a foot and a capsule which is often subtended by an elongated seta (Goffinet et al., 2008).

The two alternating generations in bryophytes are subjected to different selection pressures since they experience different environments, which derive in divergent morphologies and functions. Thus it is expected that evolutionary trajectories of sporophytes and gametophytes are sometimes uncoupled. Classifications that emphasize morphological characteristics of one generation or the other may as a consequence be substantially divergent, and this often appears to be the case (e.g. Buck, 1980; Dixon, 1932a; Miller, 1979; Rohrer, 1988). This is especially problematic in mosses, because both generations are well developed and morphologically diverse. Incongruence between classifications emphasizing gametophyte versus sporophyte characters are well exemplified by the moss order Hookeriales (e.g. Buck, 1980, 1991; Miller, 1979).

The Hookeriales belong to so called pleurocarpous mosses (core pleurocarps sensu Bell et al., 2007), where the sexual structures and thus sporophytes are produced on specialized, short, lateral branches. Comprising about 5300 to 6600 species; i.e., about half of all known mosses (Crosby et al., 1999; Shaw et al., 2003b), this well supported monophyletic group contains the orders Hookeriales, Hypnales, Hypnodendrales, and Ptychomniales (Bell et al., 2007). Although the branching order among early diverging pleurocarps (Hypnodendrales first, Ptychomniales second) is fairly well established (compare Bell et al., 2007), relationships among the crown group (Hypnales and Hookeriales) remain challenging because of extensive homoplasy in morphological traits (Buck, 2007; Hedenäs, 2007; Huttunen et al., 2004; Newton et al., 2007; Olsson et al., 2009a; Olsson et al., 2009b; Quandt et al., 2009).

As currently circumscribed by Buck et al. (2005), the Hookeriales include about 650 named species, predominantly distributed in humid forests in the tropics and south temperate zone. The sporophytic capsule of the Hookeriales opens via a lid or operculum as in other “true mosses” (Bryopsida), permitting release of haploid meiospores. Lining the mouth of the capsule are the outer and inner rows of teeth known as exostome and endostome, respectively (collectively, the peristome). Although the peristome teeth are often highly ornamented and able to perform hygroscopic movements, their true function is still speculative. It is generally agreed that the peristome participates in the regulation of spore discharge (e.g. Mueller & Neumann, 1988) but this has never been investigated experimentally, nor has the fitness significance of variations in peristome morphology, if any, been demonstrated.

1.1.1. Taxonomic importance of the peristome

The significance of sporophytes, and especially peristomes, for moss classification was emphasized in a series of studies by Philibert (for review see Taylor, 1962). Subsequently, Fleischer (1904–1923; 1920), presented a systematic arrangement of mosses that applied Philibert's observations on peristome morphology to moss classification, but only to major divisions above the ordinal rank. Fleischer considered gametophytic characters to have more importance at lower ranks. His philosophy and classification scheme is followed by Brotherus (1925) with little modifications and became the widely accepted standard. Dixon (1932a) hypothesized that sporophytic similarities define major groups (synapomorphies and clades, respectively, using modern terminology), and that within these groups, taxa can be very diverse in gametophyte morphology. It was assumed that peristomial features are not as much influenced by the external environment as are gametophyte characters, because peristomes are protected within the operculum during development (e.g., Allen et al., 1985; Fleisher, 1904-1923, 1920), or because sporophytes are significantly shorter-lived (Buck, 1980).

These thoughts, together with Philibert's view on peristome evolution, have bolstered for many decades, the idea that the sporophyte generation matters most in higher level classifications of moss diversity. Being an ardent follower of this philosophy, Crosby (1974) applied Philibert's principles of sporophyte and peristome conservatism to the family level classification of Hookeriales. As a result, the six hookerialean families previously proposed by Fleischer (1920) were shuffled into two families, separated strictly by outer exostome surface ornamentation (Crosby, 1974). Exostomes with the outer face cross-striate at the base are termed "hookeriaceous" peristomes, while those completely papillose are termed "daltoniaceous". In this scheme, several pairs of gametophytically inseparable genera that differ only in exostome ornamentation (e.g. *Lepidopilum* and *Lepidopilidium*) were arranged in different families.

1.1.2. The gametophyte strikes back

Since the late 70s, a series of studies on peristome development helped disentangling some of the evolutionary implications of its ontogeny (Edwards, 1979, 1984; Goffinet et al., 1999; Shaw & Anderson, 1988; Shaw et al., 1987; Shaw et al., 1989a; Shaw et al., 1989b). These studies, together with the advent of molecular phylogenetics (e.g. Magombo, 2003; Newton et al., 2000; Quandt et al., 2009), have evidenced how far we are from understanding peristome evolution in mosses. Moreover, Olsson et al. (2009b) showed that peristome reduction, at least in some epiphytes, is correlated with habitat shifts, and thus contradicting the traditional view that sporophytic characters are not under selection. Similarly, at least two or three distinct types of daltoniaceous peristomes have been identified, re-enforcing the view that daltoniaceous peristomes have evolved multiple times from hookeriaceous peristomes (see Buck, 1987; Tan and Robinson, 1990; Whittemore & Allen, 1989). In fact, Buck (1991) and Hedenäs (1998; 1999) have already pointed out that various peristomial structures may have evolved in parallel or convergently in many unrelated taxa in response to similar habitat conditions. These examples corroborate Buck's (1991; 2007) view that selection acts on peristome structure when it is functional, not during its development under the protection of the operculum.

Unsatisfied with the seemingly artificial sorting of Crosby (1974), Buck (1987; 1988) reversed the traditional philosophy and reassessed the Hookeriales with emphasis on gametophytic characters. He distinguished five families and discussed inferences about interfamilial relationships based on differences in gametophyte structure. Whittemore & Allen (1989) revisited Buck's (1987; 1988) system, but focused on similarities rather than differences, lumping Buck's proposed five families to two families with one exception. They were conservative about inferring a relationship for the highly reduced *Ephemeropsis* and tentatively retained it in a family of its own.

1.1.3. Other ways of using morphology

Stimulated by Bessey's (1915) dicta for flowering plants, Miller (1971) proposed a system based on 23 generalized "principles for moss systematics". It included considerations of both gametophytes and sporophytes. He recognized nine families in the Hookeriales and intuitively postulated directions of morphological evolution. In an attempt to get away from such subjective approaches Hedenäs (1996) coded 75 morphological characters from both generations and analyzed the data applying cladistic methods. This analysis resolved three clades within the Hookeriales, none with strong support from bootstraping.

1.1.4. The rise of molecular phylogeny

It is well-known that the formulation and coding of morphological characters can be biased by preconceptions about evolution. Moreover, if understanding morphological evolution is an important goal of phylogenetic analyses, it is advantageous to base the phylogenetic hypotheses on independent evidence rather than on the morphology itself.

Buck et al. (2005) conducted a molecular analysis based on four genes (*trn*L–F and *rps*4, from the chloroplast genome, *nad*5, from the mitochondrial one, and nuclear 26S) from 89 taxa traditionally classified in the Hookeriales with representatives of other pleurocarpous families as well. Evolutionary transitions in 13 morphological traits used previously to diagnose families within the Hookeriales, were reconstructed on the molecular phylogeny. Their work led to the re-arrangement of the order into seven families.

The controversial classification history and disagreement about whether gametophyte or sporophyte characters are better indicators of phylogenetic relations, would make the Hookeriales a good group to test this long-standing issue in systematic bryology. Moreover, it is particularly important to corroborate reversals in morphological characters and to determine the frequency of such reversals (Collin & Miglietta, 2008). In particular, this study focuses on the question of whether most homoplasy represents parallel changes to derived states, versus reversals to seemingly ancestral conditions. As such, this study addresses the general question of reversibility in morphological evolution.

Our study is thus undertaken with the following objectives: (1) to ascertain the monophyly of Hookeriales sensu Buck et al. (2005), (2) to resolve relationships among families and genera within the Hookeriales clade, (3) to trace the evolution of characters used in the different phylogenetic concepts utilizing ancestral state reconstruction, and (4) to identify the occurrence and frequency of reversals in morphological characters.

1.2. Materials and Methods

1.2.1. Taxon sampling and molecular protocols

DNA was sampled from 122 species representing 71 genera. The outgroup is composed of five exemplars in the moss orders Hypnodendrales and Ptychomniales. The ingroup consists of 95 species from 46 genera (out of 52) in the Hookeriales and 22 species (11 of which have been associated with the Hookeriales) currently classified in the Hypnales. Whenever possible, type species for genera were sampled. Other than the type species, sampling efforts have been made to include a few more exemplars in each genus, especially in large genera such as *Callicostella*, *Cyclodictyon*, and *Distichophyllum*, to better represent each genus in terms of their morphological and geographical diversities. In this way, relationships and monophyly, especially of the genera, could be better evaluated.

Nucleotide sequences were obtained for five DNA regions of three different genomes, namely, (1) the plastid *trn*L- F region, including the *trn*L_{UAA} group I intron as well as the *trn*L-F intergenic spacer (IGS) (hereafter *trn*LF), (2) the plastid *rps*4 gene, including the *trnS–rps4* IGS, (3) the mitochondrial *nad*5 group I intron, (4) as well as the nuclear ribosomal ITS1–5.8–ITS2 (hereafter, ITS) region and (5) the large ribosomal RNA subunit (hereafter, 26S). Table 1 provides voucher information and GenBank accession numbers when available. The identifications of all new samples were reconfirmed in this study.

Total genomic DNA was extracted using a modified CTAB protocol (Doyle & Doyle, 1990) as described by Shaw (2000). Double-stranded DNA templates were amplified by polymerase chain reaction (PCR), employing standard protocols and amplification primers as described in Shaw et al. (2003a) and Olsson et al. (2009a). Cleaned PCR products were sequenced by Macrogen Inc., South Korea (www.macrogen.com), or the DNA Sequencing Facility at the Institute for Genome Sciences & Policy, Duke University (http://www.genome.duke.edu/cores/sequencing/). All sequences will be deposited in GenBank/EMBL and included as supplementary data in the attached CDROM.

Table 1. Voucher information and GenBank accession numbers for 122 taxa (123 samples, double *Hookeria acutifolia*); ***rps*4**: all available, 35 (28%) new; ***trn*LF**: all available, 42 (34%) new; ***nad*5**: 115 available, 32 (28%) new; **ITS**: 106 available, 83 (78%) new; **26S**: 110 available, 45(41%). Total: 577 (94%) out of 615 (5 markers x 123 exemplars) available, 237 (41%) new. (a) Hypnalean taxa once associated with the Hookeriales; (h) other Hypnalean taxa; (*) type species of respective genera; and (--) missing sequences. New sequences do not have GenBank accession numbers yet and are identifiable by the lab numbers. Sequences are available as supplementary data in the attached CDROM.

Taxa	rps4	trnLF	nad5	ITS	26S	Voucher
OUTGROUP						
Euptychium cuspidatum (*)	AY631144	DQ194209	DQ200890	N88	--	New Caledonia, *A.E. Newton 5373* (BM)
Garovaglia powellii	DQ296008	DQ194217	DQ200894	NP	--	Unknown, *A.E. Newton 6496* (BM)
Hampeella pallens (*)	AY306921	AM990371	FM161266	FM161109	AY452439	Australia, Queensland, *H. Streimann 64195* (H)
Hypnodendron vitiense	AY524471	AY524499	AY524526	FM161142	--	Australia, *N.E. Bell 480* (BM)
Spiridens camusii	AY524475	AY524503	AY524530	N74	--	New Caledonia, *N.E. Bell 416* (BM)
INGROUP						
Achrophyllum crassirete	Ac470	Ac470	Ac470	Ac470	Ac470	Chile, *J.-P. Frahm 21-10* (BONN)
Achrophyllum quadrifarium (*)	AY449660	BBH01	AY452316	BBH01	BBH01	New Zealand, *W. Frey & T. Pfeiffer 98-T2* (CHR)
Actinodontium adscendens (*)	Aa471	--	Aa471	Aa471	--	Thailand, *J.-P. Frahm 2006401* (BONN)
Actinodontium sprucei	AY306855	AY306689	AY452317	BBH26	AY452397	French Guiana, *W.R. Buck 37977* (NY)
Adelothecium bogotense (*)	AY306856	AY306690	AY452318	EF680784	AY452398	Brazil, *Vital & W.R. Buck 19649* (NY)
Ancistrodes genuflexa (*)	AY306863	AY306697	AY452319	BBH68	AY452399	Chile, *I. Holz & J. Franzaring CH 00-154* (NY)
Arbusculohypopterygium arbuscula (*)	AY449665	AY449671	AY452366	EF680789	AY452445	Chile, *I. Holz & J. Franzaring CH 00-80* (NY)
Beeveria distichophylloides (*)	AY306867	AY306701	AY452320	BBH092	AY452400	New Zealand, *A.J. Fife 11150* (NY)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Benitotania elimbata (*)	AY449661	AY449669	AY452321	SB1414	AY452401	East Malaysia, *H. Akiyama & M. Suleiman*, *2002* (NY)
Brymela fluminensis	AY307005	AY306839	AY452394	--	AY452475	Brazil, *D.M. Vital & W.R. Buck 20012* (NY)
Brymela tutezona (*)	AY449662	BBH27	AY908454	--	AY452404	Panama, *N. Salazar et al. 13656* (NY)
Brymela websteri	AY306868	AY306702	AY452324	--	AY452405	Dominica, *A. Schäfer-Verwimp 17861* (NY)
Bryobrothera crenulata (*)	GOM036	GOM036	GOM036	GOM036	GOM036	Australia, *H. Streimann & T. Pócs 64341* (S)
Callicostella cf. *africana*	AM990350	AM990350	FM161247	FM161085	B333	Ghana, *J. Rikkinen et al. 21* (Priv. Enroth)
Callicostella colombica	AY449663	BBH29	--	BBH29	AY452407	French Guiana, *W.R. Buck 18797* (NY)
Callicostella pallida	AY306872	AY306706	AY452328	BBH31	AY452410	French Guiana, *I. Holz FG 00-14* (NY)
Callicostella papillata (*)	B587	B587	B587	B587	B587	Indonesia (Java), *B.C. Ho 07-003* (SING)
Callicostella prabaktiana	B588	B588	B588	B588	B588	Singapore, *B.C. Ho 07-008* (SING)
Callicostellopsis meridiensis (*)	AY306871	AY306705	AY452327	BBH32	AY452409	Venezuela, *D. Griffin PV-898* (NY)
Calyptrochaeta asplenioides	GOM003	GOM003	GOM003	GOM003	GOM003	La Réunion, *T. Pócs* (NY)
Calyptrochaeta cristata (*)	Cc474	Cc474	Cc474	Cc474	Cc474	New Zealand, *J.-P. Frahm 1-11* (BONN)
Calyptrochaeta remotifolia	Cr532	Cr532	Cr532	Cr532	Cr532	Philippines, *Linis s.n.* (SING)
Canalohypopterygium tamariscinum (*)	AY306878	AY306712	AY452331	EF680785	AY452413	New Zealand, *W. Frey & T. Pfeiffer 98-T10C* (CHR)
Catharomnion ciliatum (*)	AY306879	AY306713	AY452332	EF680786	AY452414	New Zealand, *H. Streimann 51423* (NY)
Chaetomitriopsis glaucocarpa (a*)	AY908603	MDP54	AY908681	MDP54	MDP54	China, *M.Z. Wang et al. 4046A* (MO)
Chaetomitrium borneense (a)	AY306880	AY306714	AY452333	BBH89	AY452415	Brunei, *B.C. Tan 95-1116* (NY)
Chaetomitrium dusenii (a)	AY306881	AY306715	AY452334	BBH88	AY452416	Equatorial Guinea, *P. Heras 499/94* (NY)
Chaetomitrium orthorrhynchum (a)	Co549	Co549	Co549	Co549	Co549	East Malaysia, *Suleiman 1701* (BORH)
Crosbya straminea	AY306887	AY306721	AY908490	BBH016	AY452421	New Zealand, *A.J. Fife 10379* (NY)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Crossomitrium epiphyllum (Sect. type)	AY306885	AY306719	AY452337	BBH033	AY452419	French Guiana, *W.R. Buck 33259* (NY)
Crossomitrium sintenisii	AY306886	AY306720	AY452338	BBH034	AY452420	French Guiana, *W.R. Buck 33042* (NY)
Curviramea mexicana (a)	AF143062	AF161155	AY908629	BB45	BB45	Mexico, *W.R. Buck 28242* (NY)
Cyathophorum bulbosum (*)	AY306889	AY306723	AY452339	--	AY452422	Australia, *H. Streimann 55638* (NY)
Cyclodictyon albicans	AY306892	AY306726	AY452342	BBH35	AY452425	Colombia, *S.P. Churchill et al. 18795* (NY)
Cyclodictyon blumeanum	Cb613	Cb613	Cb613	Cb613	Cb613	West Malaysia, *A. & I. Schäfer-Verwimp* (Priv. Schäfer-Verwimp)
Cyclodictyon brevifolium	Cb586	Cb586	Cb586	Cb586	Cb586	Tanzania, *T. Pócs & G. Kis 9129/BU dupl.* (EGR)
Cyclodictyon laete-virens (*)	Cl535	Cl535	Cl535	Cl535	Cl535	Portugal, *J.-P. Frahm Az-106* (BONN)
Cyclodictyon roridum	AY306893	AY306727	AY452343	--	AY452426	Ecuador, *W.R. Buck* 39563 (NY)
Daltonia apiculata	JY60	JY60	--	JY60	JY60	Bhutan, *D.G. Long 8673-C* (E)
Daltonia armata	Da576	Da576	Da576	Da576	Da576	West Malaysia, *Ho 08-007* (SING)
Daltonia jamesonii	GOM040	GOM040	GOM040	GOM040	GOM040	Bolivia, *Lewis 87373* (S)
Daltonia marginata	GOM007	GOM007	GOM007	GOM007	GOM007	Brazil, *A. Schäfer-Verwimp 9492* (NY)
Daltonia ovalis	GOM008	GOM008	GOM008	GOM008	GOM008	Ecuador, *W.R. Buck 39344* (NY)
Daltonia splachnoides (*)	GOM038	GOM038	GOM038	GOM038	GOM038	Ireland, *N. Hakelier s.n.* "B108054" (S)
Dendrocyathophorum decolyi (*)	AY306896	AY306730	AY452346	EF680790	AY452429	Japan, *T. Matsui 7264* (NY)
Dendrohypopterygium filiculaeforme	EF647955	EF657184	EF667882	--	EF680808	New Zealand, *J.-P. Frahm X7-1* (GOET)
Dimorphocladon borneense (a)	AY306898	AY306732	AY452348	BBH90	AY452430	Brunei, *B.C. Tan 95-1060* (NY)
Diploneuron connivens (*)	AY306899	AY306733	AY908457	--	AY452431	Jamaica, *M.R. Crosby 13732* (NY)
Diploneuron diatomophilum	AY306870	AY306704	AY452326	BBH30	AY452408	Cuba, *W.R. Buck* 23312 (NY)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Distichophyllidium nymanianum (*)	AY306901	AY306735	AY452350	Dn587	BBH019	West Malaysia, *Mohamed & Damanhuri 1118,* Musci Malaysiani Exsiccati, fasc. 2: #29 (NY); Indonesia (Sulawesi), *F. Müller S81* (DR)
Distichophyllum carinatum	Dc546	Dc546	Dc546	Dc546	Dc546	Germany, *M. Nebel et al. MTB 8527/3* (STU)
Distichophyllum cuspidatum	GOM012	GOM012	--	GOM012	GOM012	West Malaysia, *B.C. Tan 89-1356* (NY)
Distichophyllum flaccidum	GOM015	GOM015	GOM015	GOM015	GOM015	Chile, *W.R. Buck 46275* (NY)
Distichophyllum maibarae	Dm571	Dm571	Dm571	Dm571	Dm571	China, *D.G. Long 33943* (E)
Distichophyllum malayense	GOM049	GOM049	GOM049	GOM049	GOM049	West Malaysia, *L. Hedenäs MY92-533* (S)
Distichophyllum microcarpum	GOM055	GOM055	GOM055	GOM055	GOM055	New Zealand, *H. Streimann 51286* (S)
Distichophyllum mniifolium	GOM046	GOM046	GOM046	GOM046	GOM046	South Africa, *K. Hylander 10602* (S)
Distichophyllum paradoxum	AY306900	AY306734	AY452349	GOM020	AY452432	U.S.A., Hawaii, *T. Flynn 5151* (NY)
Distichophyllum pulchellum	AY306902	AY306736	AY452351	EF680791	AY452433	New Zealand, *H. Streimann 51380* (NY)
Distichophyllum rigidicaule var. *gabonense*	Dg585	Dg585	Dg585	Dg585	Dg585	Tanzania, *T. Pócs et al. 90057/V* (EGR)
Distichophyllum spathulatum (*)	GOM026	GOM026	GOM026	GOM026	GOM026	Indonesia (Sumatra), *L. Hoffmann* 89-181 (NY)
Ephemeropsis tjibodensis (*)	GOM048	GOM048	GOM048	GOM048	GOM048	West Malaysia, *I. Bisang & L. Hedenäs s.n.* "B57686" (S)
Ephemeropsis trentepohlioides	BBH022A	AY306740	AY908491	BBH022A	BBH022A	New Zealand, *C. Macmillan 95/94* (NY)
Glossadelphus glossoides (a)	AM990368	AM990368	FM161263	FM161106	B340	West Malaysia, *L. Hedenäs s.n.* "B57848" (S)
Gradsteinia andicola (a*)	AY908246	MDP418	AY908420	MDP418	--	Colombia, *A.M. Cleef 8236* (KRAM)
Hemiragis aurea (*)	AY306922	AY306756	AY452361	--	AY452440	Costa Rica, *G. Dauphin 2949* (NY)
Hildebrandtiella guyanensis (h)	AY306927	AF509559	FM161275	FM161119	Hg55	Unknown, *U. Drehwald 4425* (Priv. Drehwald)
Hookeria acutifolia ID	AY306929	AY306763	AY452362	BBH06	AY452441	Ecuador, *W.R. Buck 39558* (NY)
Hookeria acutifolia EC	B586	B586	B586	B586	--	Indonesia (Java), *B.C. Ho 07-004* (SING)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Hookeria lucens (*)	AY306930	AY306764	AY452363	EF680792	AY452442	USA, *W.R. Buck 37714* (NY)
Hypnella pallescens (*)	AY306932	BBH41	AY452365	--	AY452444	French Guiana, *W.R. Buck 37840* (NY)
Hypnum cupressiforme (h*)	AM990398	AM990398	FM161292	FM161143	B299	Germany, *D. Quandt s.n.* 26 XII 2005 (Priv. Quandt)
Hypopterygium didictyon	EF647956	EF657185	EF667883	EF680793	EF680809	New Zealand, *J.-P. Frahm 5-12* (GOET)
Hypopterygium hookerianum (type of *Cyathophorella**)	AY306890	AY306724	AY452340	EF680788	AY452423	Thailand, *H. Akiyama Th-39* (NY)
Hypopterygium tamarisci (*)	EF647964	EF657194	EF667887	EF680799	EF680816	Bolivia, *I. Holst 4910* (NY)
Isodrepanium lentulum (a*)	AY907964	MDP179	AY908530	MDP179	--	Suriname, *B.H. Allen 23460* (MO)
Lepidopilidium laevisetum	AY306937	AY306771	--	--	--	Brazil, *A. Schäfer-Verwimp 9237* (NY)
Lepidopilidium portoricense (*)	AY306939	AY306773	AY452369	BBH43	AY452448	French Guiana, *W.R. Buck 37825* (NY)
Lepidopilum polytrichoides	AY306938	AY306772	AY452368	BBH44	AY452447	French Guiana, *W.R. Buck* 33307 (NY)
Lepidopilum scabrisetum (*)	AY306940	AY306774	AY452370	BBH45	AY452449	Ecuador, *W.R. Buck 39436* (NY)
Lepidopilum surinamense	AF143067	AF161160	--	BB41	--	French Guiana, *W.R. Buck 33082* (NY)
Leskeodon acuminatus	ND18	ND18	--	ND18	ND18	Indonesia (Seram), *H. Akiyama C-14714* (MO)
Leskeodon auratus (*)	AY306942	AY306776	AY452371	BBH23	AY452450	Puerto Rico, *W.R. Buck 18286* (NY)
Leskeodon cubensis	GOM030	GOM030	GOM030	GOM030	GOM030	Trinidad & Tobago, *N. Djan-Chékar 94-340* (NY)
Leucodon sciuroides (h*)	AY908186	AM990405	AY908716	FM161149	A75	Unknown *T.A.J. Hedderson 8852* (RNG); Germany, *V. Buchbender 293* (Priv. Buchbender)
Leucomium strumosum (*)	AY306943	AY306777	AY908488	BBH10	AY452452	French Guiana, *I. Holz FG 00-268* (NY)
Lopidium concinnum (*)	AY306945	AY306779	AY452373	EF680800	AY452453	Australia, *H. Streimann 43706* (NY)
Myurium hochstetteri (h*)	AY908180	AF509542	AY908439	Mh26	Mh26	Scotland, *A. Solga & D. Quandt E 10017* (Priv. Quandt & Solga); Unknown, *F.J. Rumsey 17/7* (Priv. Runsey)
Neohypnella diversifolia (*)	AY306931	AY306765	AY452364	BBH40	AY452443	Ecuador, *W.R. Buck 39277* (NY)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Philophyllum tenuifolium (*)	AY306973	AY306807	AY452376	BBH11	AY452456	Brazil, *A. Schäfer-Verwimp 14548* (NY)
Phyllodon truncatulus (a*)	AY908604	MDP411	AY908682	MDP411	MDP411	French Guiana, *W.R. Buck 33300* (NY)
Pilotrichidium antillarum	AY306975	AY306809	AY452377	--	AY452458	Puerto Rico, *W.R. Buck 16127* (NY)
Pilotrichidium callicostatum (*)	AY306977	AY306811	AY908455	--	AY452460	Colombia, *J. Betancur et al. 4725* (NY)
Pilotrichum andersonii	AY306974	AY306808	--	--	AY452457	Trinidad, *N. Djan-Chékar 94-678* (NY)
Pilotrichum bipinnatum (rej. lectotype)	AY306976	AY306810	AY452378	BBH49	AY452459	French Guiana, *I. Holz FG 00-33* (NY)
Pilotrichum procerum	AY306978	AY306812	AY452379	BBH50	BBH50	Dominica, *A. Schäfer-Verwimp 17941* (NY)
Pleurozium schreberi (h*)	AY908281	MPD510	AY908642	AJ288349 + AJ288563	--	USA, *B.W. Thornton 35* (DUKE)
Pterobryon densum (h*)	AF143013	AF161106	AY908693	Pd9	BB64	Colombia, *E.L. Linares & S.P. Churchill* 3649 (MO); Honduras, *B.H. Allen 12002* (BONN)
Rhynchostegiopsis tunguraguana (*)	AY306986	AY306820	BBH13	--	AY452463	Colombia, *P. Ramírez P7690* (NY)
Rhytidiadelphus triquetrus (h)	AY908279	SB271	AY908636	SB271	SB271	USA, *B.W. Thornton 20a* (DUKE)
Rutenbergia madagassa (h*)	AY524486	AY524514	AY524542	N128	--	Madagascar, *Fisher 33* (BM)
Sauloma tenella (*)	AY306987	AY306821	AY452384	BBH051	AY452464	Australia, *H. Streimann 59726* (NY)
Schimperobryum splendidissimum (*)	AY306988	AY306822	AY452385	EF680807	AY452465	Chile, *I. Holz & J. Franzaring Ch 00-156* (NY)
Stenodesmus tenuicuspis (*)	AY908610	MDP262	AY908453	--	--	Colombia, *B.R. Ramírez et al. 8328* (MO)
Stenodictyon pallidum	AY306997	AY306831	BBH52	BBH52	AY452466	Dominican Republic, *W.R. Buck 7940* (NY)
Stenodictyon wrightii (*)	AY306998	AY306832	AY452386	BBH53	AY452467	Ecuador, *W.R. Buck* 10014 (NY)
Symphyodon imbricatifolius (a)	AY306999	AY306833	AY452387	BBH87	AY452468	Brazil, *A. Schäfer-Verwimp 14747* (NY)

Taxa	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Tetrastichium fontanum (*)	AY307000	AY306834	AY452388	--	AY452469	Portugal (Madeira), *R. Düll, Bryophyta Exsiccata Madeira #69* (NY)
Thamniopsis cruegeriana	AY307002	AY306836	AY452390	BBH55	AY452471	Trinidad, *N. Djan-Chékar 94-652* (NY)
Thamniopsis incurva	AY449668	AY449674	AY452391	BBH56	AY452472	Trinidad, *N. Djan-Chékar 94-667* (NY)
Thamniopsis pendula (*)	AY307003	AY306837	AY452392	BBH57	AY452473	Colombia, *S.P. Churchill & E.L. Lineares 18434* (NY)
Thamniopsis secunda	Hu599	Hu599	Hu599	Hu599	Hu599	China, *D.G. Long 36213* (E)
Thamniopsis sinuata	AY307004	AY306838	AY452393	BBH58	AY452474	Colombia, *R. Callejas et al. 2792* (NY)
Thamnobryum alopecurum (h*)	AM990444	AM990444	FM161334	FM161218	B238	Germany, *V. Buchbender s.n., 11 VII 2003* (Priv. Buchbender)
Trachyloma planifolium (h*)	AM990449	AM990449	FM161338	FM161234	--	New Zealand, *J.-P. Frahm 3-12* (BONN)
Trachyxiphium guadalupense (*)	BBH60	BBH60	--	--	AY452476	Trinidad, *N. Djan-Chékar 94-670a* (NY)
Trachyxiphium vagum	AY307006	AY306840	AY452395	--	AY452477	Ecuador, *W.R. Buck 39564* (NY)
Vesicularia vesicularis (h)	AY908559	MDP317	AY908406	MDP317	MDP317	Unknown, *A.E. Newton 4552* (Priv. Newton)

1.2.2. DNA sequence editing and alignment

For each sample and sequenced DNA region, forward (5'–3') and reverse (3'–5') sequences were assembled and checked for inaccurate base calling using Sequencher v4.1 (Gene Codes Corp.) or PhyDE® 0.995 (Müller et al., 2008). Consensus sequences were aligned manually in PhyDE® 0.995 following alignment rules described in Kelchner (2000) and trying to minimize substitutions and indels. The approach combines event-based and similarity criteria to produce a hypothesis about the homology of the characters (Morrison, 2006; Simmons, 2004; Simmons & Freudenstein, 2003). Simple sequence repeats were isolated based on strict motif recognition as advocated by Kelchner (2000) and Quandt & Stech (2005). The matrix was visually inspected for hairpin-associated inversions. Detected inversions were positionally separated in the alignment. Apart from the already reported inversions in the *trn*L-F IGS (Quandt & Stech, 2004) as well as in the *trn*L intron (Quandt & Stech, 2005), three additional inversions were detected (compare Table 2). Following Quandt et al. (2003), inversions were not scored for the phylogenetic analyses. Nevertheless, in order to maximize information within detected inversions; e.g.,

Table 2. Hotspots (Hs), and inversions (Iv). Genes in the merged datamatrix follow, *rps*4: 1–880, *trn*LF: 881–1753, *nad*5: 1754–3154, ITS: 3155–6894, and 26S: 6895–7958.

Nr.	position	gene	Nr.	position	gene
Iv1	166–172	*rps4*	Hs10	3236–3243	ITS
Hs1	1000–1002	*trnLF*	Hs11	3249–3649	ITS
Iv2	1012–1016	*trnLF*	Hs12	3796–4296	ITS
Hs2	1022–1026	*trnLF*	Hs13	4604–4746	ITS
Hs3	1116–1118	*trnLF*	Hs14	5102–5127	ITS
Iv3	1196–1202	*trnLF*	Hs15	5504–5509	ITS
Hs4	1341–1421	*trnLF*	Hs16	5549–5554	ITS
Hs5	1637–1641	*trnLF*	Hs17	5586–5640	ITS
Iv4	1683–1689	*trnLF*	Hs18	5892–5918	ITS
Hs6	1741–1748	*trnLF*	Hs19	6568–6578	ITS
Hs7	2224–2229	*nad5*	Iv5	7035–7037	26S
Hs8	2588–2591	*nad5*	Hs20	7424–7429	26S
Hs9	3106–3154	*nad5*			

substitutions that occurred prior the inversion event, a second alignment file was generated with the inversions included as reversed and complemented sequences for the phylogenetic analyses (cf. Borsch & Quandt, 2009; Sotiaux et al., 2009). Regions of ambiguous alignment (hotspots) in the data matrix were defined as outlined in Olsson et al. (2009a) and excluded from phylogenetic analyses (Table 2). Alignments are provided in the attached CDROM.

1.2.3. DNA data analyses

Both parsimony and Bayesian analyses were performed on the individual data sets, representing the amplified regions as well as the concatenated matrix. Analyses of the individual data sets revealed no significant conflicts (i.e. ≥ 70% bootstrap support or ≥ 95% posterior probabilities) among the different regions (data not shown).

The computer program SeqState (Müller, 2005) was used to generate a ready-to-use nexus file containing the sequence alignment with an automatically generated binary indel matrix appended based on the simple indel coding approach of Simmons & Ochoterena (2000). Command files for using the parsimony ratchet (Nixon, 1999) were generated using the program PRAP2 (Müller, 2007) applying the default settings, and executed in PAUP 4.0b10 (Swofford, 2002). Heuristic bootstrap searches under parsimony were performed with 10,000 replicates.

Bayesian analyses were performed with MrBayes v3.1.2, applying the GTR+Γ+I model for the sequence data and the restriction site model for the binary indel partition. To allow for possibly deviating substitution matrices for the different genomes as well as the indel matrix, the data set was divided into four sequence data partitions as follows: partition 1, plastid (*rps*4 + *trn*LF); partition 2, mitochondrial (*nad*5); partition 3, nuclear (ITS1 & 2 + 26S); and partition 4, the coded indel matrix. Model parameters for each partition were sampled independently. The *a priori* probabilities supplied were those specified in the default settings of the program. Posterior probability (PP) distributions of trees were created using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method. Ten runs with four chains (3×10^6 generations each) were run simultaneously. Chains were sampled every 1,000 generations and the respective trees written to a tree file. The program Tracer v1.5 (Rambaut & Drummond, 2009) was used to calculate the burnin point and to examine the log likelihoods, ensuring that the runs were in the stationary phase and adequate effective sample size (ESS) were attained. Calculations of the consensus tree and of the posterior probability of clades were performed based upon the trees sampled after the chains converged. Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph 2.0.42-187 beta (http://treegraph.bioinfweb.info/).

1.2.4. Morphological data and ancestral state reconstruction

Character state reconstruction analyses were performed under a likelihood framework (Pagel, 1999) with help of the package available for that purpose in Mesquite 2.72 (Maddison & Maddison, 2009). The model of evolution chosen was Markov k-state 1 parameter (Mk1), as described by Lewis (2001). This model is a generalization of the Jukes-Cantor model for k-states. The rate of change is the only parameter and state changes are all equally probable.

Six selected morphological characters (four gametophytic and two sporophytic) and three ecological characters (presence versus absence from a particular substrate) were coded (Table 3). The presence or absence of a laminal limbidium, presence or absence of a leaf nerve (which can be single or double when present), and the ratio of the cells at the middle of the leaf lamina (short if 1–3:1, and long if > 3:1), are three gametophyte characters that Buck (1988) highlighted as informative in his gametophyte-based classification of the Hookeriales. Ornamentation of the outer surface of the exostome teeth at their bases (smooth, papillose or weakly striate versus conspicuously striate), the presence of a furrow at the central divisural line (also found in the outer surface of the exostome when present), and the type of calyptra (mitrate versus cucullate) are also often highlighted in classifications of the Hookeriales (e.g. Crosby, 1974). In order to address the interaction of habitat shifts and morphological evolution in the Hookeriales, the occurrences of these taxa in three habitat categories were coded (Table 3). When plants were found on bare ground or decaying matter they were coded as present on the "ground". When they could grow on rocks (shaded or exposed, wet or dry) or at the base of trees or shrubs they were coded as "epilithic". Finally, when they typically grow on tree trunks and branches, or leaves, they were coded as "epiphytic". The morphological character states were obtained from literature or measured directly from herbarium collections. Similarly, habitat categories were taken from literature as well as available collection labels

Table 3. Character matrix. Limbidium (0: absent, 1: present). Costa (0: absent, 1: single, 2: double). Cell length (0: 1- 3:1, 1: > 3:1). Ex. ornam., ornamentation of the outer side of exostome at the base (0: smooth, papillose or weakly striate, 1: conspicuously striate). Div. line, outer side of the exostome divisural line (0: not furrowed, 1: furrowed). Calyptra dehiscence (0: cucullate, 1: mitrate). G, mosses found on bare ground and/or decaying matter (0: absent, 1: present). EL+TB, mosses on rocks (shaded or exposed, wet or dry) or at the base of trees or shrubs (0: absent, 1: present). EP, mosses on tree trunks, branches, and leaves (0: absent, 1: present). (?) Unknown. (-) Does not apply.

Taxon	Limbidium	Costa	Cell length	Ex. ornam.	Div. line	Calyptra	G	EL+TB	EP
OUTGROUP									
Euptychium cuspidatum	0	2	1	1	0	1	0	0	1
Garovaglia powellii	0	2	1	0	0	1	0	1	1
Hampeella pallens	0	2	1	1	1	?	0	0	1
Hypnodendron vitiense	0	1	1	1	0	0	1	1	0
Spiridens camusii	1	1	?	1	0	0	0	0	1
INGROUP									
Achrophyllum crassirete	0	1	0	1	1	1	1	0	0
Achrophyllum quadrifarium	0	1	0	1	1	1	1	1	0
Actinodontium adscendens	0	2	1	0	0	1	0	0	1
Actinodontium sprucei	0	2	1	0	0	1	0	0	1
Adelothecium bogotense	0	1	0	1	0	1	1	1	1
Ancistrodes genuflexa	0	2	1	1	1	1	1	1	1
Arbusculohypopterygium arbuscula	1	1	0	1	0	0	1	1	1
Beeveria distichophylloides	0	1	0	1	1	1	1	1	0
Benitotania elimbata	0	1	0	?	?	?	0	0	1
Brymela fluminensis	0	2	1	1	1	1	0	1	0
Brymela tutezona	0	2	1	1	1	1	0	0	1
Brymela websteri	0	2	1	1	1	1	1	1	0
Bryobrothera crenulata	0	1	0	1	0	1	1	1	1
Callicostella africana	0	2	0	1	1	1	1	1	1
Callicostella colombica	0	2	0	1	1	1	0	1	1
Callicostella pallida	0	2	0	1	1	1	1	1	0
Callicostella papillata	0	2	0	1	1	1	1	1	0
Callicostella prabaktiana	0	2	0	1	1	1	1	1	0

Taxon	Limbidium	Costa	Cell length	Ex. ornam.	Div. line	Calyptra	G	EL+TB	EP
Callicostellopsis meridiensis	0	2	0	0	0	1	1	1	1
Calyptrochaeta asplenioides	1	1	0	1	1	1	1	1	0
Calyptrochaeta cristata	1	1	0	1	1	1	1	0	0
Calyptrochaeta remotifolia	1	1	0	1	1	1	1	1	0
Canalohypopterygium tamariscinum	1	1	0	1	0	1	1	1	1
Catharomnion ciliatum	1	1	0	-	-	1	1	1	1
Chaetomitriopsis glaucocarpa	0	2	1	1	0	1	1	0	1
Chaetomitrium borneense	0	2	1	1	0	1	0	0	1
Chaetomitrium dusenii	0	2	1	1	0	0	0	0	1
Chaetomitrium orthorrhynchum	0	2	1	1	0	1	1	0	1
Crosbya straminea	1	1	0	1	1	1	0	0	1
Crossomitrium epiphyllum	0	0	1	0	0	1	1	1	1
Crossomitrium sintenisii	0	0	1	0	0	1	1	1	1
Curviramea mexicana	0	2	0	?	?	?	0	1	0
Cyathophorum bulbosum	1	1	0	1	0	1	1	1	1
Cyclodictyon albicans	1	2	0	1	1	1	1	1	0
Cyclodictyon blumeanum	1	2	0	1	1	1	1	1	1
Cyclodictyon brevifolium	1	2	0	1	1	1	1	1	0
Cyclodictyon laete-virens	1	2	0	1	1	1	1	1	0
Cyclodictyon roridum	1	2	0	1	1	1	1	1	0
Daltonia apiculata	1	1	0	0	0	1	1	1	1
Daltonia armata	1	1	0	0	0	1	0	0	1
Daltonia jamesonii	1	1	0	0	0	1	1	1	0
Daltonia marginata	1	1	0	0	0	1	0	0	1
Daltonia ovalis	1	1	0	0	0	1	0	1	1
Daltonia splachnoides	1	1	0	0	0	1	0	0	1
Dendrocyathophorum decolyi	1	1	0	1	0	0	1	1	1
Dendrohypopterygium filiculiforme	1	1	0	1	0	0	1	1	1
Dimorphocladon borneense	0	2	1	1	0	0	0	0	1
Diploneuron connivens	0	2	0	1	1	1	0	1	0
Diploneuron diatomophilum	0	2	0	1	1	1	1	0	0
Distichophyllidium nymanianum	1	0	0	0	0	1	0	1	1
Distichophyllum carinatum	1	1	0	?	?	1	1	1	0
Distichophyllum cuspidatum	1	1	0	1	1	1	0	1	1
Distichophyllum flaccidum	1	1	0	1	1	1	1	1	0

Taxon	Limbidium	Costa	Cell length	Ex. ornam.	Div. line	Calyptra	G	EL+TB	EP
Distichophyllum maibarae	1	1	0	1	1	1	1	1	0
Distichophyllum malayense	1	1	0	1	1	1	1	0	0
Distichophyllum microcarpum	0	1	0	1	1	1	1	1	1
Distichophyllum mniifolium	1	1	0	1	1	1	1	0	0
Distichophyllum paradoxum	1	1	0	1	1	1	1	1	1
Distichophyllum pulchellum	1	1	0	1	1	1	1	1	0
Distichophyllum rigidicaule	1	1	0	1	1	1	1	0	0
Distichophyllum spathulatum	1	1	0	1	1	1	1	0	0
Ephemeropsis tjibodensis	-	-	-	1	1	1	0	0	1
Ephemeropsis trentepohlioides	-	-	-	1	1	1	0	0	1
Glossadelphus glossoides	0	2	1	1	0	0	0	1	0
Gradsteinia andicola	0	2	1	?	?	?	1	0	0
Hemiragis aurea	0	2	1	1	1	1	1	1	1
Hildebrandtiella guyanensis	0	0	1	0	0	1	0	1	1
Hookeria acutifolia (Ecuador)	0	0	0	1	0	1	1	0	0
Hookeria acutifolia (Java)	0	0	0	1	0	1	1	0	0
Hookeria lucens	0	0	0	1	0	1	1	0	0
Hypnella pallescens	0	2	1	1	1	1	1	0	1
Hypnum cupressiforme	0	2	1	1	0	0	1	1	1
Hypopterygium didictyon	1	1	0	1	0	0	1	1	1
Hypopterygium hookerianum	1	1	0	0	0	1	1	1	1
Hypopterygium tamarisci	1	1	0	1	0	0	1	1	1
Isodrepanium lentulum	0	1	1	1	0	?	0	0	1
Lepidopilidium laevisetum	0	2	1	1	1	1	0	1	1
Lepidopilidium portoricense	0	2	1	1	1	1	1	1	1
Lepidopilum polytrichoides	1	2	1	0	0	1	0	1	1
Lepidopilum scabrisetum	0	2	1	0	0	1	1	1	1
Lepidopilum surinamense	1	2	1	0	0	1	1	1	1
Leskeodon acuminatus	1	1	0	0	0	1	0	0	1
Leskeodon auratus	1	1	0	0	0	1	1	1	1
Leskeodon cubensis	1	1	0	0	0	1	1	1	1
Leucodon sciuroides	0	0	1	0	0	0	0	0	1
Leucomium strumosum	0	0	1	1	1	0	1	1	0
Lopidium concinnum	1	1	0	1	0	0	1	1	1
Myurium hochstetteri	0	2	1	1	0	0	1	1	0

Taxon	Limbidium	Costa	Cell length	Ex. ornam.	Div. line	Calyptra	G	EL+TB	EP
Neohypnella diversifolia	0	2	1	1	0	1	1	0	1
Philophyllum tenuifolium	0	2	1	1	1	1	0	1	1
Phyllodon truncatulus	0	2	1	1	0	0	1	1	1
Pilotrichidium antillarum	0	2	0	1	1	1	0	1	1
Pilotrichidium callicostatum	0	2	0	1	1	1	1	1	1
Pilotrichum andersonii	0	2	0	0	0	1	1	1	0
Pilotrichum bipinnatum	0	2	0	0	0	1	1	1	1
Pilotrichum procerum	0	2	0	0	0	1	0	1	1
Pleurozium schreberi	0	2	1	0	0	0	1	0	0
Pterobryon densum	0	1	1	0	0	1	0	0	1
Rhynchostegiopsis tunguraguana	0	2	1	1	1	0	1	1	1
Rhytidiadelphus triquetrus	0	2	1	1	0	0	1	0	0
Rutenbergia madagassa	1	1	0	0	0	1	0	0	1
Sauloma tenella	0	1	1	1	1	1	1	1	1
Schimperobryum splendidissimum	0	1	1	1	0	1	0	0	1
Stenodesmus tenuicuspis	0	2	1	0	0	1	1	0	0
Stenodictyon pallidum	0	2	1	1	1	1	1	0	0
Stenodictyon wrightii	0	2	1	1	1	1	1	0	0
Symphyodon imbricatifolius	0	2	1	0	0	0	0	1	1
Tetrastichium fontanum	0	2	1	1	1	1	1	1	0
Thamniopsis cruegeriana	0	2	1	1	1	1	1	1	0
Thamniopsis incurva	0	2	1	1	1	1	1	0	0
Thamniopsis pendula	0	2	0	1	1	1	1	1	1
Thamniopsis secunda	0	2	0	1	1	1	1	1	0
Thamniopsis sinuata	0	2	1	1	1	1	1	1	1
Thamnobryum alopecurum	0	1	0	1	0	0	1	1	0
Trachyloma planifolium	0	2	1	0	0	0	1	0	1
Trachyxiphium guadalupense	0	2	1	1	1	1	1	1	1
Trachyxiphium vagum	0	2	1	1	1	1	1	0	0
Vesicularia vesicularis	0	2	1	1	0	0	1	1	1

1.3. Results

13.3. Sequence amplification

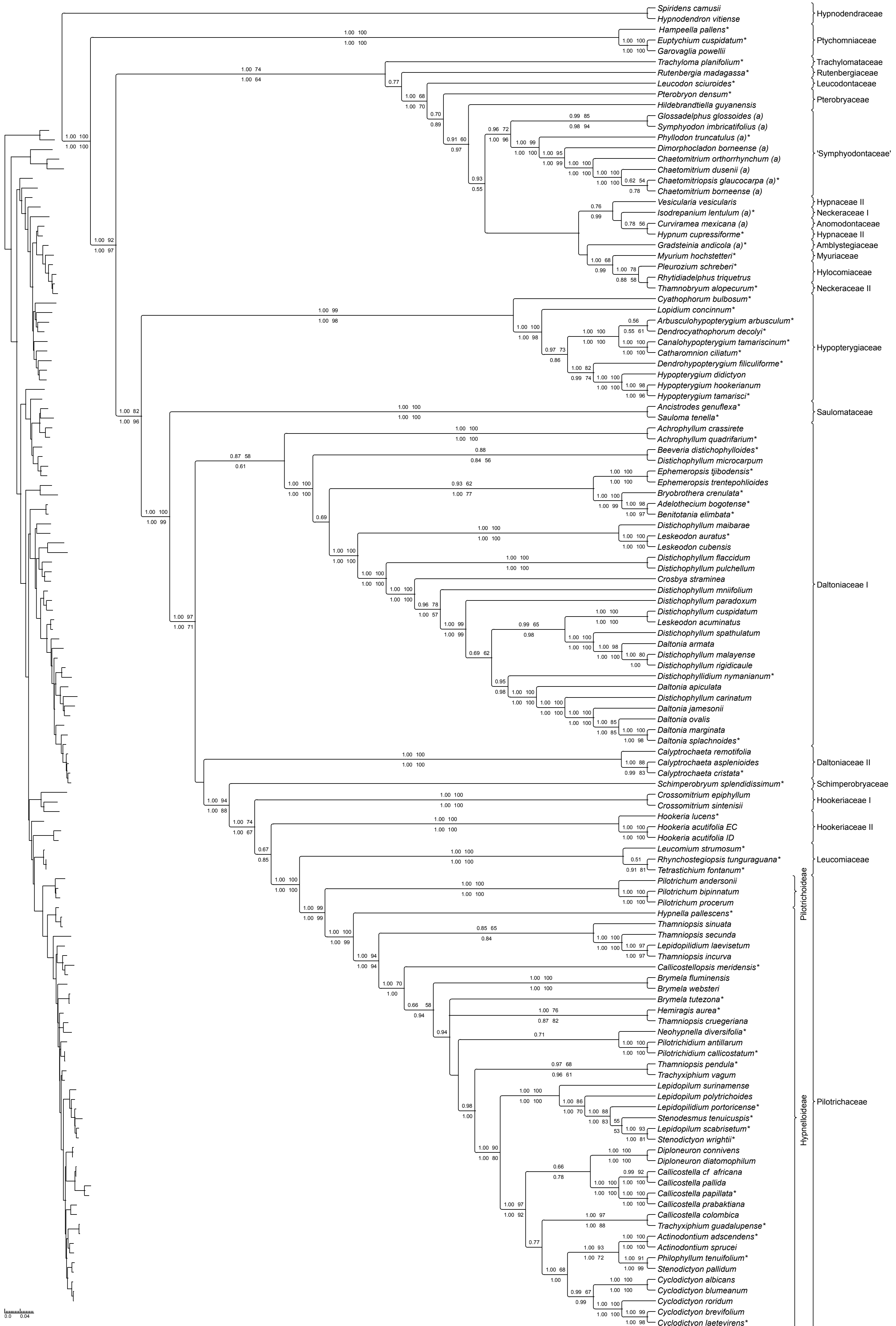
We were successful obtaining *rps*4 and *trn*LF for all accessions, 35 (28%) and 42 sequences (34%), respectively, were newly generated for this study. For *nad*5 the final data matrix includes 115 sequences, 32 of which (28%) are new. For the nuclear ITS we sequenced 106 sequences, 83 of them (78%) are new, and we used 110 26S sequences, 45 (41%) new. In total, the combined matrix includes 577, out of 615 (5 markers × 123 samples — 94%), 237 (41%) were generated for this study. Missing data represents 6% of the combined data matrix.

The combined dataset constitutes a total of 6627 characters with an additional of 1502 characters from the indel coding. The coded indels increases the number of parsimony informative characters (PI) from 1336 to 1958 characters. The highest level of increase in PI with the addition of indels as characters is seen in the nuclear ribosomal genome with a ca. 78% raise (from 644 to 1149). Among the three genomes, the highest PI is also found in the nuclear genome (644), followed by the plastids (407) and mitochondria (285).

1.3.2. Phylogenetic analyses

All data partitions converged to nearly identical topologies with no significant disagreement among supported clades (Figure 1). Two main clades were resolved corresponding to the Hypnales and Hookeriales, which are therefore monophyletic.

→ **Figure 1**. Topology obtained after ML (Morrison ratchet approach) analyses of the combined dataset without any indel coding. Miniature phylogram of the same ML tree is shown on the left. Support values shown above branches are, posterior probability (PP) for a homogeneous model followed by ML bootstrap support. Values below branches denote PP for a heterogeneous model and maximum parsimony bootstrap support (with ratchet) from 10,000 replicates. All values are from analyses of the dataset without indels with the exception of the parsimony bootstrap support. Bayesian analyses for 3,000,000 generations, 10 runs and 4 chains.


Spiridens camusii
Hypnodendron vitiense
Hypnodendraceae
Hampeella pallens*
Euptychium cuspidatum*
Garovaglia powellii
Ptychomniaceae
Trachyloma planifolium*
Trachylomataceae
Rutenbergia madagassa*
Rutenbergiaceae
Leucodon sciuroides*
Leucodontaceae
Pterobryon densum*
Hildebrandtiella guyanensis
Pterobryaceae
Glossadelphus glossoides (a)
Symphyodon imbricatifolius (a)
Phyllodon truncatulus (a)*
Dimorphocladon borneense (a)
Chaetomitrium orthorrhynchum (a)
Chaetomitrium dusenii (a)
Chaetomitriopsis glaucocarpa (a)*
Chaetomitrium borneense (a)
'Symphyodontaceae'
Vesicularia vesicularis
Hypnaceae II
Isodrepanium lentulum (a)*
Neckeraceae I
Curviramea mexicana (a)
Anomodontaceae
Hypnum cupressiforme*
Hypnaceae II
Gradsteinia andicola (a)*
Amblystegiaceae
Myurium hochstetteri*
Myuriaceae
Pleurozium schreberi*
Rhytidiadelphus triquetrus
Hylocomiaceae
Thamnobryum alopecurum*
Neckeraceae II
Cyathophorum bulbosum*
Lopidium concinnum*
Arbusculohypopterygium arbusculum*
Dendrocyathophorum decolyi*
Canalohypopterygium tamariscinum*
Catharomnion ciliatum*
Dendrohypopterygium filiculiforme*
Hypopterygium didictyon
Hypopterygium hookerianum
Hypopterygium tamarisci*
Hypopterygiaceae
Ancistrodes genuflexa*
Sauloma tenella*
Saulomataceae
Achrophyllum crassirete
Achrophyllum quadrifarium*
Beeveria distichophylloides*
Distichophyllum microcarpum
Ephemeropsis tjibodensis*
Ephemeropsis trentepohlioides
Bryobrothera crenulata*
Adelothecium bogotense*
Benitotania elimbata*
Distichophyllum maibarae
Leskeodon auratus*
Leskeodon cubensis
Distichophyllum flaccidum
Distichophyllum pulchellum
Crosbya straminea
Distichophyllum mniifolium
Distichophyllum paradoxum
Distichophyllum cuspidatum
Leskeodon acuminatus
Distichophyllum spathulatum
Daltonia armata
Distichophyllum malayense
Distichophyllum rigidicaule
Distichophyllidium nymanianum*
Daltonia apiculata
Distichophyllum carinatum
Daltonia jamesonii
Daltonia ovalis
Daltonia marginata
Daltonia splachnoides*
Daltoniaceae I
Calyptrochaeta remotifolia
Calyptrochaeta asplenioides
Calyptrochaeta cristata*
Daltoniaceae II
Schimperobryum splendidissimum*
Schimperobryaceae
Crossomitrium epiphyllum
Crossomitrium sintenisii
Hookeriaceae I
Hookeria lucens*
Hookeria acutifolia EC
Hookeria acutifolia ID
Hookeriaceae II
Leucomium strumosum*
Rhynchostegiopsis tunguraguana*
Tetrastichium fontanum*
Leucomiaceae
Pilotrichum andersonii
Pilotrichum bipinnatum
Pilotrichum procerum
Pilotrichoideae
Hypnella pallescens*
Thamniopsis sinuata
Thamniopsis secunda
Lepidopilidium laevisetum
Thamniopsis incurva
Callicostellopsis meridensis*
Brymela fluminensis
Brymela websteri
Brymela tutezona*
Hemiragis aurea*
Thamniopsis cruegeriana
Neohypnella diversifolia*
Pilotrichidium antillarum
Pilotrichidium callicostatum*
Thamniopsis pendula*
Trachyxiphium vagum
Lepidopilum surinamense
Lepidopilum polytrichoides
Lepidopilidium portoricense*
Stenodesmus tenuicuspis*
Lepidopilum scabrisetum*
Stenodictyon wrightii*
Diploneuron connivens
Diploneuron diatomophilum
Callicostella cf africana
Callicostella pallida
Callicostella papillata*
Callicostella prabaktiana
Callicostella colombica
Trachyxiphium guadalupense*
Actinodontium adscendens*
Actinodontium sprucei
Philophyllum tenuifolium*
Stenodictyon pallidum
Cyclodictyon albicans
Cyclodictyon blumeanum
Cyclodictyon roridum
Cyclodictyon brevifolium
Cyclodictyon laevirevens*
Hypnelloideae
Pilotrichaceae
0.0
0.04

In the Hypnales clade, the genera *Rutenbergia* and *Trachyloma* appear sister to the core Hypnales though their relative position within this clade is not supported. Sampling within the Hypnales was not extensive since our study focuses on the Hookeriales. There were taxa included for which an ordinal placement has been debated in extent. In that regard, a well-supported clade (i.e. “Symphyodontaceae”) consisting of *Chaetomitriopsis, Chaetomitrium*, *Dimorphocladon*, *Glossadelphus, Phyllodon* and *Symphyodon* resolved within the Hypnales is noteworthy, since most of the taxa it comprises have often been associated to the Hookeriales.

Monophyly of the order Hookeriales sensu Buck et al. (2005) is corroborated with strong support (maximum PP for both the homogeneous and the heterogeneous Bayesian models, 82 ML bootstrap and 96 MP bootstrap). Within the Hookeriales clade, the first divergence presents Hypopterygiaceae as sister to all other families in this order. Relationships in the Hypopterygiaceae clade do not differ from those reconstructed in Shaw et al (2008) when support is strong. *Ancistrodes genuflexa* and *Sauloma tenella* form a well supported monophyletic clade sister to the remaining taxa in the Hookeriales minus the Hypopterygiaceae. Following, the topology reconstructed presents the genus *Achrophyllum* in a clade with most of the Daltoniaceae (hereafter Daltoniaceae I) but for *Calyptrochaeta*, which is reconstructed as sister to this clade and all other Hookeriales. The position of *Achrophyllum* and *Calyptrochaeta* is not supported. Within Daltoniaceae earlier nodes split into a series of clades mostly composed of monotypic small-sized genera such as *Adelothecium*, *Beeveria*, *Benitotania*, and *Ephemeropsis*. Subsequently, a complex related to the large and polyphyletic genus *Distichophyllum* is found. Genera such as *Daltonia* and *Leskeodon*, which are not monophyletic themselves, are nested within this large genus. Notably the resolved clades within *Distichophyllum* and *Leskeodon* correspond rather to biogeographical entities than to groups united by morphology (see Table 1 for distributions).

Sister to *Calyptrochaeta* are *Schimperobryum*, *Hookeria*, and *Crossomitrium*, three monogeneric clades, and the Leucomiaceae (clade composed of three genera) and the Pilotrichaceae. Within the Pilotrichaceae, the first dichotomy separates to the two well-supported subfamilies recognized in the family, namely the monogeneric Pilotrichoideae, and the Hypnelloideae. Resolution within the Hypnelloideae, for the most part, is poor, and most genera in the subfamily are polyphyletic as currently circumscribed; i.e., *Callicostella*, *Lepidopilidium*, *Lepidopilum*, *Stenodictyon*, *Thamniopsis*, *Trachixyphium*. *Pilotrichum* (Pilotrichoideae) and *Cyclodictyon* (Hypnelloideae) are two of the few genera that do not show para- or polyphyly.

1.3.3. Ancestral state reconstruction

A low number of species in this study grow only in one of the habitats scored (Table 3). Thus, our resulting character state reconstruction for the habitat occupation (Figure 2 and 3), which shows no clear habitat preference for the ancestor of the Hookeriales clade, comes as no surprise.

Results of the ML character state reconstruction on the 50% majority rule Bayesian tree under a Mk1 model infer the absence of a limbidium as the ancestral condition for the Hookeriales (significant proportional likelihood, 0.976) (Figure 4A). Five origins of limbidia, with significant proportional likelihood (SPL), are detected in the order without any reversals. Similarly, the Hookeriales common ancestor is inferred to have had a single costa (SPL, 0.995), which seems to have been lost twice and regained as double (see Figure 4B). An ancestral cell ratio could not be inferred for this order (Figure 5A). Taxa on the Hypopteryigiaceae and the Daltoniaceae s.l. present smaller cell ratios when compared to the remainder of the Hookeriales. No reversals detected.

Finally, the calyptra is reconstructed as mitrate (SPL, 0.96), in the node comprising all families in the Hookeriales sister to the Hypopterygiaceae (Figure 5B). This morphology is only lost once in the Leucomiaceae. The ancestral condition for the ornamentation of the outer exostome base in the Hookeriales (Figure 6A) is reconstructed as conspicuously striate (SPL, 0.944). Ten shifts to smooth, papillose or weakly striate were detected. The ancestral condition for the divisural line found on the outer side of the exostome is reconstructed as not furrowed (SPL, 0.936) (Figure 6B). A large number of origins of median furrows take place and ca. 10 losses of furrows (reversals) are inferred. An ancestral dehiscence type for the calyptra could not be inferred, since both the Hypnales and the Hypopterygiaceae have both cucullate and mitrate calyptrae.

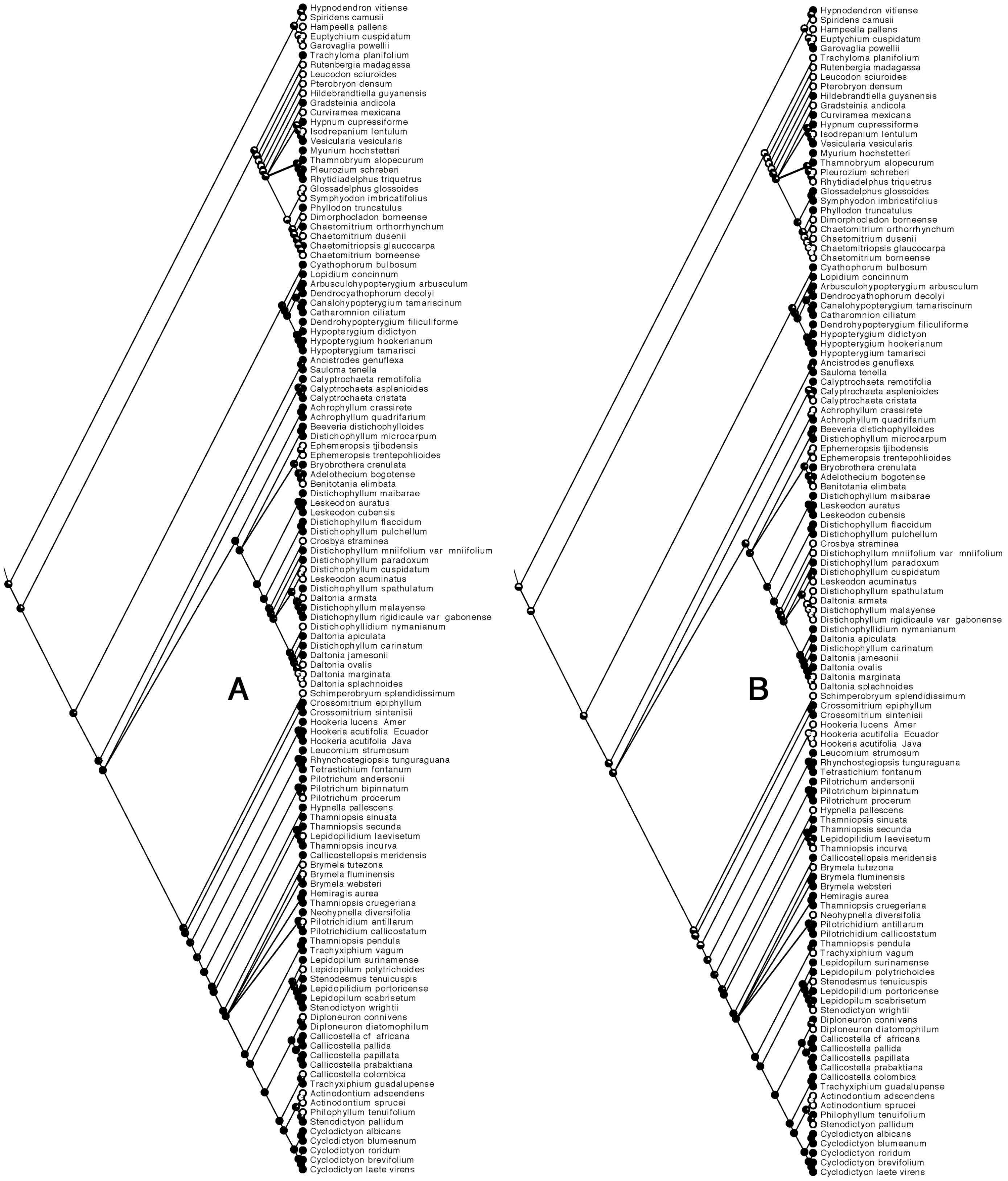


Figure 2. ML character state reconstruction in Mesquite under Mk1 for. (A) Ground, and (B) epilithic + tree bases (white = absent; black = present).

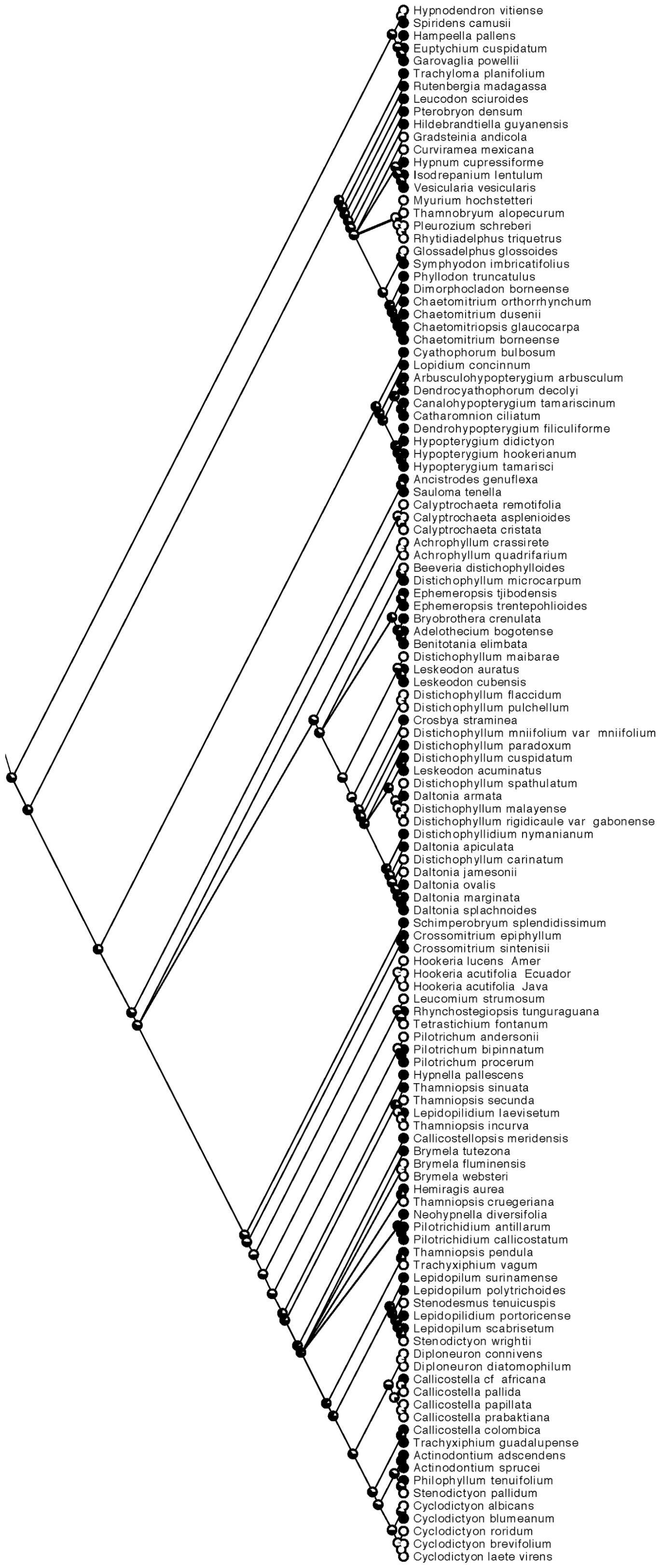


Figure 3. ML character state reconstruction in Mesquite under Mk1 for epiphytic (white = absent; black = present).

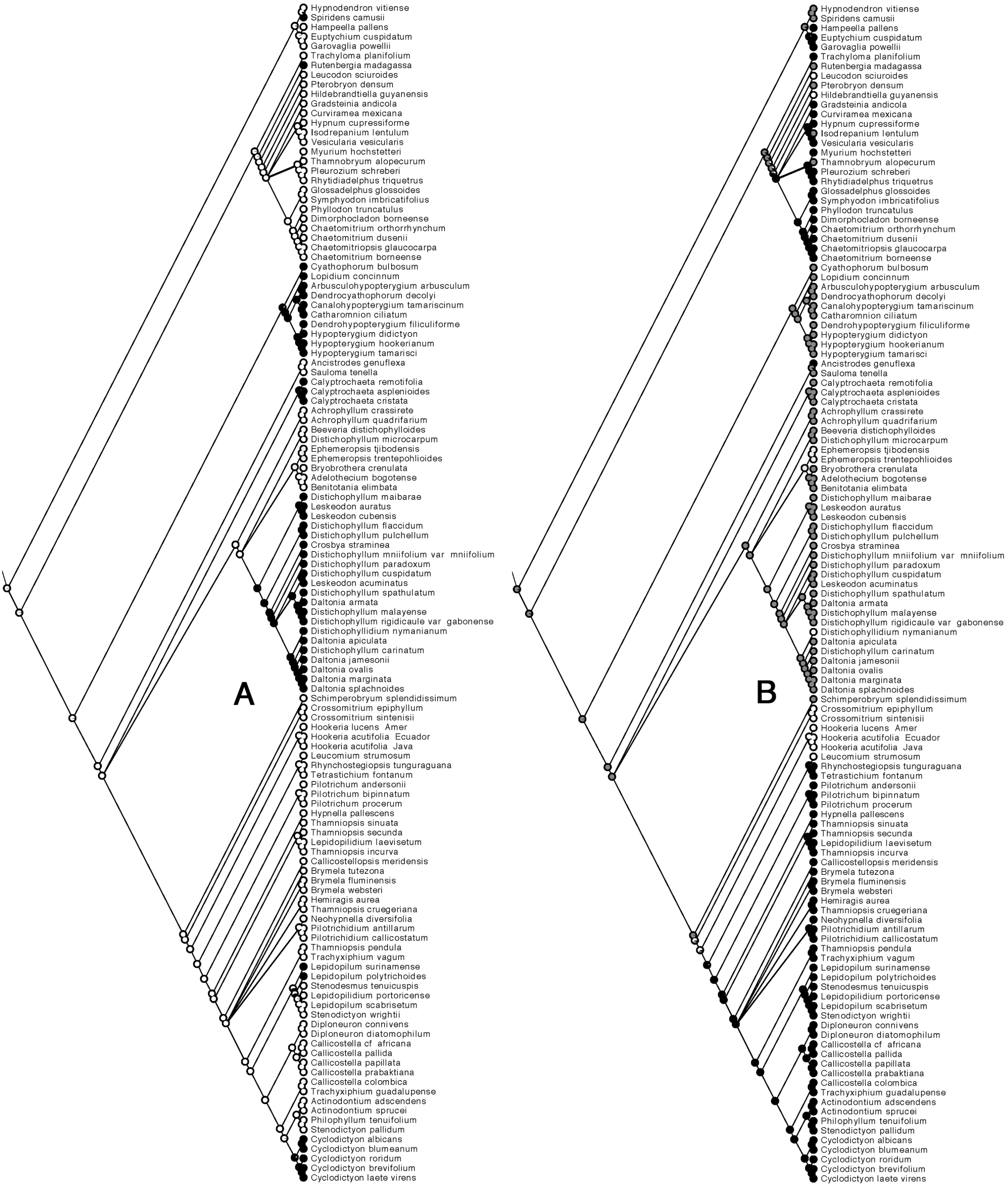


Figure 4. ML character state reconstruction in Mesquite under Mk1 for (A) limbidium (white = absent; black = present), (B) costa (white = absent; grey = single; black = double), and (C) cell ratio (white = 1-3:1, black = > 3:1).

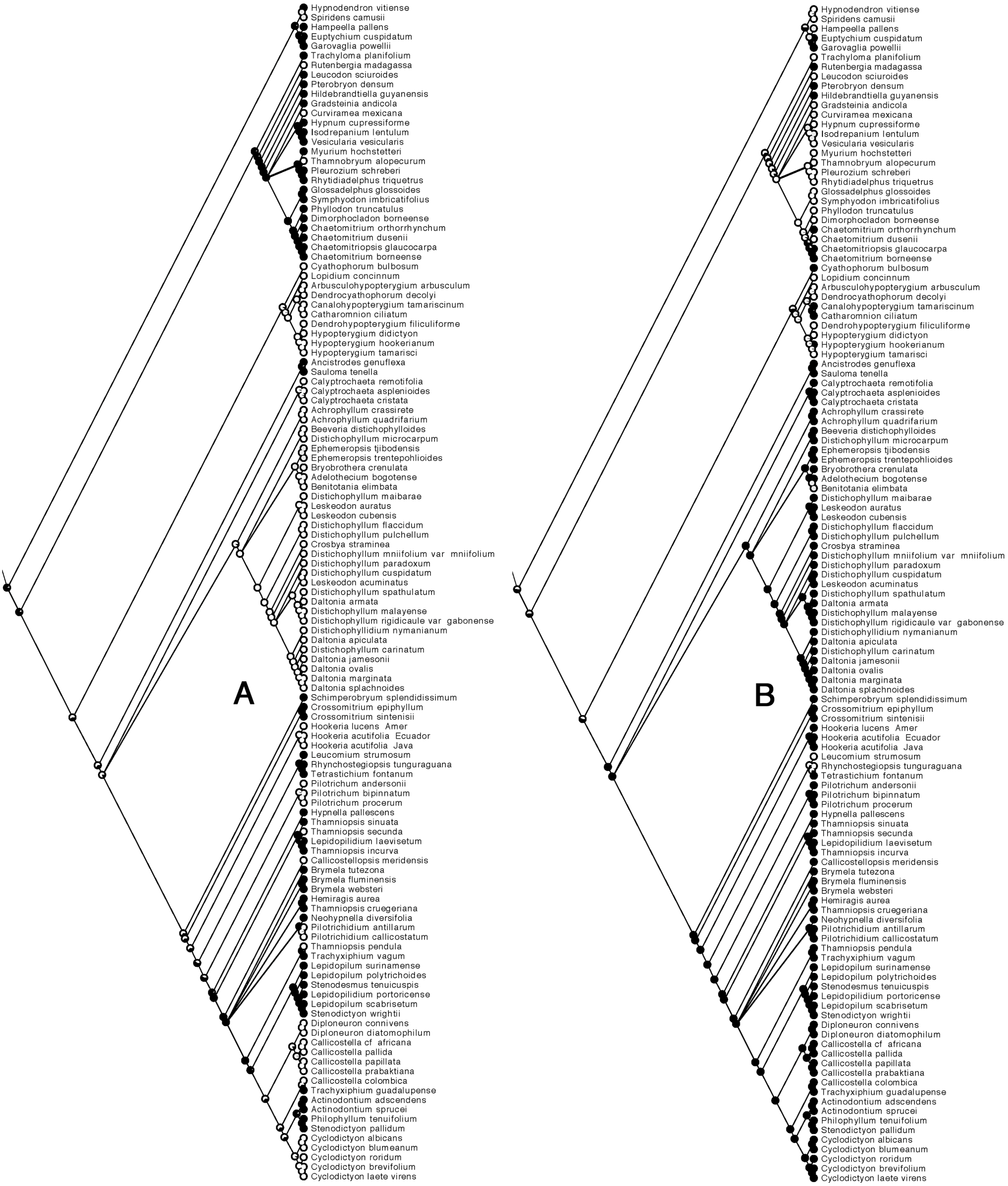


Figure 5. ML character state reconstruction in Mesquite under Mk1 for (C) cell ratio (white = 1-3:1, black = > 3:1), (B) type of dehiscence the calyptra presents (white = cucullate; black = mitrate).

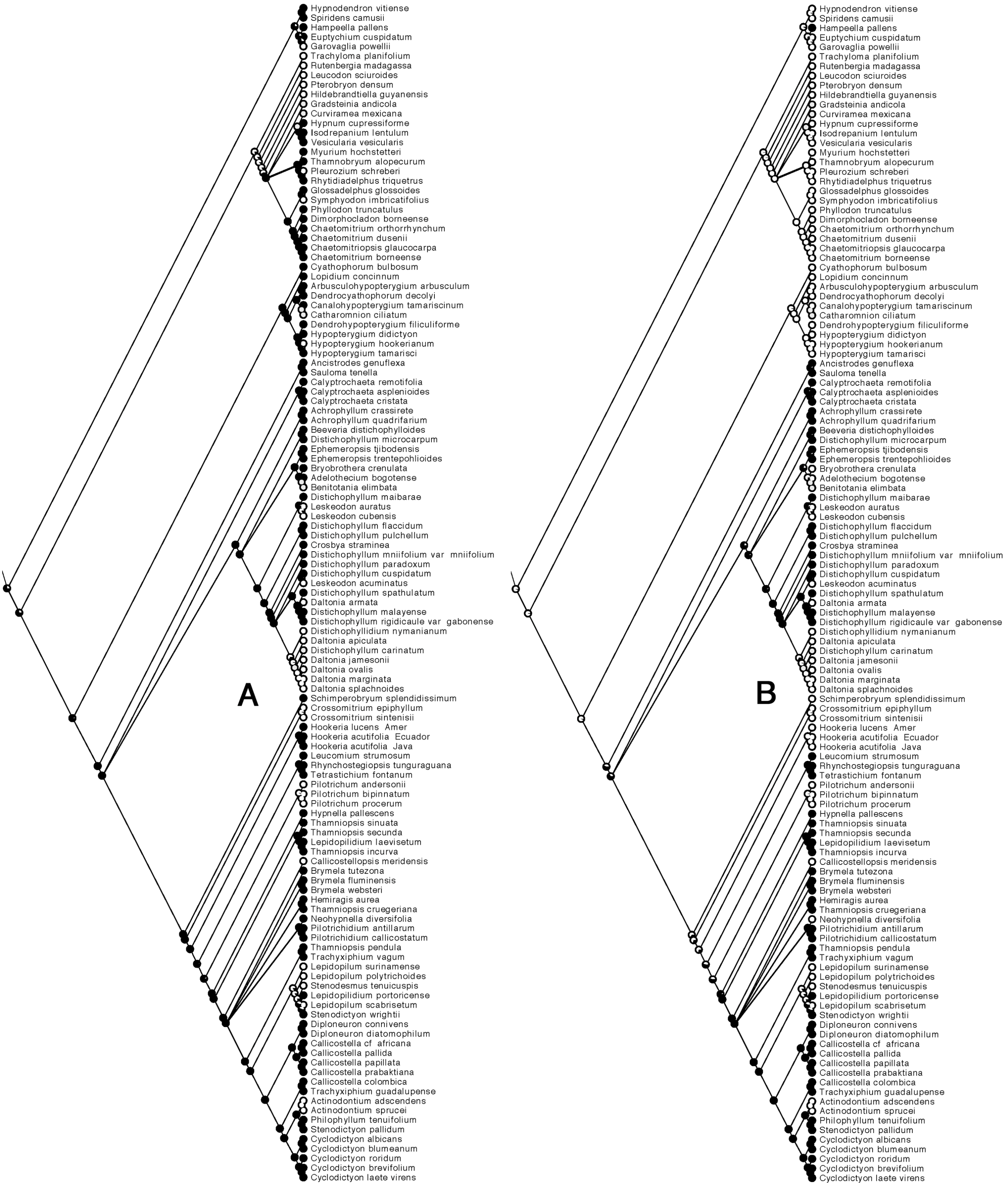


Figure 6. ML character state reconstruction in Mesquite under Mk1 for (A) ornamentation of the outer side of the exostome at the base (white = smooth, papillose or weakly striate; black = conspicuously striate), (B) central divisural line or furrow (white = absent, black = present).

1.4. Discussion

1.4.1. Is the order Hookeriales monophyletic?

Currently, the Hookeriales (sensu Buck et al., 2005) is accepted as consisting of seven families, including Daltoniaceae, Hookeriaceae, Hypopterygiaceae, Leucomiaceae, Pilotrichaceae (with two subfamilies), Saulomataceae, and Schimperobryaceae. However, Newton et al. (2007; 2009) raised reasonable doubts about the validity of these relationships. They suggested that the Hypnales are paraphyletic relative to the Hookeriales, since the affinity to the Hypnales of taxa such as *Rutenbergia* or *Trachyloma* could not be ascertained. Moreover, they recognized the independence of Hypopterygiaceae from the Hookeriales.

Nevertheless, results from this study strongly supported the monophyly of the order Hookeriales with the inclusion of Hypopterygiaceae (Figure 1), thus concurring with the findings of Buck et al. (2005). Furthermore, the genera *Rutenbergia* and *Trachyloma* come out in the Hypnales clade with maximum posterior probability, though bootstrap support is not optimum. This result seem contradictory with the ones from previous studies as pointed out by Newton et al. (2009). However, previous results are base exclusively on the plastid genome, specifically the *trn*LF and *rps*4 genes. In fact, one of the analyses of this study with only the plastid genome gave similar scenario where the relationships of Ptychomniaceae, Hypnales, Hypopterygiaceae, and the rest of Hookeriales were not resolved with good support (see Appendix 1). The greater information which arrived at the final topology presented in Figure 1 came from the nuclear genome (cf. Appendix 3).

Also within the Hypnales, the well-supported clade consisting of *Chaetomitriopsis*, *Chaetomitrium*, *Dimorphocladon*, *Glossadelphus*, *Phyllodon* and *Symphyodon*, is noteworthy. *Glossadelphus* and *Phyllodon* have never previously been associated with the Symphyodontaceae. Interestingly, all taxa in this clade were once considered allied to the Hookeriales. If the new inclusions to Symphyodontaceae are accepted, the morphological circumscription of the family sensu Buck & Goffinet (2000) seems to remain unchanged, e.g. prorate laminal cells. Nevertheless, more taxon sampling within the Hypnales, especially members of Hypnaceae, is necessary for a better delimitation of the Symphyodontaceae.

1.4.2. Familial and generic relationships in Hookeriales

The relationships of familial clades reconstructed in our analyses are in accordance to those highlighted by Buck et al. (2005). In addition, clades lacking support coincide with theirs, although the topology reconstructed is slightly different. In Buck et al. (2005), *Calyptrochaeta* is placed in a clade together with all other Daltoniaceae. In our phylogeny, *Calyptrochaeta* comes out as sister to the Schimperobryaceae, Hookeriaceae, Leucomiaceae and Pilotrichaceae. However in both scenarios, the critical nodes are without good support. Further work to resolve the placement of this genus is required.

Although Hookeriacaceae, Leucomiaceae and Pilotrichaceae forms a clade with adequate support, the relationships of *Hookeria* with *Crossomitrium* and Leucomiaceae plus Pilotrichaceae remains uncertain. In fact, in parsimony the positions of *Hookeria* and *Crossomitrium* exchange places (see Appendix 4). Hence, the elevation and segregation of *Crossomitrium* in its own family cannot be justified and thus following Buck et al. (2005) approach tentatively retaining the genus in the more traditionally defined and paraphyletic Hookeriaceae while awaiting further confirmation.

Relationships within the Hypopterygiaceae are similar to those reconstructed by Shaw et al. (2008). The only divergence from their topology lies in the position of *Lopidium concinnum*, which in this study is sister to all other Hypopterygiaceae but for *Cyathophorum bulbosum*, and in theirs is sister only to the genera *Dendrohypopterygium* and *Hypopterygium*. Though, at first, this may look as an incongruence, support values make possible this two alternative topologies.

Sauloma and *Ancistrodes* are the only two genera sampled within the Saulomataceae thus far. Position of the Chilean endemic, *Vesiculariopsis spirifolium*, hypothesized to belong in this family, remains to be tested.

All sampled Daltoniaceae, with the exception of the genera *Achrophyllum* and *Calyptrochaeta*, fall in the same clade with maximum support. Deeper nodes in this clade correspond to small genera of one to two species. Larger genera such as *Daltonia*, *Distichophyllum*, and *Leskeodon* are not monophyletic. Detailed discussion with larger taxon sampling is presented in Chapter 2. The relationship of the monotypic genera *Leskeodontopsis* and *Metadistichophyllum*, thought to belong in the Daltoniaceae, remains uncertain since sampling for DNA was not successful.

Although the Leucomiaceae is well-supported, relationships between the three genera cannot be resolved with adequate support. The double-costate Pilotrichaceae, on the other hand, presents large genera that, as currently circumscribed, are not monophyletic. Several similar topologies are already discussed in Buck et al. (2005) and thus not repeated here. With increased taxon sampling in *Cyclodictyon* to include the type species as well as representatives from other parts from the Old World, the genus remains monophyletic. Similarly the monophyly of *Actinodontium* is confirmed with the addition of the type species. Members of *Callicostella* sampled from different continents are closely relate except for *C. colombica* which has closer affinity to *Trachyxiphium guadalupense*, the type of its genus. Generic circumscriptions of *Callicostella* and *Trachyxiphium* clearly needs reassessments and adjustments. Interestingly, four type species *Lepidopilidium portoricense*, *Lepidopilum scabrisetum*, *Stenodesmus tenuicuspis*, and *Stenodictyon wrightii* showed out together in a well-support clade. If this clade would be accepted in future studies, it would be named *Lepidopilum*, the oldest name among the four. Although it is quite clear that the traditional separation of *Lepidopilum* and *Lepidopilidium* by the papillose, non-furrowed exostome can no longer hold (compare Figure 6), it is still premature to transfer all four names into synonymy with the present lack of taxonomic evaluation. The phylogeney also agrees with Buck (1987) that the traditional and broad-sensed *Hookeriopsis*, i.e. including *Brymela*, *Thamniopsis* and *Trachyxiphium*, is heterogenous, although the clades did not correspond well with the segregated genera. Other genera currently ascribed to this family that need to be included in future studies are *Amblytropis*, *Helicoblepharum*, and *Hookeriopsis.* Re-evaluations of generic boundaries within Pilotrichoideae, in conjunction with molecular phylogenetic studies is urgently needed.

1.4.3. Evolution of gametophytic versus sporophytic characters in Hookeriales,

The habitat reconstructions only indicated that most species in this order are generalists, with very few clades restricted to a single substrate, e.g. *Actinodontium* and *Ephemeropsis* (epiphytic), *Hookeria* (terrestrial). In contrast to what Olsson et al (2009b) observed in the hypnalean family Neckeraceae, no patterns of habitats preferences at the familial level can be observed.

The results of the reconstructed morphological traits show that the common ancestor of the Hookeriales should have had elimbate leaves, single costa, and a conspicuously striated outer exostome base, which was not furrowed. Although, limbate leaves have derived from elimbate ones by convergence at least five times in the Hookeriales, they represent synapomorphies for the Hypopterygiaceae, *Calyptrochaeta*, the more terminal clades within the Daltoniaceae, and *Cyclodictyon* in the Pilotrichaceae. However, in *Lepidopilum* the character is autapomorphic in only some species and the border cells when present are generally not as sharply define from adjacent ones as the other limbate taxa. Hence, the character is more useful at the generic level especially within Daltoniaceae.

It is also quite interesting how the leaf costa starts as single within the hookeriales, is lost in *Crossomitrium* and *Hookeria*, and regained in the Leucomiaceae (except for *Leucomium*) and Pilotrichaceae as double. In fact, with inference from Bell et al. (2007), all clades basal to the core pleurocarps, e.g. the Rhizogoniales, Bryales etc. have single costa leaves. Thus single costa is a pleisomorphy within the pleurocarps as well as the diplolepidous alternate mosses. This conclusion rejects earlier theories by some authors such as Miller (1971) who suggested that strong costa is primitive (pleisomorphic) while the ecostate condition is most derived (apomorphic) or Robinson (1975) who proposed evolution in the direct opposite direction as Miller (1971). Although sampling size of the Hynales is small, it is clear that leaf costa in pleurocarps evolved from the pleisomorphic unicostate state to ecostate or short bicostae. The long bicostate leaves e.g. in *Callicostella* (Pilotrichaceae, Hookeriales) and some species of *Chaetomitrium* (Symphyodontaceae, Hypnales) are secondarily developed from the (nearly) ecostate ones. In other words, the double costae are new innovations and dissimilar to the ones in unicostate taxa. In fact, the ecostate and double costate, at least between Hypnales and Hookeriales, represent homoplasy. The costae are lost and gain as double in separate evolutionary events. Nonetheless, within the Hookeriales, ecostate state is reconstructed as synapomophies for *Hookeria* and *Crossomitrium* although ambiguous due to the uncertain topologies of the two genera. The double costate state is synapomorphic for the Pilotrichaceaea clade.

The ancestral state of cell ratio is uncertain although short cells (ratio <3:1) is reconstructed as synapomophies to the clades corresponding to the Hypopterygiaceae, Daltoniaceae, *Hookeria*, *Pilotrichum*, *Diploneuron-Callicostella*, and *Cyclodictyon*. Equally uncertain is the calyptra type in the ancestor state. Nevertheless, mitrate calyptra is reconstructed as a synapomorphy corresponding to the clade uniting Saulomataceae and its sister clade, i.e. Hookeriales excluding Hypopterygiaceae. Moreover, it is shown that the cucullate calyptra in Leucomiaceae has arises from a mitrate one.

Shifts in the selected sporophytic traits are rather frequent, which in part, helps explain why classifications based exclusively on these characters give poor results with respect to natural system. Exostome striations and furrows on the outer face have lost several times in the Hookeriales. Papilose exostome without furrow on the dorsal face has been reconstructed as synapomorphies only for the genera *Daltonia* s.str. and *Actinodontim*. These characters provide no useful information in the recognition of any supported families.

1.4.4. How frequent is morphological reversibility?

Leaf limbidia in the Hookeriales have been developed from parallel evolution. Its true function is uncertain, but has been postulated to provide additional support to the lamina. On the other hand, if leaf costa has been coded as presence and absence, disregarding whether if they are single or double, then the reconstruction would have interpreted the double costa in Pilotrichaceae as a reversal. Although reconstructed with certain unambiguousities, the long-cells state seems to have lost at the beginning of the Hookeriales as short ones, but regain several times as long in some of the crown clades.

In the case of calyptra, the pleisomorphic state cannot be reconstructed with certainties. If it can be proven in future studies that, the cucullate type represent plesiomophorphy either in the order or the pleurocarps, the cucullate calyptra in Leucomiaceae is then a reversal.

Sporophyte morphology is more labile and no obvious patterns can be identified. Several switches to papillose, smooth or weaky striate ones from a strongly striate ones occur, but no reversal is identified. Gains and losses of median furrow in the outer exostome surface occur in comparable numbers, about a dozen each. Thus representing high level of homoplasy.

From the assessments of the above six selected morphologies, homoplasy due to parallel evolution seems to be more common (presence of limbidia and exostome ornamentation). Reversals in calyptra type, are uncertain and only proven as parallel in the reconstruction. The quantitative changes in the cell ratios from short to long cells and back could not be considered a lost or gain in character, but modifications of shape. Nevertheless, the presence of leaf costa(e), regardless of being single or double, is clearly a case of loss and gain of structure. Similarly, reversals are interpreted in the many regains of the exostome furrow due to the differential wall thickening of the two adjacent cell rows.

Final remarks

To summarize, the monophyly of the order Hookeriales is ascertained, however a few important nodes remains unresolved. Families in the order remain unchanged. Large genera (e.g. *Callicostella*, *Distichophyllum*, *Lepidopilum* etc.) are often not monophyletic, which signals our poor understanding on the evolution of morphological traits in this group of organisms. More work is required to disentangle internal relationships within families especially Daltoniaceae and Pilotrichaceae. Since most species in the order grow in a wide variety of habitats no obvious correlation in the morphology has emerge from our analyses. Reversals of character states, although few, are demonstrated here for the first time.

--- <<End of Chapter 1>> ---

Chapter 2:

Molecular Evolution and Diversification of the moss family Daltoniaceae (Hookeriales, Bryopsida) with emphasis on unrevealing the phylogeny of *Distichophyllum* and its allies.

To be submitted to "Systematic Botany"

Contents

2.1. Introduction

The Daltoniaceae, as currently circumscribed (Buck et al., 2005), are a prominent group of tropical and South-temperate mosses that prefer humid forest habitats. Members in the family can be found in a range of habitats from terrestrial to epiphytic; some are even adapted to live on twigs and leaves (epiphylls) or submerged under water (aquatic). Consisting of about 200 species in 14 genera, the family is characterized by (1) plants sparingly branched and usually complanate, (2) foliate axis not differentiated into stems and branches, (3) leaves almost always unicostate, rarely ecostate (only in *Distichophyllidium* M.Fleisch.) and mostly limbate, (4) laminal cells ± isodiametric and (5) calyptra mitrate. About half the number of genera consist of only one or two species each (*Adelothecium* Mitt., *Beeveria* Fife, *Benitotania* H.Akiyama, T.Yamag. & Suleiman, *Bryobrothera* Thér., *Crosbya* Vitt., *Ephemeropsis* K.I.Goebel, *Metadistochophyllum* Nog. & Z. Iwats., *Leskeodontopsis* Zanten). On the other hand, the largest genus, *Distichophyllum* Dozy & Molk., alone represents about half the number of species within the family.

2.1.1. History of Daltoniaceae Schimp.

The family Daltoniaceae Schimp. (1860) was first established to accommodate only the genus *Daltonia* Hook. & Taylor. However, Müller (1850) had earlier associated *Daltonia* and *Distichophyllum* (as *Mniadelphus* Müll.Hal.) under Mniadelphaceae. Nevertheless, the more familiar traditional classification is that of Fleischer (1908), where the Daltonieae (consisting of *Daltonia* and the segregated genus *Crosbya*, as *Bellia* Broth.) and Distichophylleae (consisting of *Achrophyllum* Vitt & Crosby as *Pterygophyllum* Broth., *Adelothecium*, *Calyptrochaeta* Desv. as *Eriopus* (Brid.) Brid., *Distichophyllidium* M.Fleisch., *Distichophyllum* and *Leskeodon* Broth.) were recognized as two separate but closely related tribes within the broad and classical definition of Hookeriaceae. Brotherus' (1907, 1925) worldwide reviews of mosses followed Fleischer's classification scheme but raised these tribes to subfamilies, Daltonioideae and Distichophylloideae, respectively. The Daltonioideae were essentially distinguished from the Distichophylloideae by the radial leaf arrangement with uniform and symmetric leaves and upright habit. Members of Distichophylloideae are more or less complanate with leaves somewhat differentiated into ventral, lateral and dorsal leaves. The lateral leaves are often asymmetric.

At least with respect to the group, Miller's (1971) system is similar to Fleischer and Brotherus, except for the inclusion of *Calyptrochaeta* (as *Eriopus*) in Hookeriaceae and for raising the two subfamilies of Brotherus to family level, i.e., Daltoniaceae and

Distichophyllaceae. In addition, the placement of *Adelothecium* in Distichophyllaceae was doubtful.

Three years later, Crosby (1974) drastically changed the whole system within the order Hookeriales by proposing a new classification which was based almost solely on two peristome types, namely the hookeriaceous peristome — exostome with the outer plate cross-striolate at the base, endostome with high basal membrane and finely papillose segments, cilia absent to rudimentary; and the daltoniaceous peristome — exostome papillose throughout with inner plates narrower than the outer ones, endostome with segments papillose, basal membrane low or absent, cilia absent (see Crosby, 1974). Pairs of genera, regardless of their gametophytic similarities, were sorted in either Hookeriaceae or Daltoniaceae according to the respective peristome types.

In Buck's (1987, 1988) reassessments of the Hookeriales based mostly on gametophytic features, the re-circumscribed Daltoniaceae included, the neotenic *Ephemeropsis*, the traditional Daltonioideae and Distichophylloideae but excluded the elimbate genera *Achrophyllum* and *Adelothecium*. *Achrophyllum* was placed together with *Cyathophorella*, *Cyathophorum*, *Dendrocyathophorum*, *Hookeria* and *Schimperobryum* in his Hookeriaceae. A new family Adelotheciaceae was also established to accommodate *Adelothecium* and, with uncertainties, *Bryobrothera*.

Whittemore & Allen (1989), in an attempt to evaluate the relationships of *Adelothecium*, had a broader concept of the Daltoniaceae and did not favor putting *Adelothecium* in a separate family. Their Daltoniaceae consisted of all unicostate Hookeriales including *Cyathophorella* and *Cyathophorum* (but not *Hypopterygium*) in the family, while all ecostate and bicostate genera were put in their Hookeriaceae. Due to the greatly reduced gametophyte, they were conservative and uncertain of the position of *Ephemeropsis*, and preferred to tentatively retain it as a separate family of its own. In Hedenäs' (1996) cladistic re-evaluation of the Hookeriales, based on 75 morphological characters, all genera in Daltoniaceae of Whittemore & Allen (1989), as well as *Ephemeropsis*, *Hookeria*, *Hookeriopsis*, and *Hypopterygium* are found together in his Hookeriaceae clade. However, the position of *Adelothecium* remains doubtful in his analysis.

Most recently, with the first phylogenetic study of the order Hookeriales based on a four-gene sequence dataset, Buck *et al.* (2005) redefined Daltoniaceae *sensu* Buck (1987, 1988) and formally incorporated Adelotheciaceae into synonymy. As currently circumscribed, Daltoniaceae consists of 14 genera, although *Metadistichophyllum* Nog. &

Z.Iwats. is sometimes treated as a synonym of *Distichophyllum* (see Crosby, 1974; Akiyama, 1990). However, phylogenetic relationships among *Achrophyllum*, *Calyptrochaeta* and the rest of the Daltoniaceae remain uncertain. Similar phylogeny and relationships were concluded in Chapter 1 to resolve the backbone phylogeny of Hookeriales, albeit with a better sampling and more gene markers. Infra-generic relationships within *Achrophyllum* and *Calyptrochaeta* have also never been assessed. Within the well-supported core Daltoniaceae, relationships among the genera with differentiated leaf borders, especially the heterogeneous *Distichophyllum*, are still in question. As Buck et al. (2005) have pointed out, clarification of the generic boundaries and relationships involving *Daltonia*, *Distichophyllum* and related genera are in need.

2.1.2. History of *Distichophyllum* and allied genera

The genus *Distichophyllum* Dozy & Molk. was a segregated from *Hookeria* Sm. (see Dozy & Molkenboer, 1845–1848). The original publication included three new combinations, namely: *D. cuspidatum* (Dozy & Molk.) Dozy & Molk., *D. spathulatum* (Dozy & Molk.) Dozy & Molk., and *D. cristatum* (Hedw.) Dozy & Molk. They also considered *Hookeria quadrifaria* Sm. (≡ *Achrophyllum quadrifarium* (Sm.) Vitt & Crosby), *Pterygophyllum microcarpon* (Hedw.) Brid. (≡ *Distichophyllum microcarpon* (Hedw.) Mitt.), and *Hookeria asplenioides* (Brid.) Steud. (≡ *Calyptrochaeta asplenioides* (Brid.) Crosby) to be included within *Distichophyllum* but no new combination was made because these species occurs outside their study area.

Two years later, unsatisfied with the misguiding name *Distichophyllum*, as the foliation is not distichous but complanate, Müller (1848) described a new genus, *Mniadelphus* Müll.Hal., to include nearly all species considered as *Distichophyllum* sensu Dozy & Molkenboer, except for *D. cristatum* and *Hookeria asplenioides* (Brid.) Steud., which both are currently species of *Calyptrochaeta* Desv. Müller (1850), in his synopsis of mosses, further argued that the genus *Distichophyllum* is heterogeneous without sharp delimitation. The confusion between the two names is discussed in Chapter 4. At first, Mitten (1859a, 1859b) accepted *Mniadelphus*, but changed his mind later (Mitten, 1863). Fleischer (1908) also rejected Müller's justifications for the use of *Mniadelphus*.

Although *Distichophyllum* started off as a genus with only three species (see Dozy & Molkenboer, 1845–1848), soon enough, Müller (1850) had already 15 species, at the time in *Mniadelphus*. About half a century later, Brotherus (1907) listed 69 names, of which more than half were described or transferred into the genus by Mitten alone (e.g. Mitten 1859a, 1869, 1882). *Distichophyllum* was already a large genus of 93 species in

Brotherus' (1925) second edition of the Pflanzenfamilien. In the recent past, Crosby et al. (1999) complied a list of 103 species of which only half have been treated in a monograph or revision, the other half being poorly known. A decade later, this situation stays almost unchanged. The current accepted concept of the genus seems to be any hookerian taxa with complanate foliation, single costa, limbate leaves and cross-striate exostome teeth.

As more and more species of *Distichophyllum* were recognized, Mitten (1869), when treating South American taxa, introduced two sections, namely section *Mniadelphus* and section *Discophyllum*. He originally distinguished section *Mniadelphus* as having sub-simple plants with erect branches and erect to inclined capsules, whereas section *Discophyllum* had prostrate plants with rarely ascending branches and horizontal capsules. In fact, nearly all taxa considered in the original section *Mniadelphus* sensu Mitten are today transferred into the genus *Leskeodon*. Modified from Mitten's original concepts of the two sections, Brotherus (1907, 1925) redefined and distinguished section *Mniadelphus* as having mostly robust plants with short and often roughened seta, whereas section *Discophyllum* had more or less slender plants with elongated smooth seta. Interestingly, species such as *D. flaccidum* and *D. procumbens* were originally considered by Mitten (1869) under the section *Mniadelphus* and *Discophyllum* respectively, but Brotherus (1907, 1925) changed these two species from one section to the other. Nonetheless, Fleischer (1908) and Matteri (1975) commented that the two sections sensu Brotherus have no standing as the key distinguishing characters present a continuous gradation. More recent regional works (e.g. Tan & Robinson 1990, Lin & Tan 1995) merely followed the concept of the two sections loosely as they have also found that some species do not fit into either section. In addition, although Müller (1900) once suggested *Adelothecium* Mitt. to be a sub-generic level, probably section, under *Distichophyllum*, no one seems to follow his view.

Upon recognizing a new Daltoniaceous species, Tan (1990) reluctantly included his new Filipino species *Distichophyllum noguchianum* in the genus. Its terete foliation, isophyllous and concave leaves do not fit into the current concept of *Distichophyllum*. However, he had the opinion that, its leaf areolation shows affinity to *Distichophyllum*, and not that of related genera such as *Leskeodon* Broth. or *Daltonia* Hook. & Taylor. Although in the absence of sporophytic material, the unique set of gametophytic characters of this species within the genus has prompted Tan (1990) to recognize a third section *Platyovatophyllum*.

Not only was the genus been subdivided into sections, but also segregated into several related genera. The first segregation was *Discophyllum*, with three species, by Mitten

(1868), but it was reduced to a section of *Distichophyllum* a year later (see above, Mitten 1869). More significantly, Brotherus (1907) segregated the largely epiphytic *Leskeodon* from *Distichophyllum*. *Leskeodon* was, and still at present is, distinguished from *Distichophyllum* only by its papillose exostome (cf. daltoniaceous peristome). In contrast, *Distichophyllum* has a cross-striolate exostome (cf. hookeriaceous peristome). In addition, Brotherus (1907) recognized two sections under *Leskeodon* — section *Longiseti* has rhomboid upper lamina cells, a long seta of about one centimeter and endostomial processes shorter than exostome teeth, whereas section *Brevisetii* (= sect. *Leskeodon*) has hexagonal upper laminal cells, a short seta of 3–4 mm long and with endostomial processes the length of exostome teeth. At present, *Leskeodon* is predominantly a neotropical genus, with few Old World representatives.

A new genus *Distichophyllidium* M.Fleisch. within the tribe *Distichophylleae* was recognized by Fleischer (1908) to include three species, based primarily on the weak to absent costa. Although he did observe the papillose exostome (cf. daltoniaceous peristome) in the type species *Distichophyllidium nymanianum*, the character was not given any emphasis. Later *D. africanum* Demaret & P. de la Varde from Southeast Africa, *D. antarense* Zant. from New Guinea and *D. muticum* Broth. & Paris from New Caledonia were described, increasing the genus to six species. However, one of the original species, *Distichophyllidium rhizophorum* M.Fleisch., was later segregated as a new monotypic genus, *Metadistichophyllum* Nog. & Z.Iwats., when sporophytic plants were found, in addition to its gametophytic peculiarities (Noguchi & Iwatsuki, 1972). Having a hookeriaceous peristome, Crosby (1974) considered the species as merely a specialized member of *Distichophyllum*, a view supported by Akiyama's (1990) observation on other gametophytic features. Its distinct morphology has also led to the independent description of *Archboldiella pilifera* E.B.Bartram from New Guinea in a genus of its own (see Bartram 1942). However, it was found later to be conspecific with *Metadistichophyllum rhizophorum* (≡ *Distichophyllum rhizophorum*, see Crosby 1974), a combination still accepted today by various authors. Mature capsules and thus peristome structures in some of the poorly known species of *Distichophyllidium* remains unknown.

About 45 years ago, van Zanten (1964) discovered a new epiphyllous species from New Guinea, which closely resembles *Leskeodon*; however, lower part of leaves, in this new species, is occupied by the elongated border cells. The species has also a spiny capsule. With justification from these unique morphological features, the monotypic *Leskeodotopsis* was thus created to accommodate this peculiar species. The autoicous species is reported to have strongly papillose exostome with a zigzag median line.

2.1.3. Exostomial structures as criteria for generic delimitation

Variations in peristome structures in several groups within pleurocarpous mosses have been shown to be correlated with habitat, rather than to provide useful information to infer familial relationships (e.g. Hedenäs, 2001, 2002; Huttunen et al., 2004; Olsson et al., 2009b; Quandt et al., 2009; Vanderpoorten et al., 2002). Chapter 1 shows, from a molecular phylogenetic perspective, that the daltoniaceous peristome has evolved several times within the Hookeriales, including Daltoniaceae. The finding corroborates with earlier postulations by Buck (1987), Tan & Robinson (1990) and Whittemore & Allen (1989) that the specialized daltoniaceous peristome has arisen from a hookeriaceous one as, most probably, the result of similar selection pressures. Shifts to a daltoniaceous peristome could be correlated to changes to a epiphytic habitat and thus, this shift to a new habitat (with higher UV levels and risk of dehydration) could probably be the ‘selective pressure’ acting upon the structure and function of the peristome. At least with regards to the pleurocarpous mosses, there is now general agreement that peristomial features are not as stable, reliable and informative for inferring familial and higher rank relationships as formerly supposed (e.g. Hedenäs, 2001, 2002; Huttunen et al., 2004; Olsson et al., 2009b; Quandt et al., 2009; Vanderpoorten et al., 2002). Nonetheless, Buck (1991, 2007) considered that peristomial features could still be valuable in recognizing genera within family.

In Daltoniaceae, there are at least two generic pairs with similar gametophytic traits but separated into different genera by the dissimilar peristome types (*Crosbya* versus *Daltonia*, *Distichophyllum* versus *Leskeodon*). Resolving the phylogeny of the group could further assess the usefulness of peristome features, especially ornamentation of exostome, to delimit genera, and to infer relationship among genera.

Objectives

The study was conducted with the following objectives: i) to resolve the relationships among the genera within the family Daltoniaceae, ii) to infer the infra-generic relationships within *Calyptrochaeta* and *Achrophyllum*, iii) to determine the best division of the heterogenous *Distichophyllum* to reflect its phylogeny, iv) to test if the proposed sections in *Distichophyllum* are phylogenetically supported, and v) to assess the relevance of exostome ornamentation in genus delimitation.

2.2. Materials and Methods

As a continuation of the earlier study to resolve the backbone phylogeny of the Hookeriales (Chapter 1), the sampling approaches, lab protocols, and analysis methods are essentially the same with minor adjustments. Names used for taxa in this study follow the currently accepted view (see www.tropicos.org), except when indicated otherwise. To have a better overview on the biogeographic distribution of clades, voucher are named by the species followed by a two-letter country code where the it was collected, following the ISO 3166-1 alpha-2 codes, in some cases a single letter suffix is added to indicate collection from different regions within a country (see Table 4)

Table 4. Voucher information and Genbank accession numbers for 126 samples; ***rps*4**: all available, 99 (79%) new; ***trn*LF**: all available, 99 (79%) new; ***nad*5**: 115 available, 82 (75%) new; **ITS**: 113 available, 85 (93%) new; **26S**: 110 available, 45(77%). Total: 592 (94%) out of 630 (5 markers x 126 exemplars) available, 478 (81%) new. (a) Hypnalean taxa once associated with the Hookeriales; (h) other Hypnalean taxa; (*) type species of respective genera; and (--) missing sequences. New sequences do not have GenBank accession numbers yet and are identifiable by the lab numbers. Sequences are available as supplementary data in the attached CDROM.

Accepted Scientific Name	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
OUTGROUP						
*Ancistrodes genuflexa** (CL)	AY306863	AY306697	AY452319	BBH68	AY452399	Chile, I. Holz & J. Franzaring CH 00-154 (NY)
*Callicostella papillata** (ID-J)	B587	B587	B587	B587	B587	Indonesia (Java), B.C. Ho 07-003 (SING)
*Catharomnion ciliatum** (NZ)	AY306879	AY306713	AY452332	EF680786	AY452414	New Zealand, (GenBank)
Crossomitrium epiphyllum (Sect type) (GF)	AY306885	AY306719	AY452337	BBH033	AY452419	French Guiana, W.R. Buck 33259 (NY)
Crossomitrium sintenisii (GF)	AY306886	AY306720	AY452338	BBH034	AY452420	French Guiana, W.R. Buck 33042 (NY)
*Cyclodictyon laetevirens** (PT)	CI535	CI535	CI535	CI535	CI535	Portugal, J.-P. Frahm Az-106 (BONN)
Hookeria acutifolia (EC)	AY306929	AY306763	AY452362	BBH06	AY452441	Ecuador, W.R. Buck 39558 (NY)
*Hookeria lucens** (US)	AY306930	AY306764	AY452363	EF680792	AY452442	U.S.A. (GenBank)
*Hypopterygium tamarisci** (BO)	EF647964	EF657194	EF667887	EF680799	EF680816	Bolivia (GenBank)
*Lepidopilum scabrisetum** (EC)	AY306940	AY306774	AY452370	BBH45	AY452449	Ecuador, W.R. Buck 39436 (NY)
*Leucomium strumosum** (GF)	AY306943	AY306777	AY908488	BBH10	AY452452	French Guiana, I. Holz FG 00-268 (NY)
*Lopidium concinnum** (AU)	AY306945	AY306779	AY452373	EF680800	AY452453	Australia (GenBank)
Pilotrichum procerum (DM)	AY306978	AY306812	AY452379	BBH50	BBH50	Dominica, A. Schäfer-Verwimp 17941 (NY)
*Rhynchostegiopsis tunguraguana** (CO)	AY306986	AY306820	BBH13	--	AY452463	Colombia, P. Ramírez P7690 (NY)

Accepted Scientific Name	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
*Sauloma tenella** (AU)	AY306987	AY306821	AY452384	BBH051	AY452464	Australia, H. Streimann 59726 (NY)
*Schimperobryum splendidissimum** (CL)	AY306988	AY306822	AY452385	EF680807	AY452465	Chile (GenBank)
*Tetrastichium fontanum** (PT)	AY307000	AY306834	AY452388	BBH54	AY452469	Portugal (Madeira), R. Düll, Bryophyta Exsiccata Madeira #69 (NY)
*Thamniopsis pendula** (CO)	AY307003	AY306837	AY452392	BBH57	AY452473	Colombia, S.P. Churchill & E.L. Lineares 18434 (NY)
INGROUP						
Achrophyllum anomalum (CL)	Aa598	Aa598	Aa598	Aa598	Aa598	Chile, J. Larrain 26248A (CONC)
Achrophyllum crassirete (CL)	Ac470	Ac470	Ac470	Ac470	Ac470	Chile, J.-P. Frahm 21-10 (BONN)
Achrophyllum dentatum (AU)	AY306853	AY306687	AY452315	EF680783	AY452396	Australia (GenBank)
Achrophyllum haesselianum (CL)	B598	B598	B598	B598	B598	Chile, M.R. Crosby 16205 (L)
Achrophyllum magellanicum (CL)	B599	B599	B599	B599	B599	Chile, M.R. Crosby 16206 (L)
*Achrophyllum quadrifarium** (NZ)	AY449660	BBH001	AY452316	BBH001	BBH001	New Zealand, H. Streimann 51258 (NY)
*Adelothecium bogotense** (BR)	AY306856	AY306690	AY452318	EF680784	AY452398	Brazil (GenBank)
*Beeveria distichophylloides** (NZ)	AY306867	AY306701	AY452320	BBH092	AY452400	New Zealand (GenBank)
*Benitotania elimbata** (MY-E)	AY449661	AY449669	AY452321	SB1414	AY452401	East Malaysia, H. Akiyama & M. Suleiman 2002 (NY)
*Bryobrothera crenulata** (AU)	GOM036	GOM036	GOM036	GOM036	GOM036	Australia, H. Streimann & T. Pócs 64341 (S)
Calyptrochaeta apiculata (CL)	GOM002	GOM002	GOM002	GOM002	GOM002	Chile, W.R. Buck 46252 (NY)
Calyptrochaeta asplenioides (MG)	GOM067	GOM067	GOM067	GOM067	GOM067	Madagascar, T. Pócs, R. E. Magill & C. La Farge-England, 90115/Q (EGR)
Calyptrochaeta asplenioides (RE)	GOM064	GOM064	GOM064	GOM064	GOM064	Reunion, T. Pócs 9612/M (EGR)
Calyptrochaeta asplenioides (ZA)	GOM070	GOM070	GOM070	GOM070	GOM070	South Africa, T. Arts RSA27/11 (EGR)
Calyptrochaeta brownii (AU)	AY306873	AY306707	AY452329	BBH14	AY452411	Australia, H. Streimann 42803 (NY)
*Calyptrochaeta cristata** (NZ)	Cc474	Cc474	Cc474	Cc474	Cc474	New Zealand, J.-P. Frahm 1-11 (BONN)

Accepted Scientific Name	rps4	trnLF	nad5	ITS	26S	Voucher
Calyptrochaeta flaccida (PH)	Cf525	Cf525	Cf525	Cf525	Cf525	Philippines, V. Linis 28 June 2007 (SING)
Calyptrochaeta flexicollis (AU)	GOM004	GOM004	GOM004	GOM004	GOM004	Australia, H. Streimann 58403 (NY)
Calyptrochaeta japonica (JP)	GOM061	GOM061	GOM061	GOM061	GOM061	Japan, M. Mizutani 15156 (S)
Calyptrochaeta otwayensis (AU)	Co534	Co534	Co534	Co534	Co534	Australia, H. Streimann 58384 -isotype (BONN)
Calyptrochaeta ramosa (ID-J)	B597	B597	B597	--	B597	Indonesia (Java), B.C.Ho 07-003 (SING)
Calyptrochaeta remotifolia (PH)	Cr532	Cr532	Cr532	Cr532	Cr532	Philippines, V. Linis s.n. 28 June 2007 (SING)
Calyptrochaeta spec. A (PH)	Cm533	Cm533	Cm533	Cm533	Cm533	Philippines, V. Linis 1459-05 (SING)
Calyptrochaeta spinosa (CN)	Cs570	Cs570	Cs570	Cs570	Cs570	China, D.G. Long 32717 (E)
Crosbya straminea (NZ)	AY306887	AY306721	AY908490	BBH016	AY452421	New Zealand, A.J. Fife 10379 (NY)
Daltonia apiculata (BT)	JY60	JY60	--	JY60	JY60	Bhutan, D.G. Long 8673-C (E)
Daltonia cf. *apiculata* (CN)	Dx565	Dx565	Dx565	Dx565	Dx565	China, D.G. Long 34759 (E)
Daltonia armata (MY-W)	Da576	Da576	Da576	Da576	Da576	West Malaysia, B.C. Ho 08-007 (SING)
Daltonia bilimbata (MY-E)	GOM005	GOM005	GOM005	GOM005	GOM005	East Malaysia, B.C.Tan 89-311 (NY)
Daltonia himalayensis (CN)	JY44	JY44	--	JY44	--	China, D.G. Long 33751 (MO)
Daltonia jamesonii (BO)	GOM040	GOM040	GOM040	GOM040	GOM040	Bolivia, M. Lewis 87373 (S)
Daltonia marginata (BR)	GOM007	GOM007	GOM007	GOM007	GOM007	Brazil, A. Schäfer-Verwimp 9492 (NY)
Daltonia ovalis (EC)	GOM008	GOM008	GOM008	GOM008	GOM008	Ecuador, W.R. Buck 39344 (DUKE)
Daltonia pulvinata (GQ)	Dm592	Dm592	Dm592	Dm592	Dm592	Equatorial Guinea, F. Müller B745 (DR)
Daltonia semitorta (NP)	JY62	JY62	--	JY62	JY62	Nepal, D.G. Long 20547 (E)
*Daltonia splachnoides** (IE)	GOM038	GOM038	GOM038	GOM038	GOM038	Ireland, N. Hakelier s.n., 18 III 1985 (S) B108054
*Distichophyllidium nymanianum**	AY306901	AY306735	AY452350	Dn587*	BBH019	West Malaysia, H. Mohamed & A. Damanhuri 1118, Musci Malaysiani Exsiccati, fasc. 2: #29; *Indonesia (Celebes), F. Müller S81 (DR)

Accepted Scientific Name	rps4	trnLF	nad5	ITS	26S	Voucher
Distichophyllum angustifolium (MY-E)	Da540	Da540	--	Da540	--	East Malaysia, M. Suleiman 1646 (BORH)
Distichophyllum angustifolium (MY-W)	--	--	Da575	Da575	Da575	West Malaysia, B.C. Ho 08-006 (SING)
Distichophyllum brevicuspis (MY-E)	Ds542	Ds542	Ds542	Ds542	Ds542	East Malaysia, M. Suleiman 1702 (BORH)
Distichophyllum carinatum (CN)	Dc566	Dc566	Dc566	Dc566	Dc566	China, D.G. Long 24419 (E)
Distichophyllum carinatum (DE)	Dc546	Dc546	Dc546	Dc546	Dc546	Germany, M. Nebel et al. MTB 8527/3 (STU)
Distichophyllum carinatum (JP)	Dc610	Dc610	--	--	--	Japan, T. Suzuki 507 (NICH)
Distichophyllum collenchymatosum var. *collenchymatosum* (JP)	GOM020	GOM020	GOM020	GOM020	GOM020	Japan, M. Mizutani 13378 (DUKE)
Distichophyllum collenchymatosum var. *collenchymatosum* (CN)	Dc561	Dc561	Dc561	Dc561	Dc561	China, L. Zhang 4307 (SZG)
Distichophyllum collenchymatosum var. *pseudosinense* (CN)	Dp562	Dp562	Dp562	Dp562	Dp562	China, L. Zhang 5807 (SZG)
Distichophyllum crispulum (AU)	GOM011	GOM011	GOM011	GOM011	GOM011	Australia, H. Streimann 47450 (NY)
Distichophyllum cucullatum 1 (ID-M)	GOM022	GOM022	--	GOM022	GOM022	Indonesia (Moluccas), H. Akiyama C-15141 (NY)
Distichophyllum cucullatum 2 (ID-M)	GOM009	GOM009	--	GOM009	GOM009	Indonesia (Moluccas), H. Akiyama C-16541 (NY)
Distichophyllum cucullatum (PH)	Dc574	Dc574	Dc574	Dc574	Dc574	Philippines, V. Linis s.n., 28 VI 2007 (SING)
Distichophyllum cuspidatum (MY-W)	B581	B581	--	Dc595	Dc595	West Malaysia, K.T. Yong 7420 (SING)
Distichophyllum dicksonii (CL)	GOM013	GOM013	GOM013	GOM013	GOM013	Chile, W.R. Buck 46173 (NY)
Distichophyllum ellipticum (CL)	De597	De597	De597	De597	De597	Chile, J. Larrain 25682A (CONC)

Accepted Scientific Name	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Distichophyllum eremitae (CL)	GOM014	GOM014	GOM014	GOM014	GOM014	Chile, W.R. Buck 46086 (NY)
Distichophyllum fernandezianum (CL)	B779	B779	--	B779	--	Chile, V. Munoz & E. Corcuera s.n., 29 II 1992 (L)
Distichophyllum flaccidum (CL)	GOM015	GOM015	GOM015	GOM015	GOM015	Chile, W.R. Buck 46275 (NY)
Distichophyllum freycinetii (US)	B777	B777	--	B777	--	U.S.A. (Hawaii), W.J. Hoe 3021.0 (EGR)
Distichophyllum jungermannioides (MY-W)	Dj577	Dj577	Dj577	Dj577	Dj577	West Malaysia, B.C. Ho 08-022 (SING)
Distichophyllum krausei (CL)	B776	B776	--	B776	--	Chile, V. Ardiles ONC-01 (CONC)
Distichophyllum krausei (NZ)	GOM018	GOM018	GOM018	GOM018	GOM018	New Zealand, A.J. Fife 46275 (NY)
Distichophyllum maibarae (JP)	GOM057	GOM057	GOM057	GOM057	GOM057	Japan, M. Mizutani 14977 (S)
Distichophyllum malayense (MY-E)	Dm541	Dm541	Dm541	Dm541	Dm541	East Malaysia, M. Suleiman 1608 (BORH)
Distichophyllum malayense (MY-W)	GOM049	GOM049	GOM049	GOM049	GOM049	West Malaysia, L. Hedenäs MY92-533 (S)
Distichophyllum mascarenicum (MG)	B594	B594	B594	Dm580	--	Madagascar, R.E. Magill et al. 9971 (L)
Distichophyllum meizhiae (CN)	Dm567	Dm567	Dm567	Dm567	Dm567	China, D.G. Long 36274 (E)
Distichophyllum microcarpum (NZ)	GOM055	GOM055	GOM055	GOM055	GOM055	New Zealand, H. Streimann 51286 (S)
Distichophyllum mniifolium (ZA)	GOM046	GOM046	GOM046	GOM046	GOM046	South Africa, K. Hylander 10602 (S)
Distichophyllum montagneanum (CN)	Dm571	Dm571	Dm571	Dm571	Dm571	China, D.G. Long 33943 (E)
Distichophyllum montagneanum (LK)	Dm528	Dm528	Dm528	Dm528	Dm528	Sri Lanka, B.C.Tan 04-077 (SING)

Accepted Scientific Name	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
Distichophyllum nigricaule var. *cirratum* (ID-J)	B584	B584	--	Dc573	Dc573	Indonesia (Java), B.C.Ho 07-005 (SING)
Distichophyllum nigricaule var. *cirratum* (ID-S)	B774	B774	--	B774	--	Indonesia (Sumatra), K.T. Yong s.n. 27 March 2009 (SING)
Distichophyllum nigricaule var. cirratum (MY-W)	GOM053	GOM053	GOM053	GOM053	GOM053	West Malaysia, L. Hedenäs MY92-335 (S)
Distichophyllum nigricaule var. nigricaule (MY-W)	GOM047	GOM047	GOM047	GOM047	GOM047	West Malaysia, L. Hedenäs MY92-556 (S)
Distichophyllum nigricaule var. nigricaule (PH)	B583	B583	Dn572	Dn572	Dn572	Philippines, Luzon, Mt Labo, V. Linis s.n., 20 VI 2007 (SING)
Distichophyllum osterwaldii (MY-E)	Do544	Do544	Do544	Do544	--	East Malaysia, M. Suleiman 1951 (BORH)
Distichophyllum osterwaldii (MY-W)	GOM045	GOM045	GOM045	GOM045	GOM045	West Malaysia, L. Hedenäs MY92-280 (S)
Distichophyllum paradoxum (US)	AY306900	AY306734	AY452349	BBH20	AY452432	U.S.A. (Hawaii), T. Flynn 5151 (NY)
Distichophyllum pulchellum (NZ)	AY306902	AY306736	AY452351	EF680791	AY452433	New Zealand, H. Streimann 51380 (NY)
Distichophyllum pulchellum 1 (AU)	GOM024	GOM024	GOM024	GOM024	GOM024	Australia, H. Streimann 36525 (Duke)
Distichophyllum pulchellum 2 (AU)	GOM044	GOM044	GOM044	GOM044	GOM044	Australia, H. Streimann 63444 (S)
Distichophyllum rakotomariae (MG)	Dr582	Dr582	Dr582	Dr582	Dr582	Madagascar, T. Pócs 9473/EB (EGR)
Distichophyllum rigidicaule var. *gabonense* (TZ)	Dg585	Dg585	Dg585	Dg585	Dg585	Tanzania, T. Pócs et al. 90057/V (EGR)
Distichophyllum rigidicaule var. *rigidicaule* (SC)	Dr581	Dr581	Dr581	Dr581	--	Seychelles, G. Kis 9345/CV (EGR)
Distichophyllum rotundifolium (AU)	GOM025	GOM025	GOM025	GOM025	GOM025	Australia, H. Streimann 65299 (NY)
Distichophyllum schmidtii (TH)	Ds609	Ds609	--	Ds609	-	Thailand, S. Chantanaorrapint 2080 (PSU)

Accepted Scientific Name	rps4	trnLF	nad5	ITS	26S	Voucher
Distichophyllum spathulatum (ID-S)*	GOM026	GOM026	GOM026	GOM026	GOM026	Indonesia (Sumatra), L. Hoffmann 89-181 (NY)
Distichophyllum spathulatum (MY-E)*	Du545	Du545	Du545	Du545	--	East Malysia, M. Suleiman 1925 (BORH)
Distichophyllum spathulatum (MY-W)*	B589	Do536	Do536	--	--	West Malaysia, K.T.Yong 4144 (KLU)
Distichophyllum subcuspidatum 1 (MY-E)	Ds543	Ds543	Ds543	Ds543		East Malaysia, M. Suleiman 921 (BORH)
Distichophyllum subcuspidatum 2 (MY-E)	GOM027	GOM027	GOM027	GOM027	GOM027	East Malaysia, B.C.Tan 89-213 (DUKE)
Distichophyllum subnigricaule var. *hainanense* (CN)	Dh569	Dh569	Dh569	Dh569	Dh569	China, L. Zhang 4153 (SZG)
Distichophyllum subnigricaule var. *subnigricaule* (ID-C)	B778	B778	--	--	--	Indonesia (Celebes), F. Müller S93 (DR)
Distichophyllum succulentum (IN)	Dy563	Dy563	Dy563	Dy563	Dy563	India, D.G. Long 23037 (E)
Distichophyllum succulentum (LK)	B593	B593	B593	B593	B593	Sri Lanka, B.C.Tan 04-754 (SING)
Distichophyllum tortile (ID-J)	B595	B595	-	B595	-	Indonesia (Java), B.C.Ho 07-006 (SING)
Distichophyllum tortile (MY-E)	Dn547	Dn547	Dn547	Dn547	Dn547	East Malaysia, M. Suleiman 1671 (BORH)
Distichophyllum tortile (MY-W)	GOM043	GOM043	GOM043	GOM043	GOM043	West Malaysia, L. Hedenäs MY92-526 (S)
Distichophyllum wanianum (TH)	Dw611	Dw611	Dw611	Dw611	Dw611	Thailand, A. Schäfer-Verwimp & I. Verwimp 23788/A (Priv. Schäfer-Verwimp)
Distichophyllum spec. B (CN)	Db568	Db568	Db568	Db568	Db568	China, D.G. Long 33796 (E)

Accepted Scientific Name	**rps4**	**trnLF**	**nad5**	**ITS**	**26S**	**Voucher**
*Ephemeropsis tjibodensis** (MY-W)	GOM048	GOM048	GOM048	GOM048	GOM048	West Malaysia, I. Bisang & L. Hedenäs s.n., 25 V 2001 (S)
Ephemeropsis trentepohlioides (NZ)	GOM050	AY306740	AY908491	BBH022A	BBH022A	New Zealand, C. Macmillan 95/94 (NY)
Leskeodon acuminatus (ID-M)	ND18	ND18	--	ND18	ND18	Indonesia (Moluccas), H. Akiyama C-14714 (MO)
Leskeodon andicola (EC)	GOM029	GOM029	GOM029	GOM029	GOM029	Ecuador, W.R. Buck 10454 (NY)
Leskeodon aristatus (BR)	ND005	ND005	ND005	ND005	ND005	Brazil, W.R. Buck 19689 (NY)
Leskeodon auratus (BZ)*	ND01	ND01	ND01	ND01	ND01	Belize, B.H. Allen 15351 (NY)
Leskeodon auratus (PR)*	AY306942	AY306776	AY452371	BBH23	AY452450	Puerto Rico, W.R. Buck 18286 (NY)
Leskeodon brevicuspidatus (FJ)	Lb583	Lb583	Lb583	Lb583	Lb583	Fiji, S. & T. Pócs 03279/DB (EGR)
Leskeodon cubensis (TT)	GOM030	GOM030	GOM030	GOM030	GOM030	Trinidad & Tobago, N. Djan-Chékar 94-340 (NY)
Leskeodon longipilus (BR)	Ll584	Ll584	Ll584	Ll584	Ll584	Dominica, A. Schäfer-Verwimp & I. Verwimp 17923/A (Priv. Schäfer-Verwimp)

2.2.1. Taxon sampling and molecular protocols

A total of 126 vouchers were sampled for DNA, including 18 selected exemplars from the other seven Hookerialean families used as outgroups. The ingroup consists of 95 species from 12 genera (out of 14) in the Daltoniaceae including *Calyptrochaeta* and *Achrophyllum*. As the phylogeny of *Daltonia* has recently been reviewed (Yu et al. in press), only a selection of representatives within *Daltonia* is included in this study. On the other hand, as many species as possible were sampled within other larger genera such as *Achrophyllum* (6 out of 8), *Calyptrochaeta* (12 out of 29) and *Leskeodon* (7 out of 20) as infra-generic relationships are still unknown in these. The sampling of *Distichophyllum* represents about a third of the c. 100 accepted species, of which only about half have been taxonomically treated at a regional scale (cf. Crosby et al. 1999). Within *Distichophyllum*, sampling efforts have been made to include more than one voucher per species that show large morphological variability and/or form species complexes that are difficult to separate morphologically. This way, each taxon is better represented in terms of their morphological and geographical diversities.

In this study, nucleotide sequences of five regions from three genomes were analyzed, i.e. (1) the *rps*4 gene, including the *trn*S–*rps*4 intergenic spacer (IGS), (2) the plastid *trn*L–F region, including the *trn*L$_{\mathrm{UAA}}$ group I intron and the *trn*L–F IGS (hereafter *trnLF*), (3) the mitochondrial *nad*5 group I intron, (4) as well as the nuclear ribosomal ITS1–5.8–ITS2 (hereafter ITS) region and (5) the large ribosomal RNA subunit (hereafter 26S). The voucher information and corresponding GenBank accession numbers, when available, are summarized in Table 4. All new vouchers used in this study are identified or confirmed by the author to ensure a common species definition, as many species have not been critically studied before.

Total genomic DNA extractions were performed from dried herbarium vouchers via a modified CTAB protocol (Doyle & Doyle 1990) following Shaw (2000). Amplification of the selected DNA regions were carried out following standard protocols and primers as outlined in Olsson et al. (2009a) and Shaw et al. (2003). Purified PCR products were sequenced by DNA Sequencing Facility at the Institute for Genome Sciences & Policy, Duke University (http://www.genome.duke.edu/cores/sequencing) or via Macrogen Inc., South Korea (www.macrogen.com). All new sequences generated in this study will be submitted to the DDBJ/EMBL/GenBank sequence database and provided as supplementary material on a CD-ROM.

2.2.2. DNA sequence editing and alignment

The generated forward and reversed sequences were assembled and edited for inaccuracy using either Phyde 0.995 (Müller et al., 2008) or Sequencher v4.1 (Gene Codes Corp.). Consensus sequences were aligned manually in PhyDE 0.995 applying guidelines outlined in Borsch et al. (2003), Kelchner (2000), Morrison (2006), Quandt & Stech (2005), Simmons (2004), and Simmons & Freudenstein (2003). Simple sequence repeats were positionally isolated based on strict motif recognition as advocated by Kelchner (2000), Quandt & Stech (2005) and Quandt et al. (2009). Regions of ambiguous alignment (hotspots) in the data matrix were defined as outlined in Olsson et al. (2009a) and excluded from phylogenetic analyses (Table 5). Detected hairpin associated inversions, which were visually identified, were positioned separately in the alignment (see Table 5). Instead of coding for the presence or absence of inversions as data for the phylogenetic analysis (e.g. Quandt & Stech, 2005), they were reversed and complemented in a second alignment file, so as to retrieve the information within the detected inversion, e.g. substitutions, that occurred before the inversion event (cf. Borsch & Quandt, 2009; Quandt et al. 2003; Sotiaux et al. 2009). Alignments are provided in the attached CD-ROM as supplementary data.

Table 5. Hotspots (Hs), and inversions (Iv). Genes in the merged datamatrix follow, *rps*4: 1–837, *trn*LF: 838–1695, *nad*5: 1696–3042, ITS: 3043–4501, and 26S: 4502–5525.

Nr.	position	gene	Nr.	position	gene
Hs1	957–960	*trn*LF	Hs8	2526-2530	*nad*5
Iv1	961–965	*trn*LF	Hs9	2993-3042	*nad*5
Hs2	970–973	*trn*LF	Hs10	3109-3111	ITS
Iv2	1131–1137	*trn*LF	Hs11	3131-3135	ITS
Hs3	1212–1215	*trn*LF	Hs12	3432-3437	ITS
Hs4	1281–1289	*trn*LF	Hs13	3601-3603	ITS
Hs5	1339–1347	*trn*LF	Hs14	3763-3766	ITS
Hs6	1553–1558	*trn*LF	Hs15	4192-4197	ITS
Iv3	1604–1610	*trn*LF	Hs16	4280-4290	ITS
Hs7	1650–1655	*trn*LF	Hs17	5016-5018	26S
			Hs18	5042-5043	26S

2.2.3. DNA data analyses

Both parsimony and Bayesian analyses were performed with or without additional information from simple indel coding (sic) approach of Simmons & Ochoterena (2000). Preliminary analyses on the concatenated nuclear and organellar datasets were first carried out to check for conflicts before the final analyses on the total combined data matrix.

The computer program SeqState (Müller, 2005) was used to generate a ready-to-use nexus file containing the sequence alignment with an automatically generated binary indel matrix appended. Command files for using the parsimony ratchet (Nixon, 1999) were generated using the program PRAP2 (Müller, 2007) applying the default settings, and executed in PAUP 4.0b10 (Swofford, 2002). Heuristic bootstrap searches under parsimony were performed with 10,000 replicates.

Bayesian analyses were performed with MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) applying the GTR+Γ+I substitution model and the restriction site model respectively for the sequence data and the binary indel partitions. To allow for possibly deviating substitution matrices for the different genomes, as well as the indel matrix, the data set was divided into four sequence data partitions including partition 1: plastid (*rps4* + *trnLF*); partition 2: mitochondrial (*nad5*): nuclear (ITS1 & 2 + 26S); and partition 4: the coded indel matrix. Model parameters for each partition were sampled independently. The *a priori* probabilities supplied were those specified in the default settings of the program. Posterior probability (PP) distributions of trees were created using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method. Four runs with four chains (4×10^6 generations each) were run simultaneously. Chains were sampled every 1,000 generations and the respective trees written to a tree file. The program Tracer v1.5 (Rambaut & Drummond, 2009) was used to evaluate the burn-in point and to examine the log likelihoods, ensuring that the runs were in the stationary phase and sufficient Effective Sample Size (ESS). Calculations of the consensus tree and posterior probability of clades were performed based upon the trees sampled after the chains converged (at generation 800,000 for dataset with sic, 1,000,000 without sic, and 250,000 without partitioning). Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph 2.0.42-187 beta (Stöver & Müller, 2010)

Part of this work was carried out by using the resources of the Computational Biology Service Unit from Cornell University which is partially funded by Microsoft Corporation.

2.2.4. Morphological data and ancestral state reconstruction

As the leaf limbidium and exostome ornamentation are key characters used to distinguish among genera in the Daltoniaceae, analyses were carried out to test their validity. First, the characters are scored based on the voucher specimen use for this study and supplemented from those reported from literature (Table 6). This is especially true for exostome structures, as sporophytes at the right stage are uncommon. Ancestral states of the coded characters were reconstructed in Mesquite version 2.72 (Maddison & Maddison, 2009) using parsimony in one of the resulting trees from the Bayesian analyses.

Table 6. Character matrix. A: Limbidium (0: absent, 1: present); B: ornamentation of the outer side of exostome at base (0: striate, 1: papillose); ?: Unknown or does not apply.

Taxa	A	B	Taxa	A	B
Achrophyllum anomalum CL	0	0	*Distichophyllum leiopogon* 1 ID M	1	0
Achrophyllum crassirete CL	0	0	*Distichophyllum leiopogon* 2 ID M	1	0
Achrophyllum dentatum AU	0	0	*Distichophyllum leiopogon* PH	1	0
Achrophyllum haesselianum CL	0	0	*Distichophyllum maibarae* JP	1	0
Achrophyllum magellanicum CL	0	0	*Distichophyllum malayense* MY E	1	0
Achrophyllum quadrifarium NZ	0	0	*Distichophyllum malayense* MY W	1	0
Adelothecium bogotense BR	0	0	*Distichophyllum mascarenicum* MG	1	0
Ancistrodes genuflexa CL	0	0	*Distichophyllum meizhiae* CN	1	1
Beeveria distichophylloides NZ	0	0	*Distichophyllum microcarpum* NZ	0	0
Benitotania elimbata MY E	0	?	*Distichophyllum mniifolium* ZA	1	?
Bryobrothera crenulata AU	0	0	*Distichophyllum montagneanum* CN	1	0
Callicostella papillata ID J	0	0	*Distichophyllum montagneanum* LK	1	0
Calyptrochaeta apiculata CL	1	0	*Distichophyllum nigricaule* var *cirratum* ID-J	1	0
Calyptrochaeta asplenioides MG	1	0	*Distichophyllum nigricaule* var *cirratum* ID-S	1	0
Calyptrochaeta asplenioides RE	1	0	*Distichophyllum nigricaule* var *cirratum* MY	1	0
Calyptrochaeta asplenioides ZA	1	0	*Distichophyllum nigricaule* var *nigricaule* MY	1	0
Calyptrochaeta brownii AU	1	0	*Distichophyllum nigricaule* var *nigricaule* PH	1	0
Calyptrochaeta cristata NZ	1	0	*Distichophyllum osterwaldii* MY E	1	0
Calyptrochaeta flaccida PH	1	0	*Distichophyllum osterwaldii* MY W	1	0
Calyptrochaeta flexicollis AU	1	0	*Distichophyllum paradoxum* US	1	0
Calyptrochaeta japonica JP	1	0	*Distichophyllum pulchellum* 1 AU	1	0
Calyptrochaeta otwayensis AU	1	0	*Distichophyllum pulchellum* 2 AU	1	0
Calyptrochaeta ramosa ID J	1	0	*Distichophyllum pulchellum* NZ	1	0
Calyptrochaeta remotifolia PH	1	0	*Distichophyllum rakotomariae* MG	1	0
Calyptrochaeta spec A PH	1	0	*Distichophyllum rigidicaule* var *gabonense* TZ	1	0
Calyptrochaeta spinosa CN	1	0	*Distichophyllum rigidicaule* var *rigidicaule* SC	1	0
Catharomnion ciliatum NZ	1	?	*Distichophyllum rotundifolium* AU	1	0
Crosbya straminea NZ	1	0	*Distichophyllum schmidtii* TH	1	0
Crossomitrium epiphyllum GF	0	1	*Distichophyllum spathulatum* ID S	1	0
Crossomitrium sintenisii GF	0	1	*Distichophyllum spathulatum* MY E	1	0
Cyclodictyon laetevirens PT	1	0	*Distichophyllum spathulatum* MY W	1	0
Daltonia apiculata BT	1	1	*Distichophyllum* spec B CN	1	?
Daltonia armata MY W	1	?	*Distichophyllum subcuspidatum* MY E	1	0
Daltonia bilimbata MY	1	1	*Distichophyllum subcuspidatum* MY W	1	0
Daltonia cf. *apiculata* CN	1	?	*Distichophyllum subnigricaule* var *hainanense*	1	0
Daltonia himalayensis CN	1	1	*Distichophyllum subnigricaule* var *subnigricaule* ID-M	1	0
Daltonia jamesonii BO	1	1			
Daltonia marginata BR	1	1	*Distichophyllum succulentum* IN	1	0
Daltonia ovalis EC	1	1	*Distichophyllum succulentum* LK	1	0
Daltonia pulvinata GQ	1	1	*Distichophyllum tortile* ID J	1	0
Daltonia semitorta NP	1	1	*Distichophyllum tortile* MY E	1	0
Daltonia splachnoides IE	1	1	*Distichophyllum tortile* MY W	1	0
Distichophyllidium nymanianum MY W	1	1	*Distichophyllum wanianum* TH	1	?
Distichophyllum angustifolium MY E	1	0	*Ephemeropsis tjibodensis* MY W	?	0
Distichophyllum brevicuspis MY E	1	0	*Ephemeropsis trentepohlioides* NZ	?	0
Distichophyllum carinatum CN	1	?	*Hookeria acutifolia* EC	0	0
Distichophyllum carinatum DE	1	?	*Hookeria lucens* US	0	0
Distichophyllum carinatum JP	1	?	*Hypopterygium tamarisci* BO	1	0
Distichophyllum collenchymatosum var *collenchymatosum* CN	1	0	*Lepidopilum scabrisetum* EC	0	1
			Leskeodon acuminatus ID M	1	1
Distichophyllum collenchymatosum var *collenchymatosum* JP	1	0	*Leskeodon andicola* EC	1	1
			Leskeodon aristatus BR	1	1
Distichophyllum collenchymatosum var *pseudosinense* CN	1	0	*Leskeodon auratus* BZ	1	1
			Leskeodon auratus PR	1	1
Distichophyllum crispulum AU	1	0	*Leskeodon cubensis* TT	1	1
Distichophyllum cuspidatum MY W	1	0	*Leskeodon longipilus* DM	1	1
Distichophyllum dicksonii CL	1	0	*Leskeodon seramensis* FJ	1	1
Distichophyllum ellipticum CL	1	0	*Leucomium strumosum* GF	0	0
Distichophyllum eremitae CL	1	0	*Lopidium concinnum* AU	1	0
Distichophyllum fernandezianum CL	1	0	*Pilotrichum procerum* DM	0	1
Distichophyllum flaccidum CL	1	0	*Rhynchostegiopsis tunguraguana* CO	0	0
Distichophyllum freycinetii US	1	0	*Sauloma tenella* AU	0	0
Distichophyllum jungermannioides MY W	1	0	*Schimperobryum splendidissimum* CL	0	0
Distichophyllum krausei CL	1	0	*Tetrastichium fontanum* PT	0	0
Distichophyllum krausei NZ	1	0	*Thamniopsis pendula* CO	0	0

2.3. Results

2.3.1. Alignment and sequence analyses

Sequences are successfully amplified from 99 % of *trn*LF, 99 % of *rps*4, 87 % *nad*5, 96 % of ITS and 87 % 26S accessions (Table 4). The concatenated and aligned datamatrix consists of 1634 positions belonging to the plastid genome, 1291 positions to the mitochondrial genome, 2439 positions to the nuclear genome; in total 5365 positions, excluding hotpots. A total of 18 hotspots were assigned, with *trn*LF and ITS having seven each, only three in 26S, one in *nad5* and none in *rps4* (see Table 5).

A total of 960 indels were coded, whereby two thirds belong to the ITS sequences alone. In this particular dataset, simple sequence repeats (SSR) contributed to most of the length variation in *trn*LF region. In *rps*4, the *rps*4-*trn*S IGS contributed to most of the sequence length variation. However, a 90 nt long repeat in the *rps*4 exon belonging to *Ephemeropsis trentepohlioides* is noteworthy. Length mutations in the nad5 and 26S sequences were rather limited and hence the alignments are straightforward.

Indel coding provided an additional 954 characters the dataset. The coded indels also increase the number of parsimony informative characters (PI) from 1117 to 1624 characters. The PI of the nuclear ribosomal genome nearly doubled with the inclusion of coded indels as characters (from 483 to 870). Among the five gene markers, ITS contributed the highest PI (380) in the combined data matrix, similar in magnitude as the ones from total plastid genome (i.e. *rps*4 + *trn*LF).

2.3.2. Phylogenetic Analyses

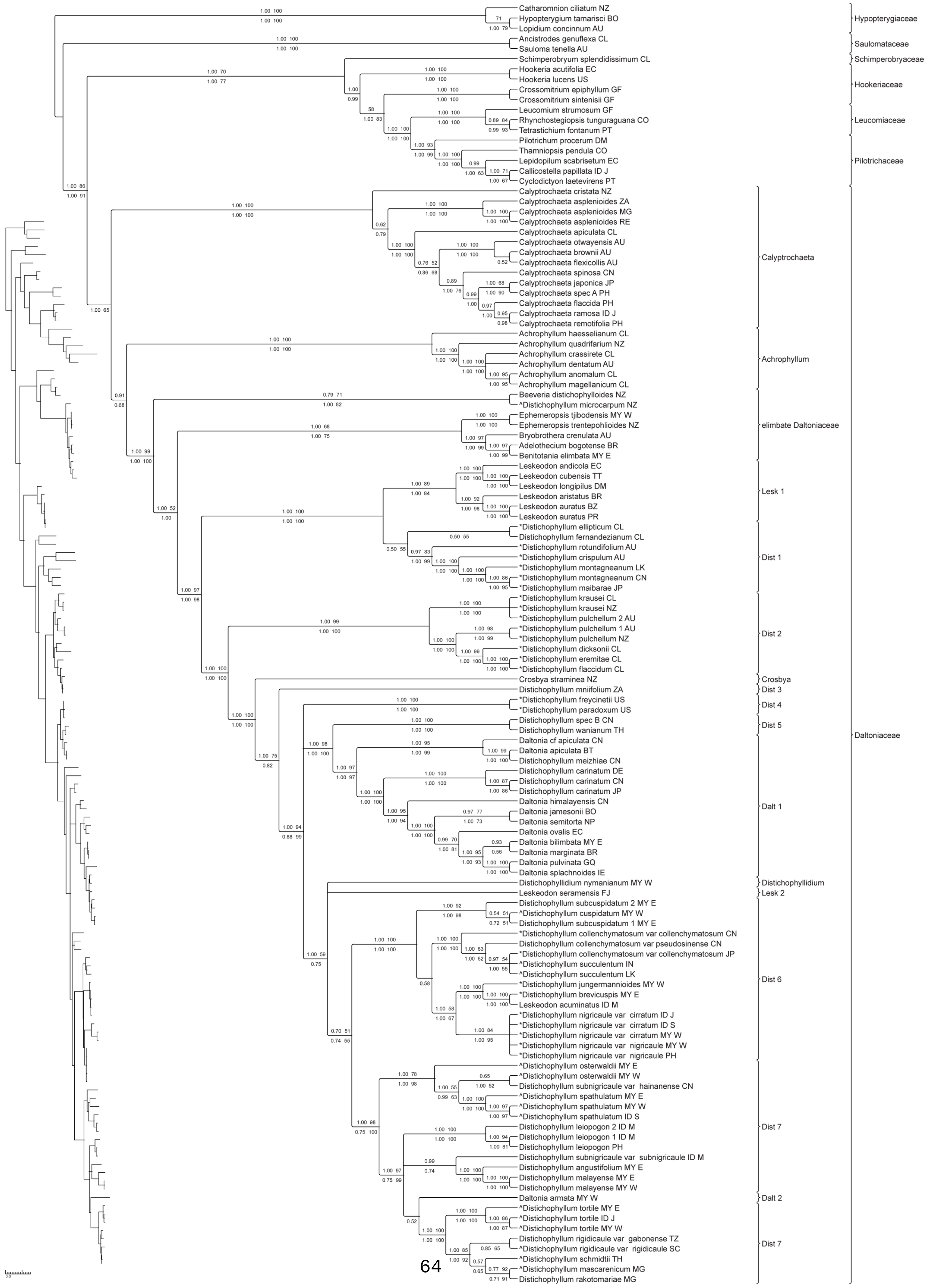
The preliminary results of both parsimony (MP) and Bayesian inference (BI) on the concatenated nuclear and organellar datasets revealed no significant conflicts; i.e., nodes with at least bootstrap support (BS) of 70% or Posterior Probabilities (PP) of 0.95 (cf. Appendices 6 & 7). The two datasets are hence combined for further analyses.

The concatenated combined datamatrix was further modified, i.e. without indels coding, with indel coding of only the organelle dataset, and with indel coding of the complete dataset. In all parsimony analyses of the three different datasets, several nodes have inadequate bootstrap support. However, parsimony analyses with dataset with simple indel coding of both the entire sequence data, and the organellar partition (abbreviated as MP_{sic} and $MP_{sic\text{-}org}$ respectively), generally give better BS values than the one without coded indels (abbreviated as $MP_{w/o}$) (see Appendix 6).

The results from Bayesian inference with the same three datasets (thereafter abbreviated as $\mathrm{BS}_{\mathrm{w/o}}$, $\mathrm{BS}_{\mathrm{sic,}}$ $\mathrm{BI}_{\mathrm{sic\text{-}org}}$) showed no conflict with the parsimony trees, and they were better resolved. The tree topologies of the three datasets with various coded indels, are almost identical except for a few end branches with low posterior probabilities (PP) (see Appendix 7). Nonetheless, $\mathrm{BI}_{\mathrm{sic}}$ gives the best ESS values, and shows no extra initial peak in Tracer, as the ones detected in $\mathrm{BI}_{\mathrm{w/o}}$ and $\mathrm{BI}_{\mathrm{sic\text{-}org}}$. Therefore, this tree is selected for illustration complemented with values of BS from parsimony analyses ($\mathrm{BS}_{\mathrm{w/o}}$, $\mathrm{BS}_{\mathrm{sic}}$) and PP of data analyses ($\mathrm{PP}_{\mathrm{w/o}}$, $\mathrm{PP}_{\mathrm{sic}}$) (Figure 7). The same tree was also used for the ancestral state reconstruction via Mesquite version 2.72.

The phylogenetic trees were rooted with the Hypopterygiaceae (*Cyathophorum*, *Hypopterygium*, and *Lopidium*), with reference to the results of Buck et al. (2005) and Chapter 1. The backbone phylogeny of the Hookeriales resembles the one in Chapter 1. The topology of the Hookeriales backbone closely resembles earlier phylogenies of this moss order. Relationships among the monophyletic *Calyptrochaeta*, the remaining unicostate Daltoniaceae, and the rest of the ecostate-bicostate Hookeriales are not resolved with adequate support, except in $\mathrm{BI}_{\mathrm{sic}}$, where support is maximal.

→ **Figure 7**. Majority consensus of trees sampled after stationary phase obtained in the Bayesian analysis of the combined dataset with simple indel coding (Simmons & Ochoterena, 2000). Miniature phylogram of the same tree is shown on the left. Values of corresponding nodes denote posterior probabilities (PP) followed by parsimony bootstrap support (BS) with ratchet from 10,000 replicates, those above branches are from analyses including indels and below excluding indels. Bayesian analyses for 4,000,000 generations, 4 runs and 4 chains. ^ = *Distichophyllum* sect. *Mniadelphus*; * = *D*. sect. *Discophyllum*.


Catharomnion ciliatum NZ
Hypopterygium tamarisci BO
Lopidium concinnum AU
Ancistrodes genuflexa CL
Sauloma tenella AU
Schimperobryum splendidissimum CL
Hookeria acutifolia EC
Hookeria lucens US
Crossomitrium epiphyllum GF
Crossomitrium sintenisii GF
Leucomium strumosum GF
Rhynchostegiopsis tunguraguana CO
Tetrastichium fontanum PT
Pilotrichum procerum DM
Thamniopsis pendula CO
Lepidopilum scabrisetum EC
Callicostella papillata ID J
Cyclodictyon laetevirens PT
Calyptrochaeta cristata NZ
Calyptrochaeta asplenioides ZA
Calyptrochaeta asplenioides MG
Calyptrochaeta asplenioides RE
Calyptrochaeta apiculata CL
Calyptrochaeta otwayensis AU
Calyptrochaeta brownii AU
Calyptrochaeta flexicollis AU
Calyptrochaeta spinosa CN
Calyptrochaeta japonica JP
Calyptrochaeta spec A PH
Calyptrochaeta flaccida PH
Calyptrochaeta ramosa ID J
Calyptrochaeta remotifolia PH
Achrophyllum haesselianum CL
Achrophyllum quadrifarium NZ
Achrophyllum crassirete CL
Achrophyllum dentatum AU
Achrophyllum anomalum CL
Achrophyllum magellanicum CL
Beeveria distichophylloides NZ
^Distichophyllum microcarpum NZ
Ephemeropsis tjibodensis MY W
Ephemeropsis trentepohlioides NZ
Bryobrothera crenulata AU
Adelothecium bogotense BR
Benitotania elimbata MY E
Leskeodon andicola EC
Leskeodon cubensis TT
Leskeodon longipilus DM
Leskeodon aristatus BR
Leskeodon auratus BZ
Leskeodon auratus PR
*Distichophyllum ellipticum CL
Distichophyllum fernandezianum CL
*Distichophyllum rotundifolium AU
*Distichophyllum crispulum AU
*Distichophyllum montagneanum LK
*Distichophyllum montagneanum CN
*Distichophyllum maibarae JP
*Distichophyllum krausei CL
*Distichophyllum krausei NZ
*Distichophyllum pulchellum 2 AU
*Distichophyllum pulchellum 1 AU
*Distichophyllum pulchellum NZ
*Distichophyllum dicksonii CL
*Distichophyllum eremitae CL
*Distichophyllum flaccidum CL
Crosbya straminea NZ
Distichophyllum mniifolium ZA
*Distichophyllum freycinetii US
*Distichophyllum paradoxum US
Distichophyllum spec B CN
Distichophyllum wanianum TH
Daltonia cf apiculata CN
Daltonia apiculata BT
Distichophyllum meizhiae CN
Distichophyllum carinatum DE
Distichophyllum carinatum CN
Distichophyllum carinatum JP
Daltonia himalayensis CN
Daltonia jamesonii BO
Daltonia semitorta NP
Daltonia ovalis EC
Daltonia bilimbata MY E
Daltonia marginata BR
Daltonia pulvinata GQ
Daltonia splachnoides IE
Distichophyllidium nymanianum MY W
Leskeodon seramensis FJ
Distichophyllum subcuspidatum 2 MY E
^Distichophyllum cuspidatum MY W
Distichophyllum subcuspidatum 1 MY E
*Distichophyllum collenchymatosum var collenchymatosum CN
Distichophyllum collenchymatosum var pseudosinense CN
*Distichophyllum collenchymatosum var collenchymatosum JP
^Distichophyllum succulentum IN
^Distichophyllum succulentum LK
*Distichophyllum jungermannioides MY W
*Distichophyllum brevicuspis MY E
Leskeodon acuminatus ID M
*Distichophyllum nigricaule var cirratum ID J
*Distichophyllum nigricaule var cirratum ID S
*Distichophyllum nigricaule var cirratum MY W
*Distichophyllum nigricaule var nigricaule MY W
*Distichophyllum nigricaule var nigricaule PH
^Distichophyllum osterwaldii MY E
^Distichophyllum osterwaldii MY W
Distichophyllum subnigricaule var hainanense CN
^Distichophyllum spathulatum MY E
^Distichophyllum spathulatum MY W
^Distichophyllum spathulatum ID S
Distichophyllum leiopogon 2 ID M
Distichophyllum leiopogon 1 ID M
Distichophyllum leiopogon PH
Distichophyllum subnigricaule var subnigricaule ID M
Distichophyllum angustifolium MY E
Distichophyllum malayense MY E
Distichophyllum malayense MY W
Daltonia armata MY W
^Distichophyllum tortile MY E
^Distichophyllum tortile ID J
^Distichophyllum tortile MY W
Distichophyllum rigidicaule var gabonense TZ
^Distichophyllum rigidicaule var rigidicaule SC
^Distichophyllum schmidtii TH
^Distichophyllum mascarenicum MG
Distichophyllum rakotomariae MG
Hypopterygiaceae
Saulomataceae
Schimperobryaceae
Hookeriaceae
Leucomiaceae
Pilotrichaceae
Calyptrochaeta
Achrophyllum
elimbate Daltoniaceae
Lesk 1
Dist 1
Dist 2
Crosbya
Dist 3
Dist 4
Dist 5
Dalt 1
Distichophyllidium
Lesk 2
Dist 6
Dist 7
Dalt 2
Dist 7
Daltoniaceae
0.0

Similarly, the topology of the monophyletic *Achrophyllum*, emerging as sister to the remaining Daltoniaceae (i.e., core Daltoniaceae), does not have adequate support in all analyses. The clade consisting of *Beeveria distichophylloides* and *Distichophyllum microcarpon* represents the most basal split within the core Daltoniaceae, with almost maximum support in all analyses. The dichotomy of *B. distichophylloides* and *D. microcarpon* receives adequate support from analyses with the indel-coded dataset (PP_{sic}=1.00; BS_{sic}=82), but support values are reduced without sic data ($PP_{w/o}$=0.79; $BS_{w/o}$=71). Subsequently, the remaining exemplars of the core Daltoniacae are divided into two sister clades of unequal size with maximum support from BI, but not MP. Within the smaller sister clade, all nodes received good support. The highly reduced *Ephemeropsis* diverged off first, followed by a clade consisting of *Bryobrothera*, which is sister to *Adelothecium* and *Benitotania*; the last three genera being monotypic and elimbate.

The well-supported larger clade consists exclusively of limbate taxa. However, the resolved clades show various combinations of species in *Daltonia*, *Distichophyllum*, *Leskeodon* and a few other smaller genera, not in accordance with the traditional generic grouping. The first basal split within this clade represents a group of neotropical *Leskeodon* ('Lesk 1') together with a few species of *Distichophyllum* each from South America, Australasia, and Asia ('Dist 1'). The 'Lesk 1-Dist 1' clade receives maximum support in all analyses, but the placement of *Distichophyllum ellipticum* and *D. fernandezianum* has inadequate support. The next diverging clade involves a well-supported group of *Distichophyllum* species confined to Australasia and Patagonia ('Dist 2'). *Crosbya straminea* and *Distichophylum mniifolium* ('Dist 3') are the next two successive splits. Following them, an unresolved trichotomy composed of a small clade of Hawaiian endemics, *Distichophyllum freycineti* and *D. paradoxum* ('Dist 4'), a clade consisting largely of *Daltonia* plus a few atypical species of *Distichophyllum* ('Dist 5 + Dalt 1'), and the '*Distichophyllidium* + Lesk 2 + Dist 5 + Dist 6' clade, is found. Within the well-supported 'Dist 5 + Dalt 1' clade, majority of the nodes receives maximum PP and at least 90 % in BS, except at the crown of 'Dalt 1'.

The '*Distichophyllidium* + Lesk 2 + Dist 5 + Dist 6' clade does not receive good support, except in $BI_{w/o}$ ($PP_{w/o}$=1.00). In fact, the relationships between these four sub-clades are not resolved with adequate support in all analyses. However, topologies in all trees indicate that at least 'Lesk 2' is sister to 'Dist 6 + Dist 7'. Nevertheless, the 'Dist 6' clade receives maximum support in all analyses. This clade consists of a group of epiphytic *Distichophyllum* species and two species complexes surrounding *D. nigricaule* and *D.*

collenchymatosum. The ‘Dist 7’ clade receives good support except in PP_{sic} (0.75). The rest of the sampled Asian-pacific *Distichophyllum*, all the Southeast African *Distichophyllum*, and the peculiar *Daltonia armata* (Dalt 2’), are nested in this clade.

2.3.3. Ancestral state reconstruction

As indicated above, the BI_{sic} gave the best scores in terms of ESS values and an absence of a secondary peak and hence taken as the reference tree for the ancestral state analyses. Results of the character state reconstruction under parsimony are shown in (Figure 8 and 9). Within the Daltoniaceae (including *Calyptrochaeta*), leaf limbidia originates twice and is reconstructed as synapomorphies for Calyptrochaeta and the clade corresponding to the Leskeodon, Daltonia, Distichophyllum complex. At least three origins of papillose exostome from a striate one have been inferred in the family.

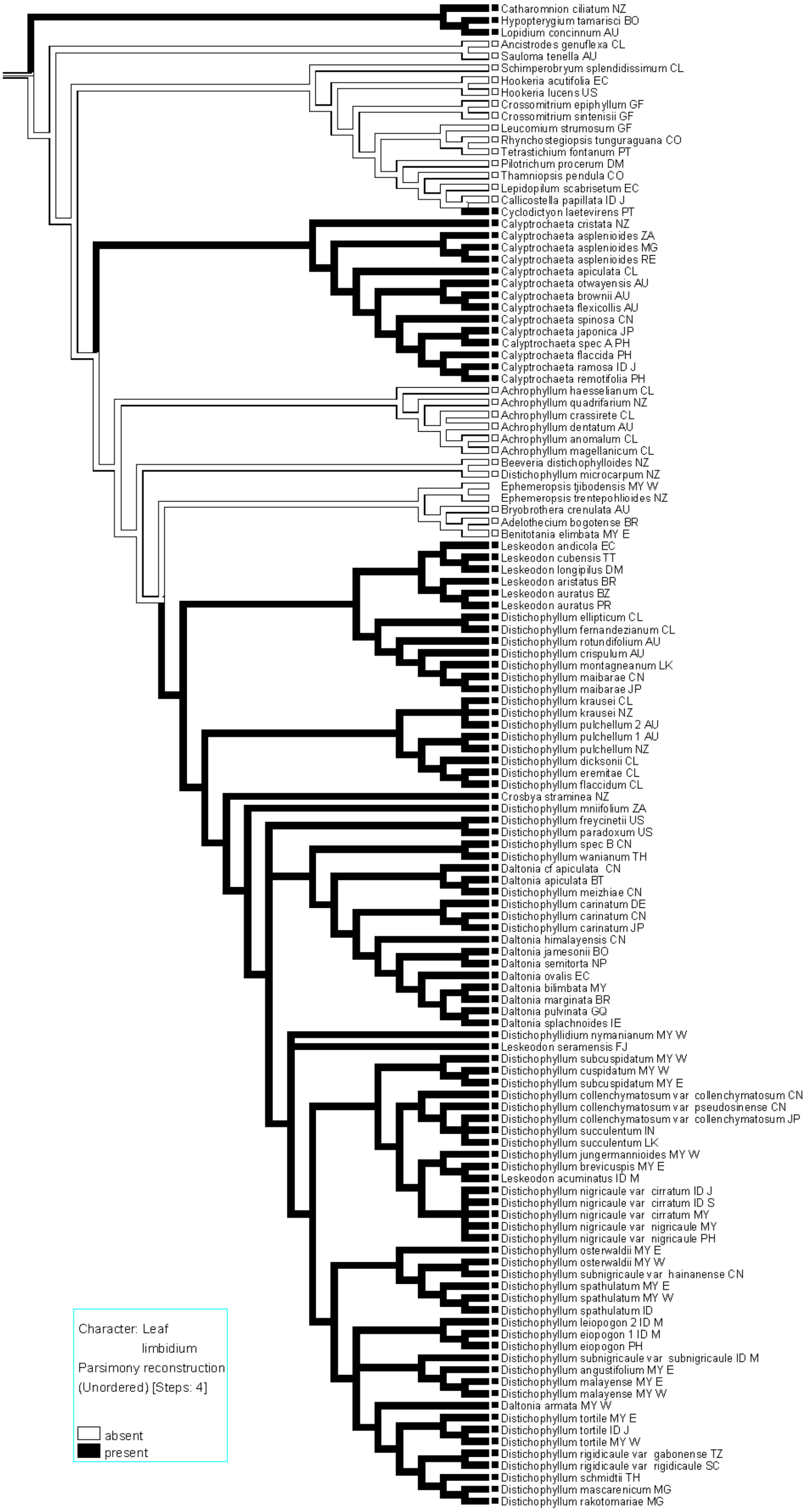


Figure 8. Parsimony character state reconstruction in Mesquite for limbidium (white = absent; black = present).

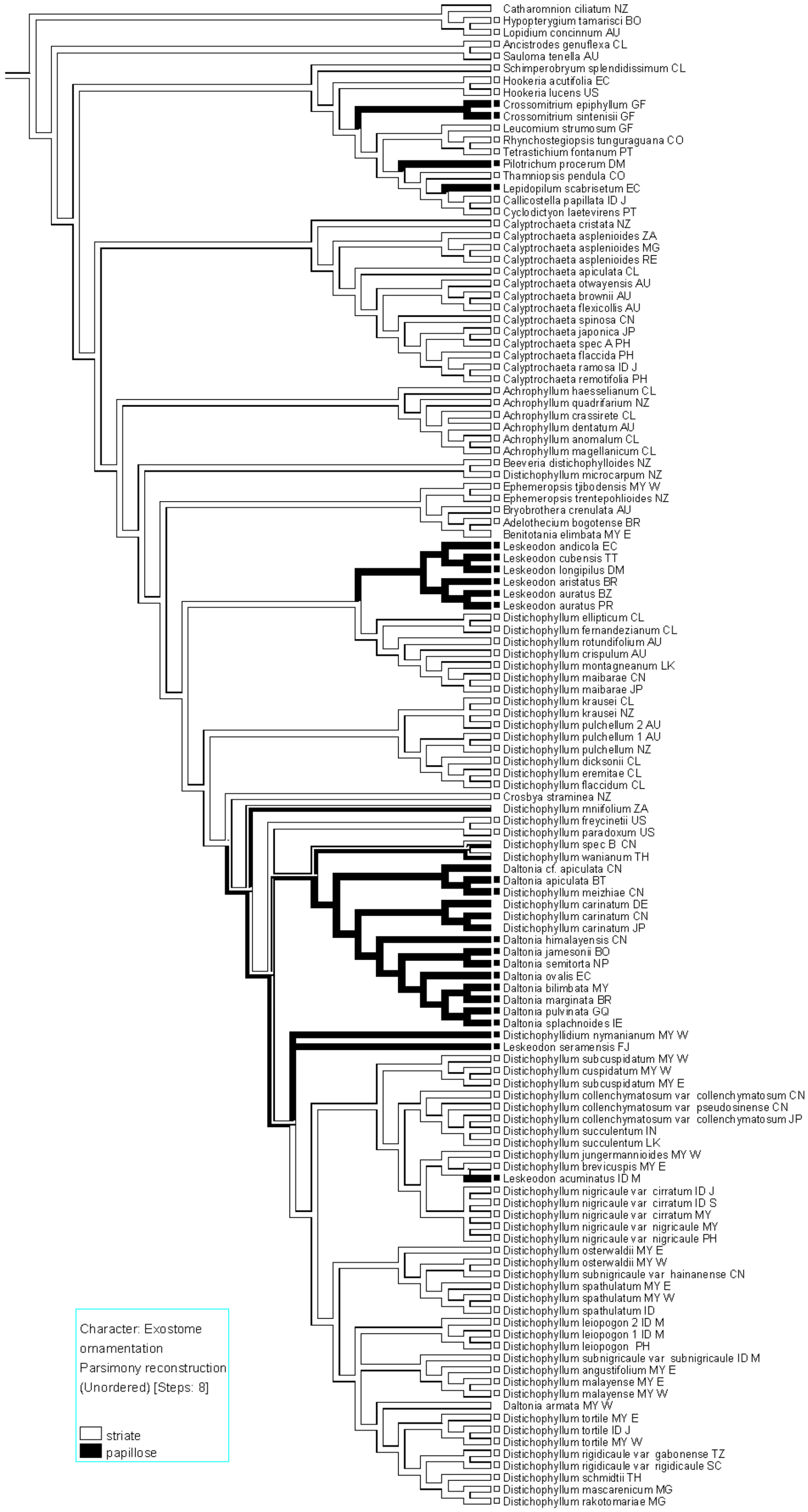


Figure 9. Parsimony character state reconstruction in Mesquite for (ornamentation of the outer side of the exostome at the base (white = conspicuously striate; black = smooth, papillose or weakly striate).

2.4. Discussion

2.4.1. Resolving relationships among the genera

In the studies of Buck et al. (2005) and Chapter 1, the relationships of *Calyptrochaeta* and *Achrophyllum* within the currently circumscribed Daltoniaceae could not be resolved with support. Despite the increase in sampling of these two genera in this study, their relationships, unfortunately, remain inconclusive. Nevertheless, both are verified to be monophyletic with good support.

The leaf limbidium provides a good indication of the phylogenetic clades (Figure 8), at least within the family. An elimbate leaf represents the plesiomorphic state in Daltoniaceae, excluding *Calyptrochaeta*, in which the exact relationship is still uncertain. The topology of the elimbate Daltoniaceae differs slightly from that reconstructed by Buck et al. (2005). In their study, *Beeveria* and *Ephemeropsis* form a clade that is sister to the rest of the core Daltoniaceae, in this study, *Beeveria* together with *Distichophyllum microcarpon* form the basal clade of the core Daltoniceae, and *Ephemeropsis* is found with the remaining elimbate taxa, with good support except for slightly lower values in $BS_{w/o}$ (68 %). At first sight, the close relationship between *Beeveria distichophylloides*, a segregate of *Achrophyllum*, and *Distichophyllum microcarpon* may seem to be a surprise. However, upon studying the specimens and descriptions of the species, it turns out that *D. microcarpon* is a peculiar Australasian *Distichophyllum*. Most strikingly, the leaves are without any differentiated leaf border or limbidium, and hence unlikely to belong to *Distichophyllum* or any of its sister genera as revealed by the phylogenetic results. The analysis of the limbate character (Figure 8) shows that the lack of limbidim is the plesiomorphic state for this character in the Daltoniaceae and that it is limited to the basal taxa. Interestingly, support values of the kinship between *B. distichophylloides* and *D. microcarpon* drop below acceptable levels without the inclusion of the coded indels ($PP_{w/o}$=0.79; $BS_{w/o}$=71). Without additional knowledge, at present, it is best to transfer *D. microcarpon* to *Beeveria* to reflect its closer affinity to *Beeveria* than to other limbate genera, instead of describing a possibly new genus.

The rest of the elimbate genera are supported in the study. However, the phylogeny of the limbate genera contradicts classical concepts for *Daltonia*, *Distichophyllum*, and *Leskeodon*. Supported clades show various combinations of species currently accepted in the above three genera. The phylogenetic evaluation of the limbate taxa will be dealt with in details in the discussion of re-organizing *Distichophyllum*.

2.4.2. Inferring the infra-generic relationships within *Calyptrochaeta* and *Achrophyllum*

This is the first attempt to evaluate the species relationships within the genera *Calyptrochaeta* and *Achrophyllum*. The monophylies of both genera are supported with maximum values. In *Calyptrochaeta*, *C. cristata* and *C. asplenioides* are most divergent from other sampled species, which form a well-support clade. In fact, the leaves of the type species, *C. cristata*, are atypical, with cells regularly thin-walled and marginal teeth consisting of variable number of cells. Typical *Calyptrochaeta* species often have thick laminal cell walls, at least at the cell corners, and marginal teeth consistently consisting of parts of two adjacent border cells. The relationship of *C. asplenioides* with *C. cristata* and the other species of *Calyptrochaeta* cannot be resolved with parsimony, and is insufficiently supported with BI. *Calyptrochaeta asplenioides* has long creeping axes with a plagiotropic growth pattern like that of *C. ramosa* (see Ho & Kruijer, 2007). The New Zealand endemic, *C. cristata* seemingly also has the same growth pattern, while the rest of the sampled taxa have an orthotropic growth pattern. It appears that in *Calyptrochaeta*, the orthotropic growth pattern is derived from a plagiotropic one, and in *C. ramosa* a reversal could have occurred. Interestingly, the three Australasian species *C. brownii*, *C. flexicollis* and *C. otwayensis* have almost identical sequences, which explain the reconstructed unresolved topology. The plants also resemble each other, suggesting that the validity of these species requires confirmation. Unfortunately, no sequences could be amplified from DNA isolated from the New World species for evaluation, especially *C. setigera* which was once segregated as a separate genus, *Piloseriopus* Sharp.

Within *Achrophyllum*, *A. haesselianum* is sister to all other species in the genus. The type of the genus *A. quadrifarium* diverges off next. Both species are conspicuous within the genus because of their pale green plants and their scarcely toothed to sub-entire leaf margin. The other species nested at the crown of the *Achrophyllum* clade are dark green plants with erose-dentate leaf margin. Congruent with the tree topology, species in the latter group are morphologically difficult to discern (Larraín, pers. comm. Jan 2010). In fact, Matteri (1972) and Robinson (1975) have different concepts for this species complex, which becomes evident when taking into account the different morphological characters they use in their respective identification keys. However, features used by both authors for identification of these species such as size of marginal teeth, length of costa, laminal cells size, degree of wall thickening at cell corners, etc., are rather variable. Robinson (1975) proposed the synonymy of *A. crassirete* and *A. magellanicum* under *A. anomalum* and *A. dentatum*, respectively. The phylogeny here presented suggests that the two basal species are clearly valid, while the delimitation of the rest of the four to six species accepted in this genus, including the Asian *A. javense* not sampled in this study, would require further critical evaluation.

2.4.3. Determining the best division of the *Distichophyllum*

The resulting phylogeny has not only confirmed the heterogeneity of *Distichophyllum*, but also shows the polyphyly of *Leskeodon* and *Daltonia* (see Figure 7). Due to the poor resolution of some of the subsequent nodes within the limbate clade (i.e., those in association with *Daltonia*, *Distichophyllum*, and *Leskeodon*), and the difficulty of finding synapomorphies to interpret the resolved internal clades, especially without adequate taxonomical knowledge, one option is to consider the entire clade, as a single genus. That would mean the generic names *Distichophyllum* and *Leskeodon* along with a few others would be sunk into the synonymy of the oldest name *Daltonia*. This approach would result in numerous new binomials and disrupt nomenclatural stability. Moreover, such a broad molecularly based interpretation of *Daltonia* has little meaning in evolutionary interpretation and would probably gain little acceptance. A better and more sensible approach is to split and adjust the traditional concepts of the genera.

Although the genus *Leskeodon* as currently defined is polyphyletic, excluding the Old World species would make the remaining neotropical members monophyletic (see ‘Lesk 1’ in Figure 7). This finding emphasized the fact that the exostome characters do not effectively reflect true phylogeny and could not be use for defining the genus (cf. Figure 9). In fact, some species currently in *Distichophyllum* (‘Dist 1’) cluster together with the neotropical *Leskeodon* (‘Lesk 1’) in a larger well-supported clade. Morphologically, all species in this clade seem to have small isodiametric laminal cells that are more or less homogenous in size except at the base particularly along the costa where cells are slightly more hexagonal or larger. Interestingly, plants of *D. maibarae* or *D. montagneanum* from Asia have remarkably similar leaf morphology with those of *L. andicola* from the New World, especially the often poorly differentiated border at the leaf apex. Hence, the transfers of the species in ‘Dist 1’ into *Leskeodon* are here proposed as the clade contains *L. auratus*, the lectotype of *Leskeodon* (see Welch, 1966). However, the phylogenetic position of the distinctive *L. palmarum* (Mitt.) Broth., which is the only species in *Leskeodon* sect. *Longeseti* Broth., unfortunately, remains uncertain as sequences of this taxon could not be successfully amplified.

The genus *Discophyllum* Mitt. is sometimes treated as an illegitimate homonym. The genus was first described along with a new species *Discophyllum flavescens* Mitt. from Samoa (see Mitten 1868). The new species was compared with *D. adnatum* (Hook.f. &

Wilson) Mitt. and *D. dicksonii* (Hook. & Grev.) Mitt., in reference to these two species of *Hookeria*. The abbreviation "D." in the citation of binomials, i.e., *D. adnatum* and *D. dicksonii,* in Mitten publication (1868) is clearly referring to *Discophyllum*, thus, they can be interpreted as new combinations and as inclusion of the two species in the genus. It is logical to assume that *Discophyllum flavescens* was intended as the type of the genus as first interpreted by Wijk et al. (1962), although this was not clearly stated in the protologue. On the other hand, *Discophyllum* (see Hall, 1847), was taken up earlier by a fossil Cnidarian, but the fossil specimen is not a plant (see Art. 54.1 in the Code, McNeill et al., 2006). Since the ICBN is independent of the ICZN, *Discophyllum* Mitt., currently a synonym of *Distichophyllum*, should not be interpreted as a later homonym and is thus legitimate for nomenclatural use. Unfortunately, no material of the type species of *Discophyllum* currently a synonym of *Distichophyllum*, was available for the study. Nevertheless, according to the original description of *Discophyllum flavescens* (in Mitten 1868), the species seems to have a closer affinity to the newly recognized *Leskeodon* clade (i.e. 'Dist 1' + 'Lesk 1'). However, without examination of authentic specimens and lack of DNA data, it cannot be ruled out that it can nest in other clades, such as 'Dist 2'.

Also noteworthy in this clade is the complex comprising the gametophytically variable *Distichophyllum maibarae* and *D. montagneanum*, which are morphologically indistinguishable when only sterile gametophytes are available. Mohamed & Robinson (1991) have suggested that *D. maibarae* can be distinguished from the more distribution-limited *D. montagneanum* by the hairy calyptrae. However, the taxonomic value of this character has been recently questioned (see Chapter 3). The Chinese voucher sampled, of this species complex, has naked calyptrae and should, thus, be named *D. montagneanum* following Mohamed & Robinson's (1991) definition. This name has never been used for Chinese plants and would represent a new country record. However, the tree topology is suggesting that this Chinese collection is closer to the Japanese plants, in which only *D. maibarae*, with hairy calyptrae, is known. Although the sampling size is small, it is evident that the use of calyptra ornamentation to distinguish the two species has no standing. In the absence of both molecular and morphological support to separate the two names, it is justifiable to synonymize them and recognize just one variable species, with *D. montagneanum* having nomenclatural priority.

The next resolved clade 'Dist 2' is a group of median to large-sized species of *Distichophyllum*, with leaves ranging from oblong to elliptic to obovate, and a rounded apex with or without a sharp point or acumen. Many of these species have distinctly concave leaves. All sampled species seems to have more or less quadrate cells at the apical lamina. This clade seems to have a so-called '*Notofagus* type' distribution (see Seki, 1973). Formal name transfer of this group of *Distichophyllm* should be done in conjunction with a generic taxonomic revision where authentic synapomorphic morphological characters could be determined to formally circumscribe the clade as a new genus.

Interestingly, one of the *D. pulchellum* sampled from Australia clusters together with the aquatic *D. krausei*, rather than with other exemplars identified as the former. Fife & Matteri (1984) have reassessed the status of these two similar-looking species and confirmed the presence of *D. krausei* in New Zealand. On the contrary, Streimann (1999) who revised the Australian taxa rejected the recognition of *D. krausei* in Australia, following characters proposed by the former authors. Morphologically, the Australian voucher of *D. pulchellum* (*H. Streimann 63444* S!, L!) and the two other specimens identified as *D. krausei* from New Zealand and Chile used in this study, could not be distinguished from each other perfectly following Fife & Matteri (1984). On the other hand, the New Zealand *D. pulchellum* (*H. Streimann 51380* NY!) and the other Australian *D. pulchellum* (*H. Streimann 36525* DUKE!), are very similar in morphology and distinct from the former. The latter specimens, in fact, look closer to *D. dicksonii*, *D. eremitae*, and *D. flaccidum* in the concave leaves with a small but distinct apiculus. These observations are congruent with the tree topology. This would mean the name *D. pulchellum* is applied to more than one entity, one of them being conspecific with *D. krausei*. It appears that the heterogenic status of *D. pulchellum* needs critical reassessment.

The position of the New Zealand endemic genus *Crosbya* is identical to the results of Buck et al. (2005) and Chapter 1. The gametophytes of *Crosbya* closely resemble those of *Daltonia*, except for the excurrent costa. However, the two species of *Crosbya* are both dioicous and have a hookeriaceous peristome (Vitt, 1977). As suggested by Vitt (1977). the gametophytic similarities of these two genera are most probably due to analogous selective pressures, since both are epiphytes. However, *Crosbya* seems to be limited to tree trunks and branches, sometimes on boulders, whereas *Daltonia* commonly grows on twigs and leaves. Perhaps these microhabitat differences could explain the differences in peristome types and sexuality.

Distichophyllum mniifolium ('Dist 3') splits off next, sister to the rest of the *Daltonia-Distichophyllum-Leskeodon* clade. In fact, when Bizot (in Bizot & Pócs, 1974) proposed the Brazillian *Leskeodon densiretis* (Broth.) Broth. as a synonym of *D. mniifolium*, he also transferred the name into *Leskeodon* probably because *L. densiretis* was included in

Leskeodon when Brotherus (1907) first proposed the genus. No material of the Brazillian *L. densiretis* has been studied to confirm the synonymy, but the sampled voucher from South Africa truly has leaves which superficially resembling those of a *Leskeodon* in leaf shape and the upper laminal cells. However, unlike most *Leskeodon*, the cells of *D. mniifolium* become larger and more lax towards the basal half of the leaves, especially those along the costa. The present lack of both morphological knowledge and molecular phylogenetic support does not allow any firm conclusion to be drawn on the placement and status of this species.

Next comes a trichotomy where relationship of the Hawaiian *Distichophyllum* (or 'Dist 4'), the largely *Daltonia* clade ('Dist 5' + 'Dalt 1'), and the crown clade consisting of almost entirely Old World taxa (*Distichophylidium* + 'Lesk 2' + 'Dist 6' + 'Dist 7'), could not be resolved. The two Hawaiian endemics *Distichophyllum freycinetii* and *D. paradoxum* are clustered together with maximum support. Although one may chose to consider the entire clade a single genus, a large group having so much morphological variation would sooner or later be spit again. However, without further knowledge and understanding of the Hawaiian plants in terms of both morphological and molecular data, they are tentatively retained in *Distichophyllum* until sufficient is known.

Nearly all species of *Daltonia* fall within the 'Dist 5' + 'Dalt 1' clade, except for *Daltonia armata*. In addition, a few curious Asian *Distichophyllum* species with more or less carinate leaves are shown to belong to this clade. Among the *Distichophyllum* within this clade, *D. meizhiae* and *D. wanianum* have gemmae producing on the dorsal side of the leaf costa (see Chapter 3), similar to some species of *Daltonia* for instance *Da. apiculata*. Noteworthy the epiphyll *D. meizhiae* and the IUCN red-listed *D. carinatum* cluster within the current definition of *Daltonia*. Leaves of these two species indeed show typical morphology of early diverging *Daltonia* (cf. Yu et al., in press), for instance, ± rectangular basal laminal cells. Hence, the transfer of *D. carinatum* and *D. meizhiae* into *Daltonia* can be justified.

In the *D. carinatum* clade the German sample is sister to the Asian collections. This is most likely, an artifact due to the small sampling size, high uniformity of the gene sequences, and the several missing data from the Japanese exemplar. Only chloroplast genes were successfully amplified for the Japanese sample and these sequences are identical to those of the Chinese exemplar. In fact, within these three exemplars, there are only five nucleotide differences out of ca. 4,500 nucleotides in the combined dataset. With reference to Yu et al. (in press) study of *Daltonia*, the early diverging lineages of *Daltonia* have a center of diversity around the Himalayan region. In this study, it is clearly shown that *D. carinatum* also belongs to the early diverging *Daltonia*. Adding to the fact that the sporophytic collections were known only from Southeast China and northern Thailand (see Chapter 3), it is most probable that the European populations migrated from continental Asia through dispersal as speculated by Dixon (1909).

Although a Chinese specimen was tentatively identified as *Da*. cf. *apiculata* (P. Majestyk, pers. comm. Oct 2009), analyses of DNA sequence data show that it is not the same species as the supposedly authentic *Da. apiculata* here sampled. However, its status can only be confirmed by comparing specimens around the Himalayan region, where the material was collected.

At this point, there is not enough information to distinguish which option would be best, whether to further expand *Daltonia* to include *Distichophyllum* spec. B and *D. wanianum*, or to treat ‘Dist 5’ as a separate new genus. *Distichophyllum* spec. B was initially identified as *D. collenchymatosum* due to the superficial resemblance to this variable species. A closer examination of the material has, however, revealed that the leaves are conspicuously keeled at the base along the costa, a character not found or reported from *D. collenchymatosum* and rare among *Distichophyllum*, but common in *Daltonia*. Although the specimen cannot be named at the moment, it could belong among the several valid existing names that have not been reexamined after their first description. Hence, the two species are tentatively staying as they are, while waiting for an in-depth morphological assessment in the future.

The small genus *Distichophyllidium* is represented in the present study only by the type species. Since the other four species in *Distichophyllidium* were not sampled, the monophyly of the genus awaits future validation. The results of Buck et al. (2005) and of Chapter 1 show that *Distichophyllium nymanianum* is sister to *Daltonia* with good support. However, in this study its relationship with the remaining Old World taxa sampled could not be resolved. Similarly, the positioning of *Leskeodon seramensis* (‘Lesk 2’) could not be determined. However, it is clear that *L. seramensis* does not belong to *Leskeodon*. Further study is necessary to ascertained if this species should be segregated as new genus or included in one of the related genera.

The remaining taxa, here interpreted as the core *Distichophyllum*, include two well-supported clades ‘Dist 6’ and ‘Dist 7 + Dalt 2’. Unfortunately, the sister relationships of these two clades lack adequate support. Nevertheless, it is best to provisionally recognize the whole clade as *Distichophyllum*. If one would choose to keep the sub-clades separate, then ‘Dist 7 + Dalt 2’ could be considered *Distichophyllum* in the strict sense, since the proposed lectotype *D. spathulatum* belongs here. However, there seems to be no distinguishing morphology to separate the two subclades.

Within ‘Dist 6’, *D. succulentum* is nested within the morphologically plastic *D. collenchymatosum*, thus rendering it paraphyletic. This result corroborates with the suggestion in Chapter 3 that the two species might be one. However, without the study of the type specimens, particularly those of the little known *D. succulentum*, to confirm the identity of samples used in this study, it is better to postpone the proposal of synonymy. Interestingly, two separate sub-clades of epiphytic species can be seen within ‘Dist 6’. In the first sub-clade, the relationships between *D. cuspidatum* and *D.* cf. *subcuspidatum* cannot be resolved with support. Without examining the type of the little-known *D. subcuspidatum*, the identities of the two voucher specimens are uncertain and may represent a variation of the typical *D. cuspidatum*. These two specimens resemble *D. cuspidatum*, but differ only by the distinct carinated leaf base and the stronger cell wall thickening. In the other epiphytic sub-clade, *D. jungermannioides*, a species commonly found at the base of trees and shrubs, is sister to two other true epiphytes including *Leskeodon acuminatus*. The papillose exostome seems to have evolved here once again in *L. acuminatus*. Consequently, the revival of the original basionym *Distichophyllum acuminatum* Bosch & Sande Lac. is proposed here.

Since all exemplars within the *D. nigricaule* complex, representing geographical and morphological variations, e.g., plant size, degree of laminal cell size differentiation, etc., are nested within the same clade, its monophyly can be confirmed. The two sampled varieties, accepted by some authors at species level, are not resolved. This indicates that the characters that are currently used to separate the two varieties or species vary greatly. Thus, the synonymy of the two names, as already proposed and accepted by some authors (e.g. Bartram, 1939; Gangulee 1977), is here supported.

Within ‘Dist 7 + Dalt 2’ some nodes are not resolved with adequate support. However, species with multiple samples from different islands, such as *D. tortile*, *D. spathulatum*, and *D. leiopogon*, are proven monophyletic with maximum support. It would be interesting to see the relationship between *D. spathulatum* and *D. mittenii*, separable only by the gametoecial morphology and sexuality, when the DNA data of the latter becomes available in the future.

Sister to *D. tortile* is an interesting well-supported clade consisting of *D. schmidtii* plus a group of species occurring in Southeast Africa and adjacent islands in the western Indian Ocean. It should be noted that identifications of the latter group of African species are difficult and thus uncertain because distinctive characters used in keys and descriptions are too variable (e.g., Crosby, 1976; Demaret, 1955), for instance, plant size, degree of leaf undulations, etc. A critical taxonomic revision is necessary to ascertain the validity of all species occurring in this region.

Another well-supported sub-clade is composed of a group of species known for their exceptional large, and lax, laminal cells and often weak costa. This group includes *D. malayense* and *D. angustifolia*. *Distichophyllum subnigricaule* var. *subnigricaule* may also belong here, but its placement has no parsimony bootstrap support. Damanhuri & Mohamed (1986), who first described *D. malayense*, have questioned if the species should be placed in *Distichophyllidium* since weak costa is the character emphasized by Fleischer (1908) to the genus. However, the reverse could also be true and species with weak costa, such as *Distichophyllidium jungermanniaceum*, may belong here.

On the other hand, paraphyly is exemplified by *D. osterwaldii*. The voucher from West Malaysia (abbreviated as MY-W) belongs to what has been interpreted as an extreme form of *D. osterwaldii* with notched leaf margins in Chapter 3. Evidence from this study, however, supports recognizing this “extreme form” as a separate new species. Similarly, *D. subnigricaule* is shown to be heterogenous appearing in two different sub-clades. This indicates that the morphological resemblances of the two recognize varieties are largely superficial. Thus, it is best to raise *D. subnigricaule* var. *subnigricaule* and var. *hainanense* to species level and to treat them as two separate species.

Contrary to Yu et al. (in press), which speculated that *Daltonia armata* (‘Dalt 2’) may belong to the basal lineages of *Daltonia*, this study supports the nesting of the species within the core *Distichophyllum*. Although the exact placement remains unresolved, the nesting of ‘Dalt 2’ within ‘Dist 7’ is clear. In fact, the removal of this species from *Daltonia* has been suggested based on several unique and exceptional morphological features among the genus (see Chapter 3). However, no transfer was made because it was uncertain where the species would belong. The current phylogeny justifies its transfer into *Distichophyllum*, which is here proposed. The long-branch length of this species indicating rapid evolution would explain its aberrant morphology.

Interesting geographic patterns are observed in the phylogeny of the complex of *Distichophyllum* and allies. The resolved clades correspond more to biogeographical entities than traditional concepts of genera (also observed in Chapter 1). In fact, several resolved clades show regular geographical boundaries. For instance, 'Lesk 1' consists of species limited to the neotropics; species in 'Dist 2' are confined to Southern South America and Southern Australasia; the two Hawaiian endemics are closely related in 'Dist 4'; all species in 'Dist 6' and 'Dist 7' only occur in the Old World, etc. On the other hand, Yu et al. (2009) have demonstrated that the crown species in *Daltonia* have transcontinental distributions, while the more basal ones are more restricted to one continent. In addition, the phylogeny here presented shows that the early diverging lineages of *Daltonia* are almost exclusively occurring in the Himalayan regions. These suggest *Daltonia* could have originated from an ancestor in this biodiversity rich region.

2.4.4. Testing the proposed sections under *Distichophyllum*

The heterogenous nature of *Distichophyllum* has been discussed above. To test the validity of the sections *Mniadelphus* and *Discophyllum*, the section to which species belong according to Brotherus (1925) is mapped in our final tree (Figure 7, ^ = sect. *Mniadelphus*; * = sect. *Discophyllum*). Other authors have a somewhat different concept of these two sections and hence these were not considered in this study. Without surprise, the two sections are indeed not monophyletic. However, some patterns can be observed. All species in 'Dist 7' treated by Brotherus (1925) were in section *Mniadelphus*. Similarly, species in 'Dist 1', 'Dist 2' and 'Dist 4' considered by Brotherus were put in section *Discophyllum*. However, the section allocation of species in 'Dist 6' would make both sections not even paraphyletic. This finding agrees with Fleischer (1908) and Matteri's (1975) observations that the sections can not hold. Interestingly, except for *D. flaccidum*, Mitten's (1869) concept of sect. *Mniadelphus* and sect. *Discophyllum* correspond with 'Lesk 1' and 'Dist 2' respectively. In any case, with the collapse of the traditional *Distichophyllum* and the nomenclatural confusions associated with the use of these names (see Chapter 4), it is best to completely abandon the use of these two sections.

Unfortunately, the status of section *Platyovtophyllum* could not be evaluated as the type species, *D. noguchianum* has been collected only once in 1987 and is not available. Based on the description and illustration of the species, the radial foliation, and isophyllous, concave leaves with rectangular basal cells, this species may be related to early diverging *Daltonia*. The other species placed in this section, *D. iwatsukii* ('*iwatsukianum*') is currently a synonym of *D. kinabaluense*. Although the two species share some superficial similarities (see Tan, 1990), they probably are not closely related. Nevertheless, this cannot be confirmed without further work.

2.4.5. Assessing the relevance of exostome ornamentation in generic placement.

The reconstructed ancestral state for ornamentation of the basal outer face of exostome is shown in Figure 9. Within the Hookeriales, shifts to papillose exostome, from a striate one, have already been demonstrated in Chapter 1. Figure 9 has evidently showed that the papillose exostome, typical of daltoniaceous peristomes, has evolved independently at least three times within the Daltoniaceae. Species with papillose exostome were traditionally put in *Leskeodon* or *Daltonia*. Although papillose exostome is fairly consistent within the clades ‘Lesk 1’ and ‘Dalt 1’ (Figure 9), some species in the traditional *Leskeodon* and *Daltonia* could be intermixed together or nested deep within species of *Distichophyllum*, a genus traditionally circumscribed as having a striate exostome. *Daltonia armata* was included into *Daltonia* based almost essentially by the superficial resemblance in leaf morphology (Bartram, 1944), while the peristome type has never been reported and thus assumed to be papillose. Although character state reconstruction of exostome ornamentation (see Figure 9) predicted that its exostome is striate, a papillose one is still possible as seen in the case of *Leskeodon acuminatus*, where a species with papillose exostome is nested deep within a clade of taxa with striate peristomes. Hence, it is proven here that, at least within the Daltoniaceae, the exostomial ornamentation is not a reliable character for distinguishing among genera.

The daltoniaceous peristome is seemingly associated with epiphytism although this relationship is not perfect. True enough, taxa traditionally put in *Daltonia* and *Leskeodon*, both with daltoniaceous type peristome, are largely epiphytes or even epiphylls. Whittemore & Allen (1989) found that in the daltoniaceous peristome, exostome teeth incurved when dry and reflexed when moist while the opposite is true of the hookeriaceous peristome (hygrocastique and xerocastique respectively, see Mueller & Neumann, 1988). The actual functions and advantages of having daltoniaceous peristome in epiphytes are unknown, but Buck (1991) has made some speculations. This could also have implications for genera within the large Pilotrichaceae that are similar gametophytically but distinguished only by peristome types, e.g. *Lepidopilum* and *Lepidopilidium*.

One would expect that there would be also specialized adaptations on the gametophyte with a switch to an epiphytic lifestyle. Here are some of the observed trends in both gametophytic and sporophytic characters that appear to be associated with epiphytism in Daltoniaceae:

- A trend towards monoeicy (autoicous and synoicous taxa). All species of *Daltonia* seem to be monoicous (bisexual). In *Leskeodon* this trend is not a rule but a tendency. Similarly in *Distichophyllum*, non-epiphytes such as *D. mittenii* are synoicous.
- Orthotropic growth habit. Epiphytes in the family tend to form orthotropic turfs rather than plagiotropic mats.
- Radial foliation. The character is typical in species of *Daltonia* probably associated with orthotropic growth. Among *Distichophyllum*, species such as *D. cuspidatum* have a less-complanate foliation. Nevertheless, species growing horizontally on leaves or adpressed to bark remain complanate even if the axes are orthotropic.
- Sharp leaf apiculus. This is found in most species of *Leskeodon* and *Daltonia*. In *Distichophyllum cuspidatum*, it is even cuspidate as the species epithet indicates. Frahm et al. (unpublished data) have shown that the hair-points in leaves of *Campylopus introflexus* (Hedw.) Brid. function as points for deposition of dew. The sharp leaf tip in leaves of epiphytic members of the Daltoniaceae, although shorter than typical hair-point, could have similar function.
- Seta becoming less rough. A spinose-papillose seta in several species of the Daltoniaceae is well-known. However, it is observed that setae in epiphytic taxa are generally less papillose or even smooth. The function of a spinose seta is unknown.

However, it should be noted that the above listed character trends are probably specific to the Daltoniaceae and thus cannot be applied to other taxonomic groups, especially outside the Hookeriales. A general trend in epiphytic pleurocarpous mosses towards shorter setae and erect capsules has been evidenced (Hedenäs, 2001). This trend may be probably true in Daltoniaceae.

2.4.6. Proposed new nomenclatural combinations and new synonymies:

I. *Beeveria microcarpos* (Hedw.) B.C. Ho & L. Pokorny, **comb. nov.** — Basionym: *Hypnum microcarpon* Hedw. *Sp. Musc. Frond.* 244. t. 59 f. 6–8. 1801. — *Pterygophyllum microcarpon* (Hedw.) *Brid. Muscol. Recent. Suppl*. 4: 149. 1819 [1818]. — *Hookeria microcarpos* (Hedw.) Hook. & Grev. *Edinburgh J. Sci.* 2: 226. 1825. "*microcarpa*" — *Mniadelphus microcarpos* (Hedw.) Müll. Hal. *Linnaea* 21: 196. 1848. "*microcarpus*" — *Distichophyllum microcarpon* (Hedw.) Mitt. *Trans. & Proc. Roy. Soc. Victoria* 19: 77. 1882. "*microcarpum*" — **Type**: "Insulae Australes". (holotype: G n.v.)

Note: Hedwig's (1801) original spelling of the species epithet is "*microcarpon*" where "-*carpon*" is the Greek neuter suffix for fruit, in reference to his observation of the small capsules or "fruits". The same spelling also appears in the index. Although, the spelling in Tab LIX (in Hedwig 1801) is "*microcarpum*", this could probably be a mistake made by the engraver, and once done, could not be readily corrected. Adopting *Hypnum microcarpon* as the basionym, Bridel (1818) made the combination *Pterygophyllum microcarpon*. However, subsequent authors adopted a Latin ending for various combination of this epithet. Following the ICBN, Art 51.1 Ex. 2 (McNeill et al., 2006), it is interpreted here that the correct spellings of the various combinations of this species should be *Hookeria microcarpos*, *Mniadelphus microcarpos*, and *Distichophyllum microcarpon*, respectively.

II. *Daltonia carinata* (Dixon & W.E. Nicholson) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Distichophyllum carinatum* Dixon & W.E. Nicholson in Dixon *Rev. Bryol.* 36: 24. f. 1–7. 1909. — **Type:** Austria, Salzburg, [Salzkammergut], St. Wolfgang See, Zinkenbach, alt. 700 m; creeping on other mosses upon dripping rocks in ravine. *H.N. Dixon & W.E. Nicholson s.n., Aug 3 1908* (holotype: BM n.v.; isotypes DUKE!, H!, S n.v.)

III. *Daltonia meizhiae* (B.C. Tan & P.J. Lin) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Distichophyllum meizhiae* B.C. Tan & P.J. Lin *Trop. Bryol.* 10: 55. f. 2, 8–12. 1995, '*meizhii*'. — **Type:** China. Yunnan Province, Gongshan-xian (county), Du-long-jiang Commune, on boulder by the Ching-lang-tang river bank, about 1300 m elev. *Mei-zhi Wang 10040*, Aug 1982 (holotype: PE n.v.).

IV. *Distichophyllum armatum* (E.B. Bartram) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Daltonia armata* E.B. Bartram Farlowia 1: 508, f. 21–24. 1944. — **Type:** Philippines, Mindanao, Lanao Prov., vicinity of Dansalan [=Marawi], alt. 700–800 m, on culm of climbing bamboo, Sacred Mountain, 3 Nov. 1938, *A. Lynn Zwickey 638*. (holotype: FH n.v.; isotype: MICH n.v.)

V. *Distichophyllum hainanense* (P.J. Lin & B.C. Tan) B.C. Ho & L. Porkorny, **stat. nov.** — Basionym: *Distichophyllum subnigricaule* var. *hainanense* P.J. Lin & B.C. Tan *Harvard Pap. Bot.* 7: 43. f. 33: E–I. 1995. — **Type:** China. "Hainan, Mt. Diao-luo, on root of tree, ca. 1050 m." *P.-J. Lin et al. 945A*, Mar 1990 (holotype: IBSC n.v.; isotype: FH n.v.).

VI. *Leskeodon crispulus* (Hook. f. & Wilson) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Hookeria crispula* Hook. f. & Wilson *Lond. J. Bot.* 3: 550. 1844. — *Mniadelphus crispulus* (Hook. f. & Wilson) Müll. Hal. *Syn. Musc. Frond.*2: 25. 1850. — *Distichophyllum* *crispulum* (Hook. f. & Wilson) Mitt. *Trans. & Proc. Roy. Soc. Victoria* 19: 77. 1882. — **Type:** New Zealand, [North Island,] Bay of Islands, *Menzies* (holotype: BM n.v., W.377 on clay earth at roots of trees in dense woods, *J.D. Hooker* Aug 1841 annotated A. Fife 1988; isotype: BM n.v.)

VII. *Leskeodon ellipticus* (Herzog) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Distichophyllum ellipticum* Herzog *Rev. Bryol. Lichénol.* 23: 83, f. 22 a–e. 1954 — **Type:** Chile, West patagonien, [Aisen,] Pto. Isla Magdalena, an quelligem Ufer des Grenzflusses, auf sandig-steinigem Grund, 13 Feb 1939, *G.H. Schwabe 20/b pp* (holotype: JE n.v.).

VIII. *Leskeodon fernandezianus* (Broth.) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Distichophyllum fernandezianum* Broth. in Skottsb. *Nat. Hist. Juan Fernandez (Botany)* 2: 435. pl. 27: f. 7–8. 1924. — **Type:** [Chile, Juan Fernández archipelago] Masafuera [= Más a Tierra, Robinson Crusoe Island]: in alpinis prope campos « Correspondencia » dictos; ad saxa humida rivuli; 1100 m s. m., *C. & I. Skottsberg 303*, 5 Feb 1917 (holotype: H n.v.; isotype: S n.v.)

Note: According to Robinson (1975), *Distichophyllum fernandezianum* is considered a synonym of *D. assimile*. In the absence of a recent revision, these taxa are kept separate and a new combination in *D. assimile* is postponed until more is known.

IX. *Leskeodon montagneanus* B.C. Ho & L. Pokorny, **comb. nov.** — Basionym: *Mniadelphus montagneanus* Müll. Hal. *Syn. Musc. Frond.*2: 22. 1850. — *Distichophyllum montagneanum* (Müll. Hal.) Bosch & Sande Lac. *Bryol. Jav.* 2: 23, t.151. 1861. **— Type**: Montes Neelgherienses [Nilgiris] ad radices fructicum, *Perrottet* [*21*?](holotype: PC n.v.).
= *Distichophyllum maibarae* Besch. *J. Bot. (Morot)* 13: 40. 1899, **syn. nov.** — **Type**: Japon, Nippon central [Honshu], Maibara, associé au *Symphyogyna sublobata*, *Faurie 11130*, 7 Nov 1893. (holotype: PC?; isotypes: FH n.v., H-Br!)
= *Distichophyllum decolyi* Gangulee *Mosses E. India* 6: 1488. f. 744. 1977, **syn. nov.** — *Distichophyllum levieri* Broth. in Brühl *Rec. Bot. Surv. India* 13(1): 125. 1931, *hom. illeg., auct. non* (Geh.) Broth. — **Type:** [India, West Bengal state,] Darjeeling district, Kurseong, Chuttakpur *Decoly & Schaul s.n. (Bryoth. Levier 2542)* (holotype: BM!; isotype: BM!)

X. *Leskeodon rotundifolius* (Hook. f. & Wilson) B.C. Ho & L. Porkorny, **comb. nov.** — Basionym: *Hookeria rotundifolia* Hook. f. & Wilson *Lond. J. Bot.* 3: 551. 1844. — *Mniadelphus rotundifolius* (Hook. f. & Wilson) Müll. Hal. *Syn. Musc. Frond.*2: 21. 1850. —

Distichophyllum rotundifolium (Hook. f. & Wilson) Müll. Hal. & Broth. *Abh. Naturwiss. Vereine Bremen* 16(3): 506. 1900. — **Type:** New Zealand, Bay of Islands, *J.D. Hooker 376* (Antarct. Exped. 1839–43) (holotype: BM n.v.; isotype: FH n.v., K n.v.).

2.5. Conclusion

The present study has revealed considerable unknown relationships among genera of the Daltoniaceae; however, precise relationships of certain genera and clades remain obscure. The infra-generic phylogenies within *Achrophyllum* and *Calyptrochaeta* have indicated that the crown species may need taxonomic re-evaluations. Genera within the limbate Daltoniaceae were shown in the present study to be rather artificially delimited in the traditional sense. The abundant homoplasy and convergence in morphological traits in this group has probably hampered traditional accurate circumscription of genera to reflect natural groupings.

Lost in a sea of similar gametophytic characters and under the influence of Philibert’s principles of peristome conservatism, it is no surprise that the more easily distinguishable exostome ornamentation was taken as the key character to delimit genera and families. Having demonstrated the heterogeneity of the papillose exostome within the limbate Daltoniaceae, traditional concepts of several genera fall apart and would require adjustments or re-circumscriptions to reflect the new improved phylogenetic hypothesis. However, finding a set of ‘good’ morphological features to delimit the recognised clades in this study is a challenging task. Critical generic revisions and delimitations of the traditional *Daltonia*, *Leskeodon* and *Distichophyllum* are essential to unveil several phylogenetic uncertainties and complement the present molecular phylogenetic study.

--- <<End of Chapter 2>> ---

Chapter 3:

New and Noteworthy records of *Distichophyllum* (Daltoniaceae, Bryopsida) and allied genera in Asia and Australasia

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Contents

Introduction

With *ca* 100 accepted species distributed largely in the tropics and southern temperate, the pleurocarpous moss genus *Distichophyllum* is characterised by complanate plants, with bordered and unicostate leaves, which are frequently rounded to spathulate, although some species have acute to acuminate leaves. The laminal cells are often large, parenchymatous, isodiametric to hexagonal, and always smooth. As a typical hookerialean moss, it has a mitrate calyptra. The exostome teeth are cross-striate on the outer face with median furrow, a main character used to separate *Distichophyllum* from the closely related *Leskeodon*. However, the true relationships between *Distichophyllum* and its allied genera remain unclear. Moreover, preliminary studies have shown that the genus itself contains a polyphyletic grade of species within Daltoniaceae (B.C. Ho, unpublished molecular data).

Phylogenetic relationship apart, a clearly defined species circumscription and accurate identification of a species is, nevertheless, important and fundamental in floristic and biogeographic studies. The present paper reports 24 new and noteworthy species records discovered during the examination of loaned materials from various herbaria in search for suitable specimen(s) for DNA systematic study as part of the doctoral dissertational research of the first author (Ho, dissertation in prep.).

Although the prevailing knowledge on the listed species below is far from complete, and the type specimens of several related species in discussion are not studied due to time constrain, we feel that reporting the new records and the diagnostic morphological information of this large and variable group of hookerialean mosses is worthwhile for identification purpose, while awaiting a monographic revision of the genus.

Clearly, the many new records reported here testify the inadequate taxonomic knowledge of this large and variable genus, which hamper accurate identifications. A thorough and critical taxonomic revision of the genus is urgently needed.

The following list of species records is arranged alphabetically for the ease of locating a name of interest. Taxonomic, biogeographic or habitat notes, where appropriate, are included after each enumerated species record. The specimens cited in this paper include only those representing the new or interesting records of a species under discussion.

New or noteworthy records

3.2.1. *Daltonia armata* E.B. Bartram (Figure 10)

The species is atypical and unique among members of the genus *Daltonia*. Majority of the species of *Daltonia* are not complanately foliated like the present species. The leaf borders in *D. armata* are narrow and weakly differentiated from adjacent laminal cells, unlike those of typical *Daltonia* which are very broad and distinct especially near the base.

The closest relative of *D. armata* is probably *Leskeodon ponapensis* H.A.Mill. (holotype BM!) described from the Caroline Islands (Micronesia) (see Miller 1978). Both have the characters of complanate foliation, leaves with margins recurved along basal half, leaf border narrow throughout and weakly defined, a weak costa at times hidden in the somewhat carinate leaves, long hexagonal laminal cells, and clusters of gemmae on dorsal face of leaf costa near base. *Leskeodon ponapensis,* however, can be distinguished by its obovate leaves with short recurved apex; *D. armata* has narrowly lanceolate to oblong-oblanceolate leaves with gradually long and narrow apex. Another interesting difference is the exceptionally long axillary hairs in *L. ponapensis* consisting of 12–18 cells long, hyaline, and numerous at the branch tips. The axillary hairs of *D. armata* consist of two short cells, including basal cell, with slightly brown walls somewhat thicken at the apex. Gemmae in *D. armata* are curved or twisted and consisting of shorter cells (length: width ratio = 1.5–2.5:1) than those in *L. ponapensis*, which are ± straight and consisting of longer cells (length: width ratio = 3–4:1). (See Figure 10).

The endemic Taiwanese taxon, *Distichophyllum pseudomalayense* T.Y Chiang & C.M. Kuo, has been suggested by Lin & Tan (1995) to be close to *Daltonia armata*. From the illustrations and descriptions of Chiang & Kuo (1989), we think they can even be synonymous. However, study of the types is necessary to confirm this.

A certain degree of sexual dimorphism of the leaves of dioicous *D. armata* has been observed from the specimens studied. It seems that plants with long narrow leaf tips are predominantly female and those with shorter tips are mostly male plants (Figure 10a–b). However, there seems to be some intermediate leaf forms. Careful study of more specimens is necessary to ascertain the observed sexual dimorphism reported here. Until the phylogenetic relationships of species within *Distichophyllum*, and between the genus and *Daltonia* are resolved, we cannot be sure where *D. armata* belongs taxonomically after its removal from *Daltonia*.

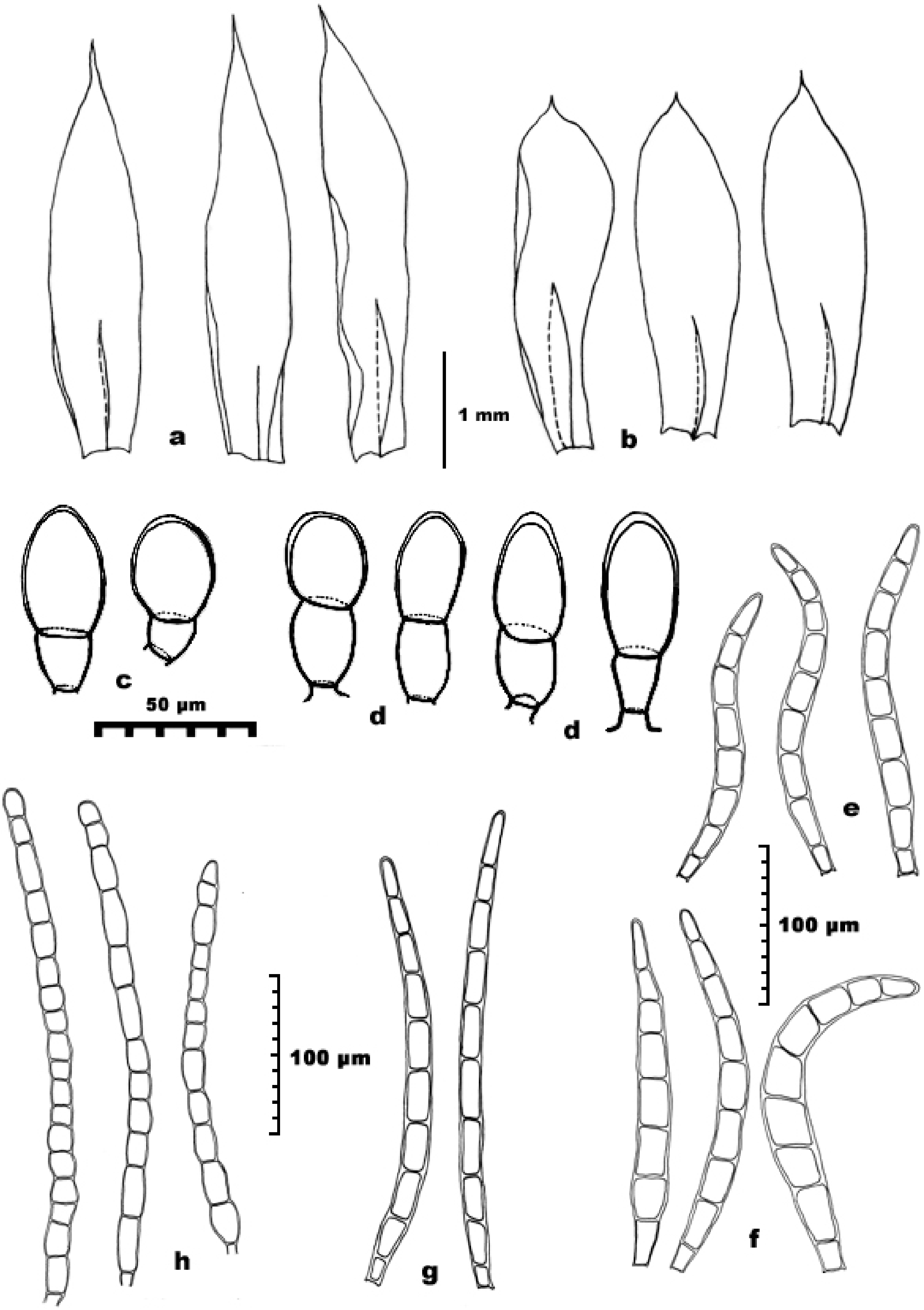

Figure 10. ***Daltonia armata***: **a.** Leaves of female plants; **b.** Leaves of male plants; **c–d.** axillary hairs; **e–f.** gemmae; ***Leskeodon ponapensis*** **g.** gemmae; **h.** axillary hairs; a–c & f based on *Ho 08-007* (SING); d–e based on *Suleiman 301* (BORH); g–h based on *Miller 6429* (holotype, BM); drawn by BCH.

From the reported type collection and few other collections seen, *D. armata* has shown to be one of the species that could grow directly on bamboo culms, although some were also found as epiphytes and epiphylls.

Specimens of new record studied: MALAYSIA: Sabah, Keningau distr., Kg. Sinua, Mt. Trus Madi, on tree trunk, partial shade, 1,180 m, 9 Oct 1996, *M. Suleiman 351*; on bamboo nodes, partial shade, 1,200 m, 9 Oct 1996, *M. Suleiman 354* (BORH). INDONESIA: C. Seram, Kecamatan Tehoru, Manusela National Park, lower montane forest, *ca* 650 m, on shrub branch, 7 Sep 1986, *H. Akiyama C-16534* (HYO) [material consists of a few fertile shoots among *Leucophanes octoblepariodes*].

Known distribution: Philippines (Mindanao), Malaysia (Pahang, Sabah), and Indonesia (Sumatra, Seram).

3.2.2. ***Distichophyllidium nymanianum*** M.Fleisch.

The small genus *Distichophyllidium*, of currently five species, is one of the related genera of *Distichophyllum*, although the true relationship is not clear. *Distichophyllidium nymanianum* is a distinctive species with ecostate leaves and the foliation is scarcely complanate. The presence of several slender, bristle like, rhizoidal gemmae along the stem axis is also diagnosis. The species is uncommon and sporadic across the range of its distribution in Malesia. The present report presents a new locality of its distribution as well as represents a new generic record for the Island of Sulawesi.

Specimen of new record studied: INDONESIA: S. Sulawesi, Gunung Lompobatang at Malino, 60 km ESE Ujung Pandang (= Makassar), montane rain forest; epiphytic, Nov 1993, *F. Müller S81* (DR).

Known distribution: Malaysia (Pahang), and Indonesia (Java, Seram, Sulawesi, Papua).

3.2.3. ***Distichophyllum albomarginatum*** D.H. Norris & T.J. Kop. (Figure 11)

The lowland species is easily distinguished by the broad and distinct leaf border of 4–6 cells wide at mid-leaf, appearing whitish when dry, as the species epithet suggests. The border becomes 2–3 cells thick towards the apex, but the border cells have always a large lumen. Other distinguishing features include the spathulate to obovate leaves and homogenous laminal cells in the upper half of leaves, which are ± isodiametric, *ca* 20–30 µm wide and thin-walled. The Seram specimens reported below have been compared to one of the paratypes (*Koponen 35686*, NY) and are identical.

Specimens of new record studied: INDONESIA: C. Seram, Kecamatan Seram Utara, on soil, *ca* 60 m, 28 Dec 1984, *H. Akiyama C-2492*; on rotten log at riverside, *ca* 60–600 m, 20 Dec 1984, *H. Akiyama C-8523*; Kecamatan Tehoru, on soil, *ca* 180 m, 14 Feb 1985, *H. Akiyama C-10241*; stream-side on boulder, *ca* 100–560 m, 18 Jul 1986, *H. Akiyama C-14626*; on tree root, *ca* 350 m, 25 Aug 1986, *H. Akiyama C-15972*; W. Seram, Kecamatan Kairatu, on boulder at streamside, *ca* 280 m, 13 Sep 1986, *H. Akiyama C-16823* (all HYO).

Known distribution: Indonesia (Seram), and Papua New Guinea (East Sepik).

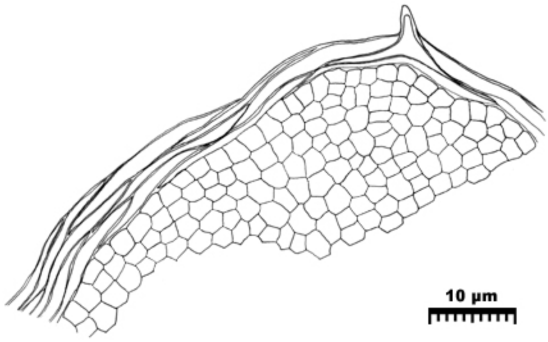

Figure 11. Leaf border and apex of *Distichophyllum albo-marginatum*; based on *Koponen 35686* (paratype NY) drawn by BCH.

3.2.4. ***Distichophyllum angustifolium*** Dixon

The species was considered endemic to Borneo. The two new collections listed below are indicative that its range is wider than reported. The large lax cells and weak costa of this species resemble those of *D. subnigricaule*, but can be distinguished by the elongate leaf outline with the length at least thrice that of the width. The species could also be confused with *D. malayense*, probably its closest relatives. Leaf apices in *D. angustifolium* are, however, obtuse, ending with a short apiculate acumen. See below the treatment of *D. malayense* for comparison.

Although Ariyanti et al. (2009) reported a Sulawesian collection (*Ariyanti 539*) to consist of a mix of *D. tortile* and *D. spathulatum*, our careful comparison of the collection with other identified specimens has revealed that the Sulawesi specimens are in fact, *D. angustifolia* and *D. mittenii* respectively (see discussion below). Both species are new to the island of Sulawesi.

Specimens of new record studied: MALAYSIA: Pahang, Genting highlands, on semi-shaded log by stream, *ca* 800 m, 04 Mar 2008, *B.C. Ho 08-004* & *08-006* (SING). INDONESIA: C. Sulawesi, trail to Mt. Nokilalaki from Tongoa Lore Lindu National Park, rotten wood, 1,650 m, 22–26 Jun 2005, *N.S. Ariyanti 539* (SINU) [with *D. mittenii*]

Known distribution: Malaysia (Pahang, Sabah, Sarawak), and Indonesia (Sulawesi).

3.2.5. *Distichophyllum brevicuspes* M.Fleisch.

The specimens studied, with somewhat carinate leaves and short apiculate leaf tip, coupled with laminal cell walls not exceptionally thicken and slightly collenchymatous, match well with the description and illustration of Philippine specimen of *D. brevicuspes* in Tan & Robinson (1990). Based on the description of *D. subcarinatum* Nog. & Z.Iwats., Tan & Robinson (1990) suggested a possible synonymy of this species with *D. brevicuspes*. Upon studying the type specimens, Akiyama & Yamaguchi (1999), however, considered *D. subcarinatum* synonymous with *D. subcuspidatum* Nog. & Z.Iwats.

On the other hand, the type specimen of *Distichophyllum torquatifolium* Dixon (holotype BM!) is probably conspecific with *D. subcuspidatum*. If the synonymy is proven, the former would have nomenclatural priority. Study and comparison of types and specimens identified as *D. subcuspidatum*, *D. subcarinatum*, and *D. brevicuspes* are necessary to resolve their true identities.

Specimens of new record studied: THAILAND: Nakhon Si Thammarat Province, Khao Luang National Park, Pharmee Mt., epiphytic on tree trunk, 1,400 m, 1 May 2009, *S. Chantanaorrapint KL7/4a* (PSU). MALAYSIA: Sabah, Tawau Hills Park, Maria Camp to Headquarters; Primary forest, along Tawau River, on leaf, 350 m, 20 Feb 2007, *M. Suleiman 1702* (BORH). INDONESIA: Kalimantan Timur, Wanariset; on treelet in vegetation bordering a stream, 750 m, 12 May 1993, *J.V. Valkenburg 1286A* (L).

Known distribution: Thailand (Nakhon Si Thammarat), Philippines (Luzon), Malaysia (Pahang, Sabah), and Indonesia (Java, Kalimantan).

3.2.6. *Distichophyllum carinatum* Dixon & W.E. Nicholson in Dixon

Plants of this species are dioicous, scarcely complanate and light yellowish in colour. Leaves are ovate to broadly lanceolate, strongly crisped when dry, spread out in wet condition, keeled along the costa, acuminate to shortly cuspidate at the leaf tip.

Nearly 50 years after the first discovery of *D. carinatum* in the Zinkenbach of Austria, Takaki (1951) found the second locality in the Akaishi Mountains (Japanese Alps) in Honshu, Japan. Later, several populations have been discovered in the European Alps (see e.g. Urmi 1984 for an overview). Redfearn et al. (1996) reported the second Asian locality of this species on Mt. Emei in Sichuan Province of China. Based on a specimen collected from the nearby Mt. Jinfu, Lin & Tan (1995) reported the first sporophytic plants, albeit immature.

We are pleased to report here the second sporophytic population from Chiang Mai, northern Thailand, also representing a new species record at its southern most limit of distribution. The seta is smooth, and up to 5 mm long. The oblong capsule is erect, 2 mm long with a distinct neck region. Exostome teeth are striate below and papillose above. The presence of this world endangered moss species on Doi Inthanon shows the urgent need to protect the remaining primary vegetation of this mountain.

Interestingly, populations of *D. carinatum* with sporophytes have been found only in continental Asia. This seems to corroborate the suggestion of Dixon (1909) that the Alps' populations may have migrated from the East. Thus far, the DNA sequences of five gene markers taken from three different genomes barely differ among samples taken from Germany, China, and Japan (Ho, dissertation in prep.). Nevertheless, judging from the biogeographical point of view and the general distributional pattern of the family, it seems most probable that the original population came from SE Himalayas.

Having a scattered and disjunct distribution, *D. carinatum* is among the first listed in the IUCN World Red List of Bryophytes (Tan et al. 2000). Known populations of this protected species are monitored periodically worldwide. Hallingbäck (2001) has reported that two of the three sites at Allgäu (Germany) have vanished. Because of its endangered conservation status, we are reporting here two new locality records of this species from Yunnan Province of China.

Specimens of new record studied: CHINA: Yunnan, Diqing pref., Sang Shang Ya, E. of Xiaozhongdian, on dripping rock face in ravine, 3,480 m, 16 Jun 1993, *D.G. Long 24419* (E); Diqing pref., Weixi Co., W side of Litiping Plateau, on wet ledges of limestone rock face, 3,095 m, 19 Jun 1993, *D.G. Long 24540* (E). THAILAND: Chiang Mai, Doi Inthanon, Kew Mae Pan, in opened deforested area of upper montane forest and grassland by a steep limestone slope; growing attached to the branch of a tree, 2,300 m, *Y. Nathi 460* (BCU, SING).

Known distribution: European Alps, Japan (Honshu), China (Sichuan, Yunnan), and Thailand (Chiang Mai).

3.2.7. *Distichophyllum collenchymatosum* Cardot (Figure 12)

Plants of this species are small to medium sized. Leaves are ovate oblong in outline with acute to acuminate tips. The distinct leaf borders consist of 2–3 rows of linear cells reaching up to leaf apex. Leaf cells are hexagonal to rounded and are, at times, only slightly collenchymatous, in spite of the species epithet.

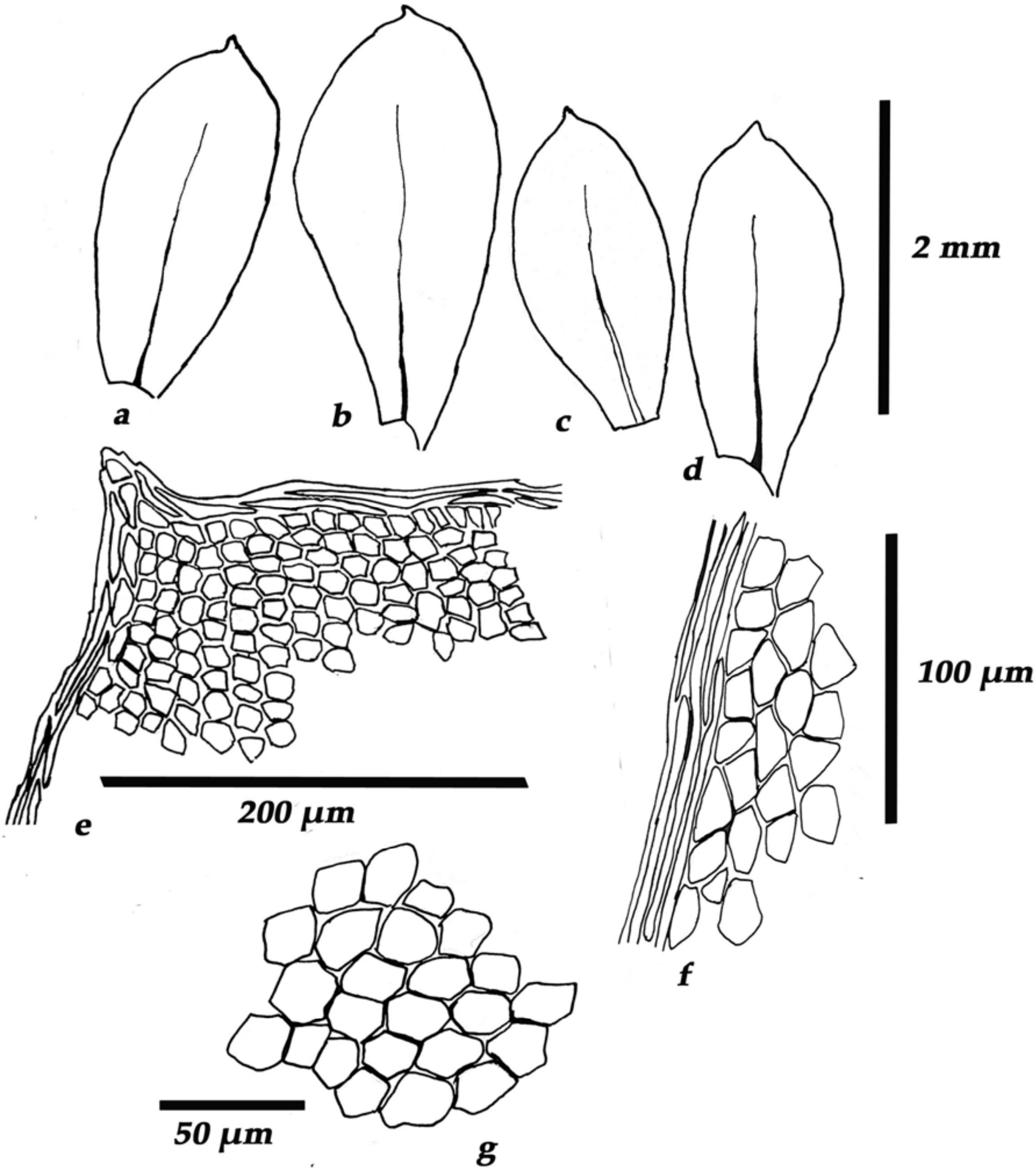

Figure 12. ***Distichophyllum collenchymatosum***: **a–d.** Leaves; **e.** Leaf apex; **f.** Cells at leaf margin; **g.** Leaf cells; based on *Y. Nathi 1040* (BCU); drawn by YN.

Distichophyllum collenchymatosum is a widespread species in south and southeast China and Japan, its occurrences in northern Thailand, northeast India, Nepal and Bhutan can be expected. However, the species shows considerable variations in leaf size and shape in terms of length: width ratio. From the illustrations and notes given by Townsend (1982), the southern Indian – Sri Lankan species, *D. succulentum* (Mitt.) Broth., might be conspecific with the variable *D. collenchymatous*. The study and comparison of more specimens including the types is necessary to prove the synonymy. If such the case is true, *D. succulentum* would have nomenclatural priority over the more widely known *D. collenchymatosum*.

Known distribution: Bhutan, Nepal, India, China, Japan, Thailand (Chiang Mai), Philippines (Negros), and Indonesia (Java).

Specimens of new record studied: BHUTAN: Geylegphug (=Sarphag) Distr., Chaley Khola, above Sham Khara, N of Gaylegphug, wet dripping rocks in ravine, *ca* 1,800 m, 3 June 1979, *D.G. Long 8209* (E) [new genus record]. NEPAL: Kangchenjunga, between Funfun and Khesewa, on dripping rocks by waterfall, *ca* 1,690 m, 30 Sep 1989, *D.G. Long 17451* (E); Rasuwa district, south bank of Langtang Khola above Syabru, on dripping rocks, *ca* 1,670 m, 27 Apr 1992. *D.G. Long 22127* (E). INDIA: West Bengal, Darjeeling District, 9 km above Mungpoo, on wet rocks by stream, *ca* 1,910 m, 3 Aug 1992, *D.G. Long 23024* (E); Sikkim, South District, S bank of Rate Chhu N of Gangtok, on wet dripping rocks, *ca* 1,630 m, 31 Jul 1992, *D.G. Long 22990* (E); Darjeeling District, 2 km W of Sukia Pokhari, on wet rocks by waterfall, *ca* 2,155 m, 5 Aug 1992, *D.G. Long 23037* (E). THAILAND: Chiang Mai, Doi Inthanon, Kew Mae Pan, *Y. Nathi 855, 992, 1040* (BCU, SING).

3.2.8. ***Distichophyllum crispulum*** (Hook. f. & Wilson) Mitt.

The New Caledonian specimen studied has oblong-oval to oblanceolate leaves with an apiculate tip, costa ¾ of leaf length, and a narrow border of 2–3 cells wide; all compare well with the description (see Streimann 1999) and specimens identified as *D. crispulum*. In spite of a distance of geographical separation of about 1,200–1,500 kilometres of New Caledonia from Australia and New Zealand, it has a few common plant species with the latter two countries. The new finding in *Distichophyllum* not only broadens the range of distribution of *D. crispulum*, but also indicates a need to evaluate the taxonomic status of several endemic species of *Distichophyllum* and related genera on New Caledonia and adjacent islands/countries.

Specimen of new record studied: NEW CALEDONIA: Païta, Mont Mou, climb to Summit, montane rain forest, on boulder, *ca* 1,200 m, 10 Sep 2001, *F. Müller NC429* (DR).

Known distribution: New Caledonia, Australia and New Zealand.

3.2.9. ***Distichophyllum*** cf. ***denticulatum*** Dixon (Figure 13)

There are confusions around the identity of Asian-Pacific species of *Distichophyllum* with toothed apical margins. They can be artificially divided into two groups. One group has leaves with incomplete border differentiation above and will be discussed later under the treatment of *D. graeffeanum*. The other group has completely bordered leaves. In addition to the feature mentioned above, the leaves of *D. denticulatum* are obtuse to acute apex. The leaf marginal teeth are, in fact, the protruding cell ends of border cells.

In the type specimen of *D. denticulatum* from Borneo, the obovate to oblanceolate leaves are up to *ca* 2 mm long, margins are toothed down to about upper third of the leaves and laminal cells are strongly collenchymatous. In the Seram materials studied, leaves are spathulate, *ca* 3 mm long and have weaker teeth limited to the apex. The laminal cells are only weakly collenchymatous. The Seram materials are intermediate between *D. denticulatum* and *D. obtusifolium* Thér. and look like a *D. obtusifolium* with slightly stronger marginal teeth. We are tentatively naming them as *D. denticulatum* and await further study.

The following new records were all formerly identified as *D. mittenii*, but the latter has strong cell size differentiation in the upper half of the leaf and a narrow cell border. For earlier record of *D. denticulatum* from Seram, see discussion under *D. graeffeanum*.

Specimens of new record studied: INDONESIA: C. Seram, Kecamatan Seram Utara, Manusela National Park, on decaying wood, *ca* 600 m, 31 Dec 1984, *H. Akiyama C-8568* (HYO); Kecamatan Tehoru, on rotten log, *ca* 620 m, 19 Feb 1985, *H. Akiyama C-10520*; *ca* 460 m, 30 Aug 1986, *H. Akiyama C-16265*; *ca* 580 m, 2 Sep 1986, *H. Akiyama C-16415*; *ca* 460 m, 2 Sep 1986, *H. Akiyama C-16431*; *ca* 540 m, 30 Aug 1986, *H. Akiyama C-16272*; *ca* 600 m, 30 Aug 1986, *H. Akiyama C16315*; *ca* 530 m, 1 Sept 1986, *H. Akiyama C-16403* (HYO).

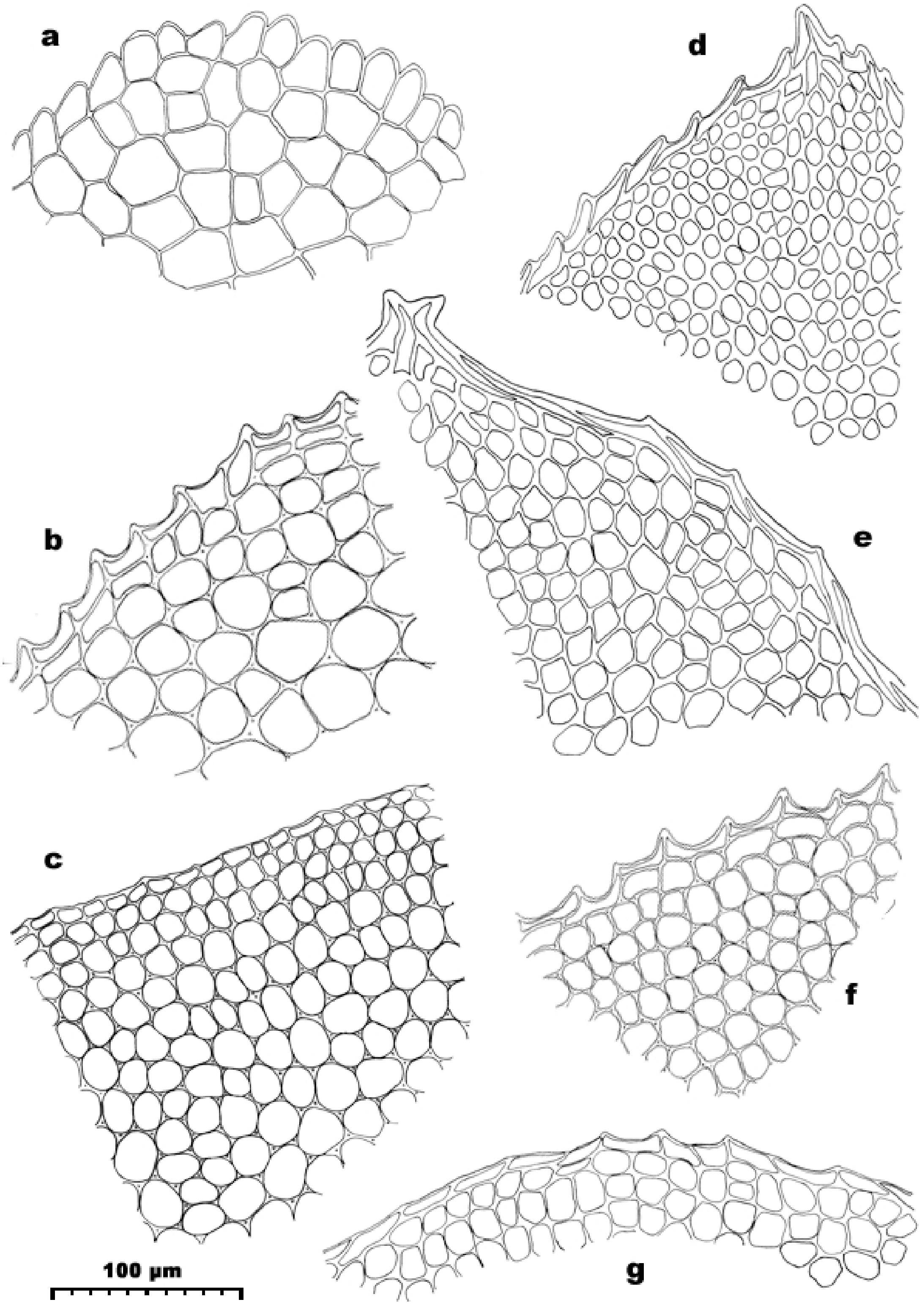

Figure 13. Leaf tips of *Distichophyllum* species with toothed margins: **a.** ***D. santosii***, based on *Mohamed & Bakar 3177a* (KLU); **b.** ***D. pterygophylloides***, based on *Ridley 1024* (original material, BM); **c.** ***D. osterwaldii***, based on *Suleiman 1951* (BORH); **d.** ***D. denticulatum***, based on *Everett s.n.* (holotype, BM); **e.** ***D.*** cf. ***denticulatum***, based on *Akiyama C-16415* (KYO); **f.** ***D. graeffeanum***, based on *Akiyama C-16268* (KYO); **g.** ***D. obtusifolium***, based on *Musci Jap. Exs.(Iwatsuki & Smith) 1262* (EGR); drawn by BCH.

Known distribution: Malaysia (Sarawak), and Indonesia (Seram).

3.2.10. ***Distichophyllum graeffeanum*** (Müll. Hal.) Broth. (Figure 13)

The most distinctive species with toothed leaf margin and incomplete border differentiation is *D. santosii* E.B.Bartram, which has lax, thin-walled leaf cells, unlike those of the others, which are variously collenchymatous (Figure 13a). The upper leaf margins of *D. santosii* are crenate, and each tooth corresponds to a protruding marginal cell (see also Bartram 1939, Pl. 19: 325). The strong marginal teeth in *D. graeffeanum* are in direct contrast with those of the former species. Each tooth composes of parts of two adjacent 'U-shape' marginal cells and the margins are serrate-dentate (see also Matsui & Iwatsuki 1993). The leaf margins of *D. osterwaldii* M.Fleisch. may be smooth to slightly notched. We have seen several Malayan specimens with stronger notched leaves identified as *D. denticulatum* Dixon that match well with the original material (BM) of what Dixon (1926) has called *D. pterygophylloides, nom. nud*. (Figure 13b) The latter is most probably an extreme form of *D. osterwaldii*. Although the strongly notched margins of specimens of *D. pterygophylloides* may resemble those of *D. graeffeanum*, other features such as size and shape of leaves, laminal cell differentiation and size etc., are similar to *D. osterwaldii*.

In the New World, two Chilean species *D. subelimbatum* Broth. and *D. theriotianum* Matteri have also incomplete leaf border differentiation and denticulate leaf margins. However, the leaves are elliptic to obovate and never spathulate or lingulate like those of the Asian-Pacific species mentioned above.

Two of the specimens reported as *D. denticulatum* in Akiyama (1990) are in fact *D. graeffeanum*, the first record of this Melanesia species in Asia. Its occurrence in the island of New Guinea can be expected.

Specimens of new record studied: INDONESIA: C. Seram, Kecamatan Tehoru, on the base of tree trunk, *ca* 460 m, 30 Aug 1986, *H. Akiyama C-16266*; on shrub branch, *ca* 460 m, 30 Aug 1986, *H. Akiyama C-16268* (HYO).

Known distribution: Indonesia (Seram), Vanuatu, and Fiji (Viti Levu).

3.2.11. ***Distichophyllum jungermannioides*** (Müll.Hal.) Bosch & Sande Lac.

This delicate species has been collected often from the base of tree trunks, an observation corroborated by Mohamed and Robinson (1991). The species is distinct in having a spathulate or obovate leaf outline with narrow base, and often a short but stout cuspidate leaf tip, and more or less homogenous cells in the upper half of the leaf. Although the majority of the slightly concave leaves have a short costa, costal length can vary from 1/3 to 2/3 of total leaf length even in the leaves of a single branch. The leaves, as already observed by Fleischer (1908), are easily detached and may act as a means of asexual reproduction.

In Malay Peninsular, this species was known at one time as *D. ulukaliense* Damanhuri & Mohamed, a synonym of *D. jungermannioides* proposed by Mohamed & Robinson (1991) which are sometimes overlooked.

Although several specimens of *D. jungermannioides* (as *D. jungermaniaceum* see Akiyama 1990) has been reported from Seram, Indonesia, they were mostly misidentified specimens of *D. nigricaule* (see below). Nevertheless, *D. jungermannioides* is found among one of the Seram collections growing mixed with the equally minute *D. catinifolium* J.Froehl.

Specimens of new record studied: THAILAND: Nakhon Si Thammarat Province, San Yen, Khao Nan National Park, growing on base of tree trunk along trail, 1,000–1,300 m, 19 Apr 2007, *S. Chantanaorrapint 1486* (PSU); Khao Luang National Park, Pharmee Mt., growing on base of tree trunk, 1,400 m, 30 Apr 2009, *S. Chantanaorrapint KL6/9a* (PSU). INDONESIA: C. Seram, Kecamatan Tehoru, Mansela National Park, on tree trunk & base of tree trunk, *ca* 560 m, 27 Aug 1986, *H. Akiyama C-16121* (HYO) [mixed with *D. catinifolium*].

Known distribution: Thailand (Nakhon Si Thammarat), Malaysia (Malay Peninsula, Sabah, Sarawak), Indonesia (Java, Sumbawa, Seram), and Papua New Guinea.

3.2.12. *Distichophyllum leiopogon* Dixon *J. Bot.* 80: 27. 1942 (Feb). **Type:** Papua [New Guinea], Alola, epiphytic on fern, on decaying log in forest, 3,800 m, 5 Jan 1936, *Carr 14185* (holotype BM!)

= *Distichophyllum cucullatum* E.B. Bartram, *Lloydia* 5: 279. f.43. 1942 (Dec), ***syn. nov*.** **Type:** [Indonesia, Papua (= Irian Jaya),] Lake Habbema, trunks of trees in moist, closed forest, 3,223 m, *Brass 9500*. (holotype FH, n.v.)

The species is distinct in having at least some leaves narrowly cucullate at the leaf apex, especially the dorsal leaves. The type specimen of *D. leiopogon* has been studied and the leaves have the same characteristic features of authenticated specimens of *D. cucullatum*. Interestingly, both names were published on the same year. Upon checking the original publications, *D. leiopogon* has several months' priority over *D. cucullatum*, a better known name reported to occur also in the Philippines (Tan & Robinson 1990)

The relative robust plant with spathulate leaves may be confused with *D. mittenii*. However, the submarginal laminal cells are only slightly smaller than the paracostal ones. The following herbarium specimens were all erroneously identified as *D. mitteniii*, which has leaves with much stronger cell size differentiation and smaller upper submarginal cells.

Specimens of new record studied: PHILIPPINES: Camiguin Island, Mt. Timpoong; montane forest, on wet rocks, 1,530 m, 28 Jun 2007, *V. Linis* s.n. (SING) [mixed with a few plants of *D. spathulatum*]. INDONESIA: C. Seram, Kecamatan Tehoru, Manusela National Park, on tree trunk base, *ca* 1,860 m, 29 Jul 1986, *H. Akiyama C-15141*; on trunk of tree fern, 1,450 m, 8 Sep 1986, *H. Akiyama C-16730* (HYO).

Known distribution: Philippines (Mindanao, Camiguin Island), Indonesia (Seram, Papua), and Papua New Guinea.

3.2.13. ***Distichophyllum maibarae*** Besch. (Figure 14)

Distichophyllum maibarae looks like a small *D. collenchymatosum*, but the two species differ in the length of the leaf border. In *D. maibarae* the differentiated border often does not reach the leaf apex. In addition, its leaf apiculus is also shorter than that in *D. collenchymatosum*, and the upper leaf cells are consistently smaller.

Akiyama (2006) reported an Indian endemic, *D. decolyi* Gangulee, new to Thailand. This name has been proposed earlier to be a synonym of *D. maibarae* (see Tan & Lin 1991). The new discovery of *D. maibarae* in northern and southern Thailand is not surprising because the country is situated geographically at the middle of the distribution range of the species. One of the Thai specimens examined has a young calyptra with long erect hairs, a feature separating it from *D. montagneanum* (see below treatment).

Specimens of new record studied: THAILAND: Chiang Mai, Doi Inthanon, Kew Mae Pan, Ang Ka area, on wet soil nearby a streamlet and a small shaded canal, *Y. Nathi 9, 640, 652, 689, 856, 1025* (BCU, SING); 15 ha Plot, near Check Point 2, *ca* 1,600 m; at stream in upper montane forest, on wet submerged rock, 31 Dec 2008, *H. Akiyama et al. 229, 230, 237* (HYO); on moist wet rock, 31 Dec 2008, *H. Akiyama et al, 243, 246* (HYO); on wet rock, 2 Jan 2009, *H. Akiyama et al. 269*; on moist-wet rock, 5 Jan 2009, *H. Akiyama et al. 377* (HYO); on wet rock, 6 Jan 2009, *H. Akiyama et al. 399* (HYO); Nakhon Si Thammarat Province, San Yen, Khao Nan National Park, growing on wet rocks, along streamlet, 1,000–1,300 m, 20 Apr 2007, *S. Chantanaorrapint 1591* (PSU).

Known distribution: India (Chuttapur), China, Japan, Thailand (Chiang Mai, Nakhon Si Thammarat), Vietnam, Philippines (Luzon, Batan Is.), Malaysia (Pahang, Sabah), and Indonesia (Java).

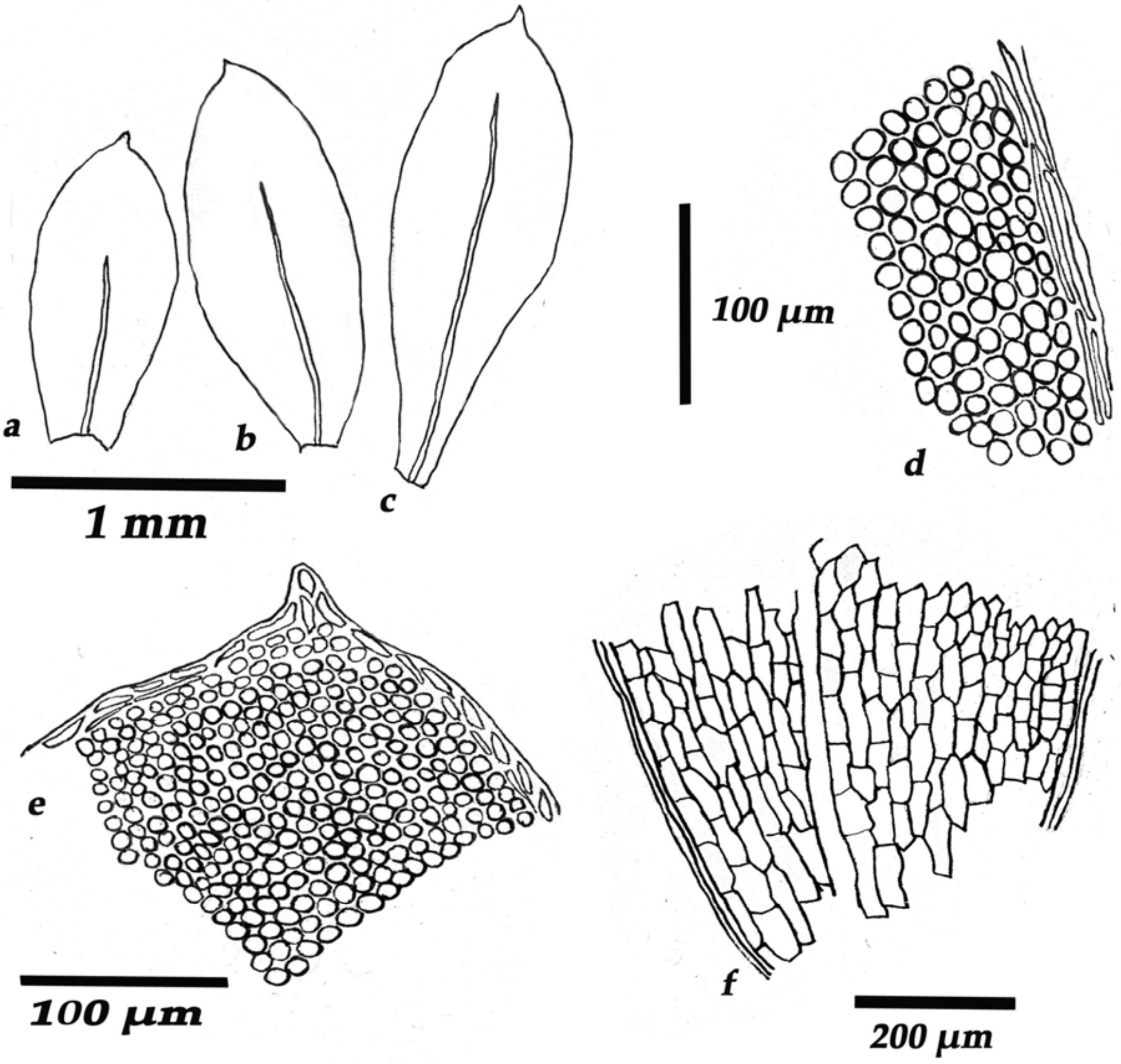

Figure 14. ***Distichophyllum maibarae***: **a–c.** Leaves; **d.** Cells at leaf margin; **e.** Leaf tip; **f.** Leaf base; based on *Y. Nathi 640* (BCU); drawn by YN.

3.2.14. ***Distichophyllum malayense*** Damanhuri & Mohamed

This is a relatively small-sized species with large lax cells. It can be separated from the similar *D. angustifolia* by its typically oblanceolate leaves with gradually acute apex ending in a long and slender acumen. For a comparison of leaf morphology, see discussion under *D. angustifolium*. The species was first described from Peninsular Malaysia, and later reported from Borneo (as *D. scabrisetum*) and recently from Java (Akiyama & Yamaguchi 1999; Tan et al. 2006). The present report further extends its range to eastern Malesia.

Specimen of new record studied: INDONESIA: C. Seram, Kecamatan Tehoru, en route from Nihehata to the top of Gunung Hoale Besar, Manusela National Park, on rotten log, *ca* 1,540 m, 8 Sep 1986, *H. Akiyama C-16706* (HYO).

Known distribution: Malaysia (Pahang, Sabah), and Indonesia (Java, Seram).

3.2.15. ***Distichophyllum meizhiae*** B.C.Tan & P.J.Lin

This is a beautiful and unique species, easily recognised by its highly differentiated gemmiferous dorsal leaves forming a hood to keep and protect the developing gemmae. Known only from the type before this paper, we report here three more specimens, two of these were collected along the Dulong-jiang (River) located at northwest corner of Yunnan province of China, but at slightly higher elevations from the type locality. The third and most interesting specimen is an old but fertile collection from the Abor Hills of India. This collection was reported in Dixon (1914) and followed by Gangulee (1977) as *D. griffithii* (Mitt.) Paris. In fact, some of the illustrations of *D. griffithii* in Gangulee (1977: Fig. 742) were based on the collection identifiable to *D. meizhiae*. Dixon (1914) and Gangulee (1977) were probably misled by the undulate non-gemmiferous lateral leaves and may have overlooked the hooded gemmiferous leaf character in the specimen. It would be of relevant scientific interest to study all specimens of *D. griffithii* cited in Gangulee (1977), including its type, to check if this Indian species and *D. meizhiae* are conspecific. All the three Chinese collections, including the type, of *D. meizhiae* were collected along the same river between 1,300 m and 1,735 m, whereas the Abor specimen was collected at slightly lower elevation (3000 ft = 1000 m). In terms of geography, Abor Hills is located at the western edge of Hengduan Mountain range in SE Himalayas, about 400 km west of the Dulong River. The newly identified collections seem to indicate that *D. meizhiae* has a preference for epiphyllous habitats.

While the type specimen is non-fruiting, one of the Chinese specimens (*Long 36274*) has several juvenile sporophytes with seta about 2 mm long and a mitrate calyptra. The calyptrae are smooth with fringes at the base, reddish brown at the apex and becoming very pale and discoloured below. The Indian specimen on the other hand, has several old decapitated seta of 5–6 mm long. The setae in both collections are smooth and reddish-brown. Fortunately, one horizontal capsule was found in the latter specimen with intact peristome. Interestingly the outer face of the exostome teeth of *D. meizhiae* is papillose with a faint zig-zag line and the exothecial cells are not collenchymatous. These sporophytic characters indicate that either the present systematic position of this species in *Distichophyllum* is not appropriate, or the validity of using these characters, especially the exostomial ornamentation (papillose versus striate), to discern between distichophylloid genera needs a re-evaluation.

Specimens of new record studied: CHINA: Yunnan Prov., Gongshan Co., Dulong Xiang, W slope of Gaoligong Shan, small valley with stream in subtropical forest, epiphyllous on large fern frond by stream, *ca* 1,735 m, 3 Sept 2006, *D.G. Long 36274* (E); Gongshan Co., Dulong River, 1,600 m, 22 Aug 1982, *Zang Mu 2938* (SINU). INDIA: Arunachal Pradesh, Abor, on tributary of the Egar stream, epiphyllous, at 3000 ft.,18 Jan 1912, *I.H. Burkill 36106* (SING).

Known distribution: India (Abor Hill), and China (Yunnan).

3.2.16. *Distichophyllum mittenii* Bosch & Sande Lac. (Figure 15)

Distichophyllum mittenii, *D. spathulatum* (Dozy & Molk.) Dozy & Molk. and *D. undulatum* Bosch & Sande Lac. are three species with overlapping characters. All have spathulate leaves with thin border consisting of 1(–2) row of cells at apex and a distinct band of smaller laminal cells near the margin in the upper half of the leaves. These species seem to be indistinguishable by only vegetative characters. According to Fleischer (1908) the main distinguishing character is sexuality: dioicous in *D. spathulatum* versus heteroicous in both *D. mittenii* and *D. undulatum*, consisting of bisexual perichaetia and male perigonia. Hence, Mohamed & Robinson (1991) interpreted wrongly that *D. mittenii* is autoicous, i.e., with archegonia and antheridia in separate gametoecia on the same plant. In fact, out of the four specimens cited by Mohamed & Robinson’s (1991) under *D. mittenii*, three are dioicous, thus, are *D. spathulatum* and one (*Manuel 2341*) is not found among the loan from KLU. Refer to treatment of *D. spathulatum* for more distinguishing features of these related taxa.

Distinguishing between *D. mittenii* and *D. undulatum* are more challenging. Fleischer (1908) separated them by size of laminal cells and leaf margins above, denticulate vis-à-vis entire. However the size range given in his descriptions for the two species overlaps and could not be used as the diagnostic character to separate the species with confidence. Studying the types would be critical in evaluating the true identity of *D. undulatum*.

Figure 15. Gametangia of ***Distichophyllum mittenii***: **a.** bud-like male perigonium; **b.** Bisexual perichaetium; based on *Wray 945* (SING); and ***D. spathulatum***: **c.** Long-stalked perigonium, **d.** Female perichaetium; based on *Mohamed & Damanhuri 5057* (KLU).

Mohamed & Robinson (1991) has excluded *D. undulatum* from Malaya. However, the following heteroicous Malayan specimen with weakly denticulate margin could well be *D. undulatum*: Malaysia, Kelantan, Dabong, Gunung Stong Forest Reserve, valley between the summit of Mount Stong and Mount Ayam, *ca* 1,080 m; lower montane forest to upper montane forest zone, on tree base, 27 May 2003, *K.T. Yong 4124* (KLU).

A specimen of *D. mittenii* from Sulawesi of Indonesia was reported as *D. spathulatum* (Ariyanti et al. 2009). However, the heteroeicy and morphology of the gametangia points its identity to *D. mittenii*, a new species record for Sulawesi.

Specimen of new record studied: INDONESIA: C. Sulawesi, trail to Mt. Nokilalaki from Tongoa Lore Lindu National Park; rotten wood, 1650 m. 22–26 Jun 2005, *N.S. Ariyanti 539* (SINU) [with *D. angustifolia*].

Known distribution: Widely distributed in East Asia, Sri Lanka, Indochina, Malesia, Australia (Queensland), Melanesia, and Polynesia. In Indonesia, reported from Sumatra, Java, Kalimantan Timur, Flores, Sulawesi and Papua.

3.2.17. ***Distichophyllum montagneanum*** (Müll. Hal.) Bosch & Sande Lac.

According to Mohamed & Robinson (1991), the main distinguishing character of the two gametophytically inseparable species, *D. maibarae* and *D. montagneanum*, is in the ornamentation of the calyptra. The calyptrae of *D. maibarae* possess long erect hairs whereas those in *D. montagneanum* are smooth. We have identified several collections from SW China and Nepal that belong to this group. Among them, four specimens were found to have (at least young) sporophytes with intact calyptra. The calyptrae are all smooth, and thus should be named *D. montagneanum* by definition of Mohamed & Robinson (1991) who suggested a restricted distribution of this species to India and Sri Lanka. On the other hand, a recent fertile Sri Lankan specimen of *D. montagneanum* (*Tan 04-077*, SING) has, instead, a calyptrae with long erect hairs near the apex. Moreover, an isotype (TNS) of *D. madurense* Thér. & P. de la Varde, a name sunk into synonymy of *D. montagneanum* by Townsend (1982), has a few young developing sporophytes with hairy calyptrae. In Japan, *D. maibarae* is reported and illustrated by Noguchi (1956) to have hairy calyptrae. Consequently, the validity of using calyptra hairiness to distinguish the two species is questionable. Future studies with the aid of DNA molecular data may help to unveil the relationships between *D. maibarae* and *D. montagneanum* Here, we tentatively report the four fertile specimens with smooth calyptra as *D. montagneanum*, new to China and Nepal, although *D. maibarae* is a common species in China (*fide* Lin & Tan 1995) and has been reported from Nepal by Gangulee (1977) erroneously as *D. sinuosulum* (see Tan & Robinson 1990).

Specimens of new record studied: NEPAL: Kangchenjunga, N-facing slopes of Dobala Danda above Kabeli Khola, on wet rocks by stream, *ca* 2,350 m, 28 Sep 1989, *D.G. Long 17388* (E); Sankhuwasabha district, forested ridge between Tashigaon and Kauma, on wet rocks under overhang, *ca* 2480 m. 25 Sep 1991, *D.G. Long 20566* (E). CHINA: Yunnan Prov., Gongshan Co., Dulong Xiang, Gaoligong Shan, W bank of Dulong Jiang, amongst mosses on shady dripping cliff face, *ca* 1,425 m, 5 Nov 2004, *D.G. Long 33943* (E); N bank of Dulong Jiang valley, on shady soil bank, *ca* 1,875 m, 30 Aug 2006, *D.G. Long 31635* (E).

Known distribution: Sri Lanka, India, Nepal, China (Yunnan), Vietnam, and Japan (Ryukyu).

3.2.18a. ***Distichophyllum nigricaule*** Mitt. ex Bosch & Sande Lac. var. ***nigricaule***

The specimens reported below were originally identified as either *Distichophyllum jungermannioides* or *Distichophyllidium jungermanniaceum* (also *Distichophyllidium jungermannioides*, see Akiyama 1990). However, *D. nigricaule*, in comparison, is a larger plant. For other distinguishing features of *D. jungermannioides*, please refer to the species treatment above.

Distichophyllum nigricaule has typically a number of rows of smaller submarginal cells in the upper 2/3 of leaves. The mostly broad elliptic to oblong leaves are never concave like those of *D. jungermannioides* and have a thicker border of 3–5 rows of linear cells.

Specimens of new record studied: INDONESIA: W. Seram, Kecamatan Seram Barat, stream-side on boulder, 760 m, 12 Aug 1986, *H. Akiyama C-15627*; Kecamatan Kairatu, stream-side on soil, 650 m, 18 Aug 1986, *H. Akiyama C-15775*; C. Seram, Kecamatan Tehoru, Manusela National Park, on soil, 110–810 m, 20 Jul 1986, *H. Akiyama C-14686*; on tree trunk base, *ca* 710 m, 30 Aug 1986, *Akiyama C-16305*; on tree trunk base, *ca* 1,670 m, 8 Sep 1986, *H. Akiyama C-16684* (all HYO).

Known distribution: Nepal, Japan (Ryukyu), China (Hainan, Taiwan), Vietnam, Thailand, Philippines (Batan, Luzon, Palawan), East and West Malaysia, Singapore, Indonesia (Sumatra, Java, Bali, Seram), and Papua New Guinea.

3.2.18b. ***Distichophyllum nigricaule*** var. ***cirratum*** (Renauld & Cardot) M.Fleisch.

The following specimens have leaves much crisped when dry and more rows of smaller sub-marginal cells, which are characteristic of the var. *cirratum*. This variety seems to be more common than the main variety in eastern Malesia.

Specimen of new record studied: INDONESIA: C. Seram, Kecamatan Tehoru, Manusela National Park, on humus, *ca* 1,720 m, 21 Feb 1985, *H. Akiyama C-10723* (HYO).

Known distribution: Nepal, Japan (Ryukyu), Taiwan, Philippines (Luzon), Thailand, Malaysia (Perak, Pahang, Sabah, Sarawak), and Indonesia (Sumatra, Java, Seram).

3.2.19. ***Distichophyllum osterwaldii*** M.Fleisch.

This is a distinctive species with a differentiated border disappearing above mid-leaf. It is apparently not a rare species but in Indonesia known only from Java. The species seems to have a close relationship with *D. mittenii* and *D. spathulatum*. They are all robust plants, with similar leaf outline and also have a size differentiation between submarginal and paracostal laminal cells (see Figure 13c). However, in *D. mittenii* and *D. spathulatum*, the leaf margins are completely bordered with at least one row of narrow elongated cell.

Specimens of new record studied: INDONESIA: Sumatra, highland of Brastagi, ascent from Lake Lao Kawar to Gunung Sinabung, Primary Rain forest, on rock, 1,720 m, 19 May 2005 *A. Schäfer-Verwimp & I. Verwimp 24990* (Hb. Schäfer-Verwimp); W. Seram, Kecamatan Kairatu, en route from Tihulale to the upper elevation of Gunung Totaniwel, streambed, 650 m, 18 Aug 1986, *H. Akiyama C-15765* (HYO); C. Seram, Kecamatan Tehoru, on boulder beside a stream, 110 m, 20 Jul 1986, *H. Akiyama C-14689*; on boulder covered with soil, 730 m, 24 Jul 1986, *H. Akiyama C-14884*; on boulder, 980 m, 27 Aug 1986, *H. Akiyama C-16162B*; *ca* 570m, 1 Sep 1986, *H. Akiyama C-16396*; on wet boulder, 730 m, 7 Sep 1986, *H. Akiyama C-16545* (HYO).

Known distribution: China (Guangxi, Taiwan), Japan (Ryukyu), Vietnam (Tam Dao), Philippines (Negros, Mindoro, Luzon, Leyte), Malaysia (Pahang, Sabah, Sarawak), and Indonesia (Sumatra, Java, Seram).

3.2.20. ***Distichophyllum schmidtii*** Broth.

A species of tropical lowland, *D. schmidtii* has oblong-ovate to obovate leaves and ± homogenous upper laminal cells. The specimen cited below was identified as *Distichophyllum nigricaule* var. *cirratum* in the herbarium. However, the latter has shorter ± oblong elliptic leaves that are much crisped when dry and laminal cell distinctly differentiated in size.

Distichophyllum schmidtii seems to be the only species of the genus recorded from Singapore and is probably extinct today on the island country. The plants were initially identified as *Distichophyllum singapurense* Dixon *nom. ined*. but Dixon changed his identifications later to *D. schmidtii*. The reported record of *D. gracilicaule* M.Fleisch., now a synonym of *D. nigricaule*, from Singapore by Johnson (1980), is most likely based on misidentification. The only Singapore specimen (*Holttum 18313B*, SING!) identified as *D. gracilicaule* collected from Bukit Timah, has only few small stems, and represents a juvenile or underdeveloped collection of *D. schmidtii*.

Specimen of new record studied: VIETNAM: Ha Tinh Province, Vu Quang Nature Reserve, between Vu Quang Village and Kim Quang Village, degraded roadside along Truoi River; degraded lowland rain forest, *ca* 25–180 m; 20 May 2002, *B.C. Tan 02-235* (SINU).

Known distribution: S. India, Bangladesh, Thailand, Vietnam (Ha Tinh), Malaysia (Kedah, Selangor, Pahang, Langkawi, Sarawak), and Singapore.

3.2.21. ***Distichophyllum spathulatum*** (Dozy & Molk.) Dozy & Molk. *Musci Frond. Ined. Archip. Ind.*4: 103, t. 34 et 35A. 1846. (Figure 15)

= *Distichophyllum macropodum* Dixon, *Ann. Bryol.* 5: 36. 1932b, ***syn. nov*. Type**: [Indonesia] Sumatra East Coast, Summit of Deleng Baroes, Karoland (Tanah Karo), 21 Jun 1927, *H.H. Bartlett 8505* (holotype BM!, isotypes BM!).

Apart from using sexuality to distinguishing between *D. spathulatum* and *D. mittenii* as outlined above in the treatment of *D. mittenii*, the gametangia in *D. spathulatum* seem to be unique and could be used for the species identification. The perigonia are consistently subtended on a conspicuous stalk and each resembles a typical tulip flower (Figure 15c, see also Tab. XXXIV: f. 5 in Dozy & Molkenboer, 1845–1848). They are quite common and easily seen in fresh plants. The perichaetial leaves are much elongated, about 3–5 times the length of the archegonia (Figure 15d), a character also noticed by Fleischer (1908). The gametangia of *D. mittenii* are also common, but more bud-like and without a distinct stalk. In addition, the perichaetial leaves are only about 2–3 times the length of the archaegonia. The differences of the two species are outlined in Table 7.

The types of *D. macropodum* Dixon consist of only robust female plants (thus, dioicous). The perichaetial leaves are much elongated like those of *D. spathulatum*, and the synonymy is hence proposed here. Dixon (1932b) has compared his species with *D.mittenii* and the main difference is in its exceptionally long seta, a character we consider variable.

In Malay Peninsula, *D. spathulatum* seems to be larger in plant size and more common than *D. mittenii*. However, no authentic specimens have, hitherto, been reported from adjacent Thailand. Similarly, only *D. mittenii* is known from the Philippines. However, we have come across a sterile collection from the Philippines, which consist of only few dioicous female plants with long perichaetial leaves, typical of *D. spathulatum*. Careful examination of *D. mittenii* from Philippines may probably prove that at least some reported specimens of *D. mittenii* are *D. spathulatum*. In Borneo, the species has been reported only once from Kalimantan Barat (Indonesia) (Brotherus 1928).

Table 7. Distinguishing features between *D. spathulatum* and *D. mittenii* from Fleischer (1908) and personal observation.

Features	*D. spathulatum*	*D. mittenii*
Sexuality	Dioicous	Heteroicous
Gametangia	♂ & ♀ on different plants	♂ + ⚥ on same plant (axis)
Perichaetial leaves	> 3× longer than archegonia	2–3× longer than archegonia
Perigonia	Conspicuously long stalked	Almost sessile

Specimens of new record studied: THAILAND: Nakhon Si Thammarat Province, San Yen, Khao Nan National Park, growing on base of tree trunk and rotten wood along a trail, 1,000–1,300 m, 18. Apr 2007, *S. Chantanaorrapint 1472*; 20 Apr 2007, *S. Chantanaorrapint 1570* (PSU). PHILIPPINES: Camiguin Island, Mt. Timpoong; montane forest, on wet rocks, 1,530 m, 28 Jun 2007, *V. Linis s.n*. (SING) [only a few plants mix with *D. cucullatum*]. MALAYSIA: Sabah, Mt. Kinabalu, on moist rotten log along trail in forest, 1,780 m, 19 Jan 1997, *H. Akiyama et al. 672*; on moist rotten log along stream, 19 Jan 1997, H. *Akiyama et al. 717* (BORH); Tambunan, Mahua, to Minunduk Sirung Hill, primary forest, partial shade, on rotten log, 1,127 m, 13 Dec 2003, *M. Suleiman 1392* (BORH); Tawau Hills Park, primary forest, by trail, on rotten log, 880 m, 18 Feb 2007, *M. Suleiman 1633* (BORH). INDONESIA: E. Kalimantan, Nunukan District, Krayan Subdistr., Pa' Raya Village, primary forest, in open area by stream, on decaying log, 990 m, 4 Apr 2003, *M. Suleiman 1077* (BORH) [Second report].

Known distribution: China (Taiwan), Thailand (Nakhon Si Thammarat), Malaysia (Pahang, Perak, Sabah), Philippines (Camiguin Is.), Indonesia (Sumatra, Java, Kalimantan, Sumbawa), Melanesia (New Caledonia), and Society Is. (Tahiti).

3.2.22a. *Distichophyllum subnigricaule* Broth. **var. *subnigricaule***

This species belongs to a group of *Distichophyllum* including *D. angustifolium* and *D. malayense* with large, hexagonal and thin-walled laminal cells. All three species have also leaves with thin differentiated border. Apart from the obovate to broadly lingulate leaves, *D. subnigricaule* could be distinguished from *D. angustifolium* by the short and weakly defined costa, and from *D. malayense* by the obtuse to rounded leaf tip.

Specimen of new record studied: INDONESIA: Sumatra, Barisan Range, Harau Valley, in shaded wet bank of riverine forest and wet sandstone cliff, July 2009, *B.C. Tan & Nana Hernawati s.n.* (SING, ANDA); C. Sulawesi, Air Terjun Salopa, 15 km W Tentena, on N-bank of Danau Poso, Montane rain forest, on tuff rocks by waterfall, Nov 1993, *F. Müller S93* (DR).

Known distribution: Philippines (Luzon, Leyte, Mindanao), Malaysia (Sabah), Indonesia (Seram, Java, Sulawesi), and Papua New Guinea.

3.2.22b. ***Distichophyllum subnigricaule* var. *hainanense*** P.J. Lin & B.C. Tan

The two specimens from Vietnam were identified as *D. mittenii* and *D. undulatum*. Both these two species have leaves with very narrow border and a large band of strongly differentiated narrow sub-marginal cells. The specimens, however, have wider border of 1–2 cells and only a few rows of slightly smaller cells near the margin. The larger leaf cells and the slightly serrulated margins resemble *D. obtusifolium*, but the latter has a poorly differentiated border at the apex. We therefore identified the two collections in question as *D. subnigricaule* var. *hainanense*.

Specimens of new record studied: VIETNAM: Vinh Phuc Province, Tam Dao, Yen my, on tree in lower montance evergreen forest, 1,200 m, 10 Dec 1968, *Tran Ninh 68204a* (EGR); Hòa Bình Province, Montes Núi Biêu, near Tu-Ly, on putrefied trunk in montane forest Nuí Vói, 500 m, 5 Jan 1966, *Pócs, T. & Tran Ninh 3148/s* (EGR).

Known distribution: The variety was reported before only for Hainan Island (China), and now in Vietnam.

3.2.23. ***Distichophyllum wanianum*** B.C.Tan & P.J.Lin (Figure 16)

In northern Thailand, *Distichophyllum wanianum* is rather common growing on branches and bark of trees in forest. The plants are small, with stems often measuring less than 10 mm long. The leaves are strongly crisped when dry. When wet, the leaves are broadly spathulate and narrow at base. The leaf apices are broadly round, obtuse, and occasionally with a small apiculus. The thick leaf margin is made up of two rows of linear cells. Laminal cells are round to hexagonal in shape. The Thai specimens produce plenty of filamentous gemmae on leaf costa, not seen in the Chinese specimen of this species. Setae of Thai specimens are smooth to slightly papillose distally.

Akiyama (2006) reported a specimen of *Distichophyllum* from Doi Inthanon as *D. obovatum* (Griff.) Paris, new to Thailand. The latter taxon is an Indian endemic in the Darjeeling and Khasia Hill area (Gangulee 1977). We could not locate the type of *D. obovatum* in BM, BR and NY. However, the Indian specimens of *D. obovatum* kept at NY are found to consist of two species. Four large plant specimens mounted on the same sheet and collected by Griffith from Thumathaya (*Griffith 27*, *371*, *372*, *s.n*, NY-Mitten) are the same as the original illustration of *D. obovatum* in the protologue [see Griffith 1849: Pl. XCIX, f. I(1)] with spathulate to obovate leaves and a distinctly papillose seta. Yet, one other specimen collected from Darjeeling named “*D. obovatum*” (*NICH 201055*), which was cited by Gangulee (1977) is a small plant with similar leaf outline, and has seta smooth to weakly papillose distally. The latter fits into our concept of *D. wanianum*. Hence, it is noteworthy to report that the illustration of *D. obovatum* in Gangulee (1977: Fig. 740) consists of a mixture of drawings of *D. obovatum* and *D. wanianum*.

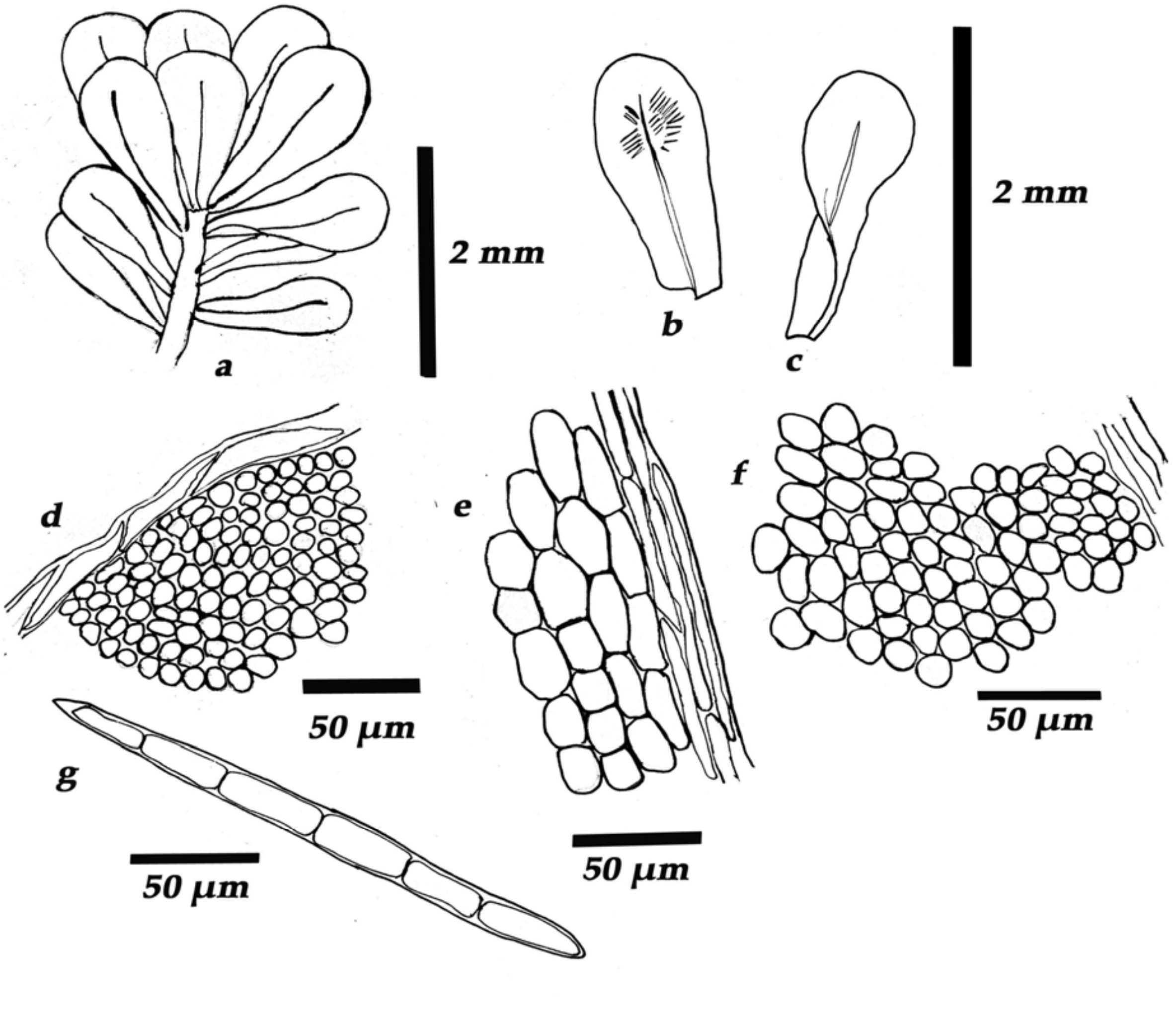

Figure 16. ***Distichophyllum wanianum***: **a.** Plant habit; **b–c**. Leaves; d. Leaf tip; **e.** Leaf base; **f.** Leaf cells; **g.** Gemma; based on *Y. Nathi 772* (BCU); drawn by YN.

Specimens of new record studied: INDIA: Darjeeling, Takdah, 1,660–1,700 m, 18 Apr 1960, *H. Hara, Togashi & Wada [ex NICH] 201055* (NY, TNS). THAILAND: Chiang Mai, Doi Inthanon, Kew Mae Pan and Ang Ka areas, on tree trunks and branches, *Y. Nathi 164, 204, 256, 772* (BCU, SING); Gipfelbereich, Primärwald mit *Rhododendron arboretum* ssp. *delavayi*, epiphytisch, 2,530 m, 7 Apr 2004, *A. Schäfer-Verwimp & I. Verwimp 23788/A* (Herb. Schäfer-Verwimp); 15 ha Plot, near Check Point 2, *ca* 1,650 m, on tree trunk, 27 Dec 2008, *H. Akiyama et al. 22* (HYO); on branch of fallen tree along a stream, 28 Dec 2008, *H. Akiyama et al. 122* & *134* (HYO); on tree trunk at ridge, 2 Jan 2009, *H. Akiyama et al. 317* (HYO).

Known distribution: India (Darjeeling), China (Guangdong, Hainan, Yunnan), and Thailand (Chiang Mai).

3.2.23. *Leskeodon seramensis* H. Akiyama

The genus *Leskeodon* as defined at present differs from *Distichophyllum* in having papillose exostome teeth. *Distichophyllidium* and *Daltonia* also have papillose exostome teeth, but are never complanate foliated like in *Leskeodon*. With majority of the species occurring in the neotropics, we agree with Tan & Robinson (1990) that the present definition of *Leskeodon* is probably heterogeneous.

The leaves of *L. seramensis* are oblong to obovate with cells hexagonal. In contrast to the spathulate leaved *L. acuminatus* (Bosch & Sande Lac.) M.Fleisch., its costa never reached the apex. Specimens of *L. seramensis* identified by Dr. Akiyama have a similar leaf shape but seem to have shorter leaf tip. However, these characters are unstable. Our Fujian specimen may belong to one of the little known species already described in Melanesia. However, due to the lack of knowledge in species of this region, and its similarity to the Seram plants, we are tentatively identifying the specimen as *L. seramensis*. Future studies may prove that *L. seramensis* is conspecific with one of the known species occurring in Melanesia.

Specimens of new record studied: FIJI: central part of Taveuni Island, NE side of Des Voeux Peak, on branches, 1,040–1,150 m, 27 Aug 2003, *S. & T. Pócs 03279/DB* (EGR) [with *D. graeffeanum*].

Known distribution: Philippines (Mindanao), Indonesia (Seram), Papua New Guinea (mainland and D'Entrecasteaux Islands), and Fiji.

Other notes:

1. Eddy (1996) in his treatment of *Splachnobryum* for the Handbook of Malesian Mosses, indicated that a specimen at BM which purported to be a duplicate of the type of *Splachnobryum wiemansii* M.Fleisch. is a small *Distichophyllum* species. However, the label of this specimen at BM was collected by Ruttner on 11.XI.1928, i.e., 20 years after the formal description of *S. wiemansii* in 1908, and thus cannot be the type. The material is clearly an acrocarpous moss with terminal perichaetia and thus also could not be a *Distichophyllum*. Moreover, the specimen was verified as *S. wiemansii* by Arts (2001) and cited it in his revision of the Splachnobryaceae.

2. The type specimen of *Distichophyllum pullei* Dixon, is unlike any *Distichophyllum*. The atypical rhomboid leaf cell areolation has already been pointed out by Dixon (1942) in his original description. In addition, its recurved lower leaf margin, excurrent costa, carinated lower half of leaf, clusters of gemmae on ventral side of middle costa, all fit to the concept of *Leskeodon acuminatus*. Thus we proposed here the new synonymy:

Leskeodon acuminatus (Bosch & Sande Lac.) M.Fleisch. *Musci Buitenzorg* 3: 971. 1908.

= *Distichophyllum pullei* Dixon *J. Bot.* 80: 28. 1942, ***syn. nov*****. Type:** [Indonesia, Papua,] Monte Parameles, on *Medinilla*, 1,200 m, 28 Jan 1912, *Pulle 480* (holotype, BM!)

--- <<End of Chapter 3>> ---

Chapter 4:

Proposal to conserve the name *Distichophyllum* Dozy & Molk. (Daltoniaceae) with a conserved type

A modified version has been submitted to “Taxon”.

Distichophyllum Dozy & Molk., *Musci Frond. Ined. Archip. Ind.* 99. 1846. *nom. cons. prop*.
Typus: *Distichophyllum spathulatum* (Dozy & Molk.) Dozy & Molk. (*Hookeria spathulata* Dozy & Molk., *Mniadelpus spathulatus* (Dozy & Molk.) Müll. Hal.), *typ. cons. prop.* (selected by Buck et al. 2005 [2004])

The genus *Distichophyllum* was first described in 1846 (see Dozy & Molkenboer, 1845–1848) including three new combinations, namely: *D. cuspidatum* (Dozy & Molk.) Dozy & Molk., *D. spathulatum* (Dozy & Molk.) Dozy & Molk., and *D. cristatum* (Hedw.) Dozy & Molk. [based on *Leskea cristata* Hedw. ≡ *Calyptrochaeta cristata* (Hedw.) Desv.], without specifying the type species. In addition, *Hookeria quadrifaria* Sm. (≡ *Achrophyllum quadrifarium* (Sm.) Vitt & Crosby), *Pterygophyllum microcarpon* (Hedw.) Brid. (≡ *Distichophyllum microcarpos* (Hedw.) Mitt.), and *Hookeria asplenioides* (Brid.) Steud. (≡ *Calyptrochaeta asplenioides* (Brid.) Crosby) were also mentioned in the discussion of *Distichophyllum* by Dozy & Molkenboer (1845–1848).

On the other hand, the genus *Calyptrochaeta* Desv. (1824) was created to replace *Chaetephora* Brid. *hom. illeg*. 1818, *non Chaetophora* Schrank 1783, to accommodate one species, *Chaetephora cristata* (Hedw.) Brid. (≡ *Leskea cristata* Hedw.). Hence, *Leskea cristata* Hedw. is unequivocally the type of *Calyptrochaeta*. Unfortunately, Dozy & Molkenboer (1845–1848) had included the names *C. cristata* (Hedw.) Brid. and *L. cristata* Hedw. under *Distichophyllum cristatum* (Hedw.) Dozy & Molk. The last mentioned taxon sensu Dozy & Molkenboer (1845–1848) is a misconstrued species of *Distichophyllum* and was subsequently corrected to *Eriopus remotifolia* (Müller, 1847) (≡ *Calyptrochaeta remotifolia*), and accepted by Dozy & Molkenboer (1861–1870) and Fleischer (1908).

Although taxonomically misinterpreted, the inclusion of the type species (*Leskea cristata* Hedw.) of another earlier genus (*Calyptrochaeta* Desv.) in the protologue of *Distichophyllum* has made the name superfluous and nomenclaturally illegitimate as defined in Art. 52.2. of the ICBN Vienna code (McNeill et al., 2006). Hence, *Distichophyllum* is automatically typified by *Leskea cristata* Hedw. under Art. 7.5. Therefore, the supposed lectotypification of the genus with *D. spathulatum* designated by Buck et al. (2005) is neither effective as the name already had a type, nor making the name legitimate according to Art. 6.4.

Since, the type of which ought to have been adopted has been overlooked in the past, *Mniadelphus* Müll. Hal. (1848) was generally accepted as illegitimate as it includes nearly all of *Distichophyllum* sensu Dozy & Molkenboer (1861–1870) (see Wijk et al. 1964.). *Mniadelphus* has since fallen into little use other than, in a few publications, as a section of *Distichophyllum*. However, the protologue of *Mniadelphus* (in Müller, 1848) did not include the element of the superfluity and illegitimacy of *Distichophyllum*. In fact, none of the four species first included in *Mniadelphus* (*Hookeria cuspidata* Dozy & Molk., *Hookeria spathulata* Dozy & Molk., *Hookeria quadrifaria* Hook. and *Pterygophyllum microcarpum* Brid.) is a type of a previously published generic name. The later selection of *H. quadrifaria* as the type of *Achrophyllum* (see Vitt & Crosby, 1972) does not affect the legitimacy of *Mniadelphus*. Consequently, *Mniadelphus* is legitimate according to the *Code*, contrary to previous general acceptance.

With the presumed illegitimacy of *Mniadelphus*, Buck et al. (2005) considered *Distichophyllum* sect. *Mniadelphus* Mitt. (1869) non Müll.Hal. (1848) as the first legitimate use of the name and proposed the latter to be a synonym of *Leskeodon* Broth. To formalise their nomenclatural interpretation, Buck et al. (2005) lectotypified *Distichophyllum* sect. *Mniadelphus* Mitt. with *M. auratus* Müll. Hal. (1850). However, since *Mniadelphus* is in fact legitimate, Mitten's (1869) name must be treated as a new combination, and require to be typified by an element from the protologue (Art. 7.4). The species *M. auratus* was described two years after *Mniadelphus*, and thus not included in its protologue (cf. Müller, 1848). Moreover, the same species has already been earlier selected as the lectotype of *Leskeodon* (Welch, 1966), a lectotypification that is generally overlooked. Although Crosby et al. (1985) have pointed out that Welch's choice of lectotype appears to be mechanically selected, having *M. auratus* as the lectotype of *Leskeodon* poses no conflict with its protologue (see Brotherus, 1907). Hence, the lectotypification of the section *Mniadelphus* proposed by Buck et al. (2005) cannot be accepted.

Instead of formally recognising the use of the section *Mniadelphus* by Mitten (1869) in having a different taxonomic concept sensu Müller (1848), it is best not to introduce further confusion by recognising the name in the original sense i.e. treating *Distichophyllum* and *Mniadelphus* as applying to the same taxonomic group of plants. To formalise this, *Mniadelphus cuspidatus* (≡ *D. cuspidatum*) is most appropriate to be selected as the lectotype as it was included in both the protologues of both genera and available for use.

> *Mniadelphus* Müll. Hal. *Linnaea* 21: 196. 1848*.* ≡ *Hookeria* sect. *Mniadelphus* (Müll. Hal.) Hook.f. & Wilson in Hook.f., Bot. Antarct. Voy. II (Fl. Nov. Zel.) 2: 122. 1854. ≡ *Distichophyllum* sect. *Mniadelphus* (Müll. Hal.) Mitt., *J. Linn. Soc., Bot.* 12: 393. 1869. ≡ *Hookeria* subg. *Mniadelphus* (Müll. Hal.) Hampe, *Verh. Zool. Bot. Ges. Wien* 21: 391. 1871.
> Typus: *Mniadelphus cuspidatus* (Dozy & Molk.) Müll.Hal. (*Hookeria cuspidata* Dozy & Molk., *Distichophyllum cuspidatum* (Dozy & Molk.) Dozy & Molk.), *hic designatus*.

Having the nomenclatural status of *Distichophyllum* and *Mniadelphus* resolved, it becomes clear that all current names under the former genus are illegitimate and ought to be transferred. With about 100 to 103 accepted species in the genus today (Crosby et al., 1999; see also http://www.tropicos.org/), the conservation of this large and well-established generic name *Distichophyllum* is here proposed, with the proposed conserved type, *D. spathulatum*, following the selection of Buck et al. (2005). Conserving the name would avoid replacing many species binomials in the genus that are of wide acceptance in publications, thus, maintaining the nomenclatural stability and preserving their long usage. Although currently ongoing phylogenetic research on *Distichophyllum* suggested that the genus is polyphyletic (see Chapter 2), a majority of the species would still belong together in the to-be-re-defined genus, *Distichophyllum*, after a revision.

-- <<End of Chapter 4>>--

Summary

Unbiased by human intuition in interpreting morphological criteria and by convergence of morphological traits, recent methods in molecular phylogeny is offering an independent option to guide our postulations on phylogeny. This is especially significant in evolutionary studies of mosses as morphological variations are rather limited and their phylogenetic relevance difficult to interpret. Past conflicting systems of classifications with emphasis on few morphologies on either generations of the plant life cycle has been exemplified in the Hookeriales. Recent phylogenetic studies based on DNA sequence data have repeatedly proven useful in the re-interpretation of evolutionary concepts in mosses (e.g. Huttunen et al., 2004; Olsson et al., 2009a, 2009b; Quandt et al., 2009; Sotiaux et al., 2009).

In the first study, the monophyly of the Hookeriales as currently circumscribed was confirmed with a sampling size of 122 taxa and a five-gene- sequence data representing three different genomes. The previous controversial position of the Hypopterygiaceae was also resolved within the order. The relationships of the families, in the greater part, have been resolved. At the generic level, several larger genera, especially within Daltoniaceae and Pilotrichaceae, are shown to be not monophyletic. Additionally six selected morphological characters (four gametophytic and two sporophytic ones), were scored to trace their evolution by means of ancestral state reconstruction in the resulting phylogeny. The common ancestor of the Hookeriales was reconstructed as having elimbate leaves, single costa, and a conspicuously striated outer exostome base without a furrow. From the study, it shows that the selected gametophytic features flared better in defining supported clades than the sporophytic ones. The many losses and regains of the exostome furrow were interpreted as reversals. Similarly, the presence of leaf costa(e), regardless of being single or double, is clearly a case of loss and gain of structure. It points to the fact that strong costae in unicostate leaves and bicostate ones are not homologous.

In Chapter 2, the phylogeny between and within genera in Daltoniaceae is inferred with the same approach as Chapter 1, but with significant increase in the sampling size within the family, especially in the genus *Distichophyllum*. This study also represents the first attempt to assess infra-generic relationships within *Achrophyllum* and *Calyptrochaeta*. The monophyly of both genera are proven but definitions of some crown species require re-evaluations. Within the core Daltoniaceae, relationships among the elimbate taxa (including *Ephemeropsis*) are generally resolved. Contrastingly, topology of the limbate taxa show various combined clades of species in *Daltonia*, *Distichophyllum* and *Leskeodon*, not in accordance with the traditional generic concepts. Attempt to re-organize these taxa is a major challenge. Transfers and combinations are not made without adequate statistical and known morphological supports. Similarly, no new genera are proposed in the absence of critical morphological evaluation. Nevertheless, nine new combinations are made including: *Beeveria microcarpos*, *Daltonia carinata*, *Da. meizhiae*, *Distichophyllum armatus*, *Leskeodon crispulus*, *L. ellipticum*, *L. fernandezianus*, *L. montagneanus*, and *L. rotundifolius*. *Distichophyllum acuminatum* is revived from *Leskeodon acuminatus* as the accepted name. *Distichophyllum decolyi*, and *D. maibarae* are proposed as new synonyms of *L. montagneanus*. *Distichophyllum hainanense* stat. nov. is elevated from a varietal level. Peristome types, particularly exostome ornamentations, are shown not useful for distinguishing genera at least in Daltoniaceae. Although considerable phylogenetic knowledge has been revealed, several significant nodes remains ambiguous. Critical generic revision is crucial to bridge the lacking morphological knowledge, especially circumscriptions of the newly recognize clades.

Chapter 3 presents the outcomes of re-confirming specimens for use in the molecular phylogenetic studies. In total, 24 new distributional records of species of *Distichophyllum* and allied genera in Asia and Australasia are reported along with several illustrations of the species. For each new species record, taxonomic, biogeographic and habitat notes, where appropriate, are included. Three new synonyms (*Distichophyllum cucullatum* E.B. Bartram, *D. macropodum* Dixon, and *D. pullei* Dixon) are proposed and several probable synonymies are pointed out.

The proposal to conserve the illegitimate name *Distichophyllum* with a conserved type *D. spathulatum* has been drafted and submitted to the nomenclature committee and awaits the decision and voting in the forthcoming XVIII International Botanical Congress, to be held in Melbourne, Australia, in July 2011.

In conclusion, the present dissertation covers research at different levels of classification and aspects with focus on *Distichophyllum*. This includes the phylogenetic studies of the order Hookeriales and the family Daltoniaceae, as well as resolving relationships between and within several genera. At a species levels, some taxonomical puzzles are resolved along with several new species records for countries and sub-regions. Attempts were also made to untangle some nomenclatural confusion and to assess their consequences due to earlier misinterpretations. Henceforth, several essential skills have been acquired during the course of this dissertation project.

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List of Abbreviations

26S	:	Large subunit of the nrDNA
BI	:	Bayesian Inference
BS	:	Bootstrap Support
ca.	:	circa
cf.	:	*confer* in Latin, meaning "compare" or "consult"
cpDNA	:	Chloroplast DNA
CTAB	:	Cetrimonium bromide $((C_{16}H_{33})N(CH_3)_3Br)$
DNA	:	Deoxyribonucleic acid
ESS	:	Effective Sample Size
GTR	:	general time reversible
I	:	proportion of invariant sites
IGS	:	Intergenenic spacer
Indel	:	Insertion-Deletion
ITS	:	Internal Transcribed Spacer of nrDNA
MCMC	:	Markov chain Monte Carlo algorithm
Mk1	:	model ("Markov k-state 1 parameter model
ML	:	Maximum Likelihood
MP	:	Maximum parsimony
mtDNA	:	Mitochrondrial DNA
n.v.	:	*non vidi* in Latin, meaning “not seen” (of specimens)
*nad*5	:	gene encoding subunit 5 of β-nicotinamide adenine dinucleotide (NADH) dehydrogenase
nrDNA	:	nuclear ribosomal DNA
PCR	:	Polymerase chain reaction
PI	:	number of parsimony informative characters
PP	:	Bayesian Posterior Probability
*rps*4	:	gene encoding ribosomal protein S4
Spec.	:	species
SPL	:	significant proportional likelihood
tRNA	:	Transfer ribonucleic acid
*trn*F	:	tRNA gene *trn*$\mathrm{F}_{\mathrm{GAA}}$ coding for Phenylalanine
*trn*L	:	tRNA gene *trn*$\mathrm{L}_{\mathrm{UAA}}$ coding for Leucine
*trn*LF	:	IGS between *trn*L and *trn*F, including *trn*L group 1 intron
*trn*S	:	tRNA gene *trn*$\mathrm{S}_{\mathrm{GGA}}$ coding for Serine

List of Symbols

= : heterotypic synonym, also known as taxonomic synonym

≡ : homotypic synonym, also known as nomenclatural synonym

! : specimen examined

Γ : gamma distribution of rates

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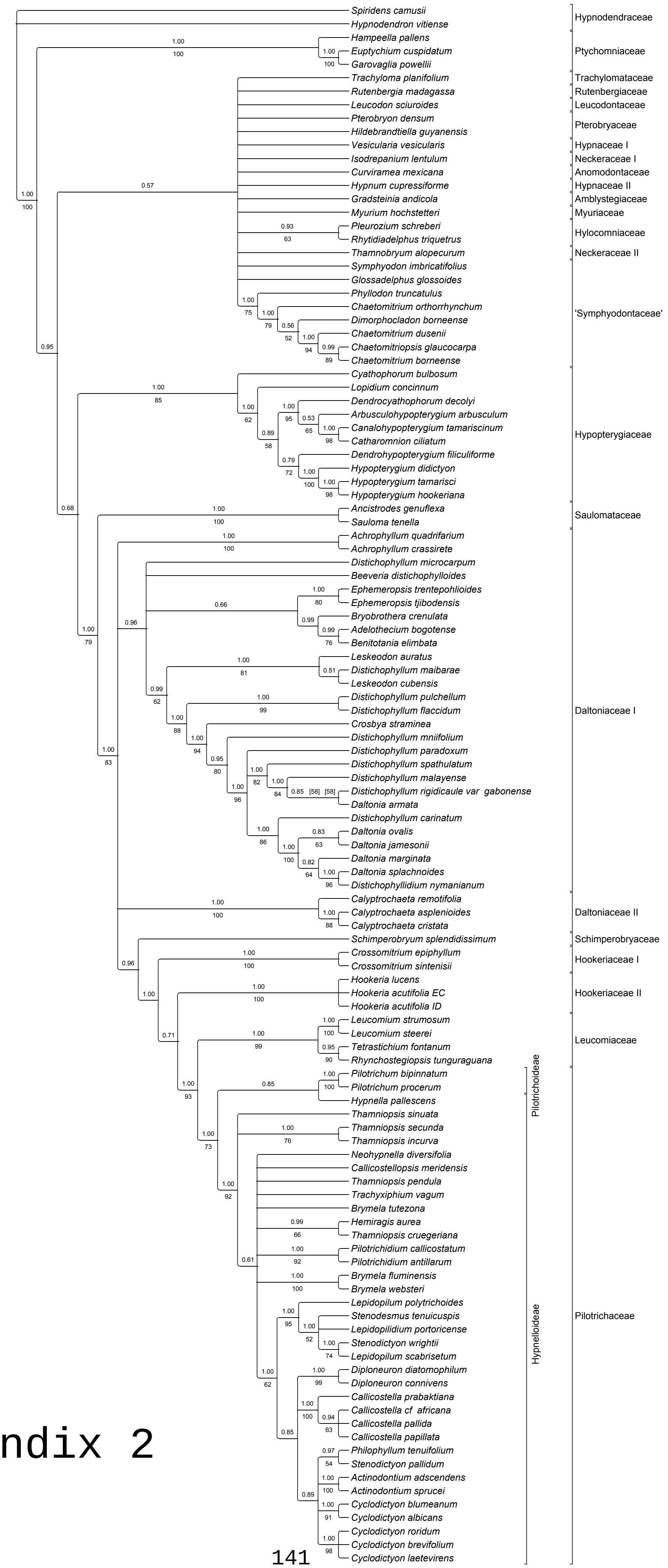
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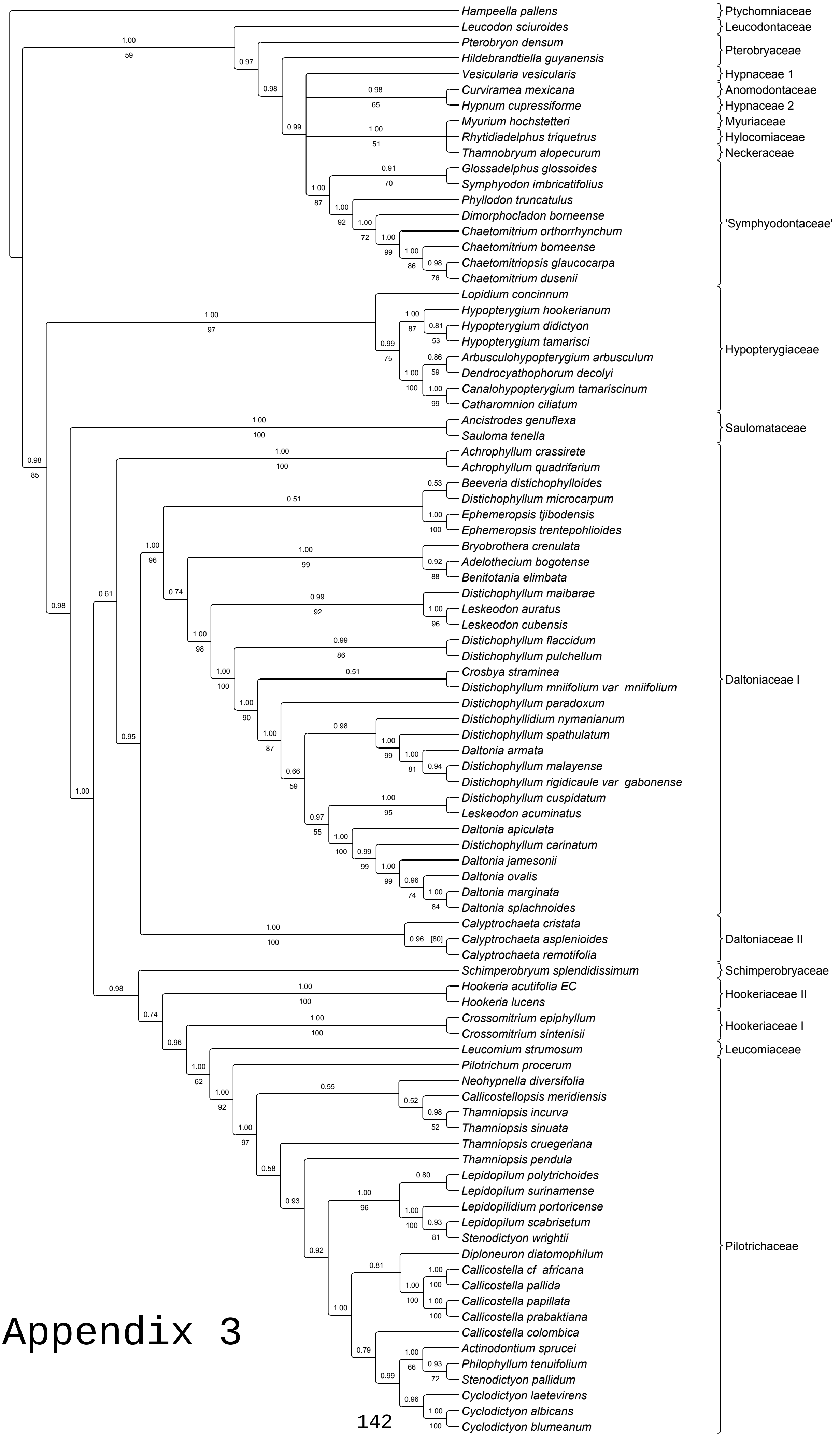
Callicostella papillata
Philophyllum tenuifolium
Stenodictyon pallidum
Actinodontium adscendens
Actinodontium sprucei
Cyclodictyon blumeanum
Cyclodictyon albicans
Cyclodictyon roridum
Cyclodictyon brevifolium
Cyclodictyon laetevirens
Hypnelloideae
Pilotrichaceae

Appendix 2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Pterobryaceae
0.98
Vesicularia vesicularis
Hypnaceae 1
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65
Curviramea mexicana
Anomodontaceae
Hypnum cupressiforme
Hypnaceae 2
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Myurium hochstetteri
Myuriaceae
Rhytidiadelphus triquetrus
Hylocomiaceae
Thamnobryum alopecurum
Neckeraceae
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Glossadelphus glossoides
Symphyodon imbricatifolius
1.00
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Phyllodon truncatulus
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92
Dimorphocladon borneense
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72
Chaetomitrium orthorrhynchum
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99
Chaetomitrium borneense
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86
Chaetomitriopsis glaucocarpa
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Chaetomitrium dusenii
'Symphyodontaceae'
Lopidium concinnum
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Hypopterygium hookerianum
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Hypopterygium didictyon
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Hypopterygium tamarisci
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Arbusculohypopterygium arbusculum
0.86
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Canalohypopterygium tamariscinum
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99
Catharomnion ciliatum
Hypopterygiaceae
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100
Ancistrodes genuflexa
Sauloma tenella
Saulomataceae
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Achrophyllum quadrifarium
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Distichophyllum microcarpum
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Ephemeropsis tjibodensis
Ephemeropsis trentepohlioides
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Bryobrothera crenulata
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Adelothecium bogotense
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Benitotania elimbata
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Distichophyllum maibarae
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Leskeodon auratus
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Leskeodon cubensis
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Distichophyllum flaccidum
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Distichophyllum pulchellum
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Distichophyllum mniifolium var mniifolium
Daltoniaceae I
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Distichophyllidium nymanianum
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1.00
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Distichophyllum spathulatum
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99
Daltonia armata
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Distichophyllum malayense
0.94
0.95
Distichophyllum rigidicaule var gabonense
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Distichophyllum cuspidatum
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Leskeodon acuminatus
1.00
0.97
55
Daltonia apiculata
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100
Distichophyllum carinatum
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Daltonia marginata
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Thamniopsis sinuata
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Lepidopilidium portoricense
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Lepidopilum scabrisetum
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Pilotrichaceae
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Callicostella pallida
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Callicostella papillata
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Callicostella prabaktiana
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Callicostella colombica
Actinodontium sprucei
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0.99
Stenodictyon pallidum
Cyclodictyon laetevirens
0.96
Cyclodictyon albicans
1.00
100
Cyclodictyon blumeanum

Appendix 3


Hypnodendron vitiense
Spiridens camusii
Hypnodendraceae
Hampeella pallens
Euptychium cuspidatum
Garovaglia powellii
Ptychomniaceae
Rutenbergia madagassa
Rutenbergiaceae
Trachyloma planifolium
Trachylomataceae
Leucodon sciuroides
Leucodontaceae
Pterobryon densum
Pterobryaceae
Curviramea mexicana
Anomodontaceae
Hypnum cupressiforme
Hypnaceae II
Isodrepanium lentulum
Neckeraceae I
Vesicularia vesicularis
Hypnaceae I
Gradsteinia andicola
Amblytheciaceae
Hildebrandtiella guyanensis
Pterobryaceae
Myurium hochstetteri
Myuriaceae
Pleurozium schreberi
Rhytidiadelphus triquetrus
Hylocomiaceae
Thamnobryum alopecurum
Neckeraceae II
Glossadelphus glossoides
Symphyodon imbricatifolius
Phyllodon truncatulus
Dimorphocladon borneense
Chaetomitrium orthorrhynchum
Chaetomitrium borneense
Chaetomitriopsis glaucocarpa
Chaetomitrium dusenii
'Symphyodontaceae'
Cyathophorum bulbosum
Lopidium concinnum
Arbusculohypopterygium arbusculum
Dendrocyathophorum decolyi
Canalohypopterygium tamariscinum
Catharomnion ciliatum
Dendrohypopterygium filiculiforme
Hypopterygium didictyon
Hypopterygium hookerianum
Hypopterygium tamarisci
Hypopterygiaceae
Ancistrodes genuflexa
Sauloma tenella
Saulomataceae
Achrophyllum quadrifarium
Achrophyllum crassirete
Beeveria distichophylloides
Distichophyllum microcarpum
Ephemeropsis tjibodensis
Ephemeropsis trentepohlioides
Bryobrothera crenulata
Adelothecium bogotense
Benitotania elimbata
Distichophyllum maibarae
Leskeodon auratus
Leskeodon cubensis
Distichophyllum flaccidum
Distichophyllum pulchellum
Crosbya straminea
Distichophyllum mniifolium var mniifolium
Distichophyllum paradoxum
Distichophyllidium nymanianum
Distichophyllum spathulatum
Distichophyllum rigidicaule var gabonense
Daltonia armata
Distichophyllum malayense
Distichophyllum cuspidatum
Leskeodon acuminatus
Daltonia apiculata
Distichophyllum carinatum
Daltonia jamesonii
Daltonia ovalis
Daltonia marginata
Daltonia splachnoides
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Calyptrochaeta asplenioides
Calyptrochaeta cristata
Daltoniaceae II
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Schimperobryaceae
Hookeria lucens
Hookeria acutifolia EC
Hookeria acutifolia ID
Hookeriaceae II
Crossomitrium epiphyllum
Crossomitrium sintenisii
Hookeriaceae I
Leucomium strumosum
Rhynchostegiopsis tunguraguana
Tetrastichium fontanum
Leucomiaceae
Pilotrichum andersonii
Pilotrichum bipinnatum
Pilotrichum procerum
Pilotrichoideae
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Thamniopsis secunda
Lepidopilidium laevisetum
Thamniopsis incurva
Callicostellopsis meridensis
Neohypnella diversifolia
Brymela tutezona
Hemiragis aurea
Thamniopsis cruegeriana
Thamniopsis pendula
Trachyxiphium vagum
Pilotrichidium antillarum
Pilotrichidium callicostatum
Brymela fluminensis
Brymela websteri
Lepidopilum surinamense
Lepidopilum polytrichoides
Lepidopilidium portoricense
Stenodesmus tenuicuspis
Lepidopilum scabrisetum
Stenodictyon wrightii
Diploneuron connivens
Diploneuron diatomophilum
Callicostella cf africana
Callicostella pallida
Callicostella papillata
Callicostella prabaktiana
Callicostella colombica
Trachyxiphium guadalupense
Cyclodictyon albicans
Cyclodictyon blumeanum
Cyclodictyon roridum
Cyclodictyon brevifolium
Cyclodictyon laetevirens
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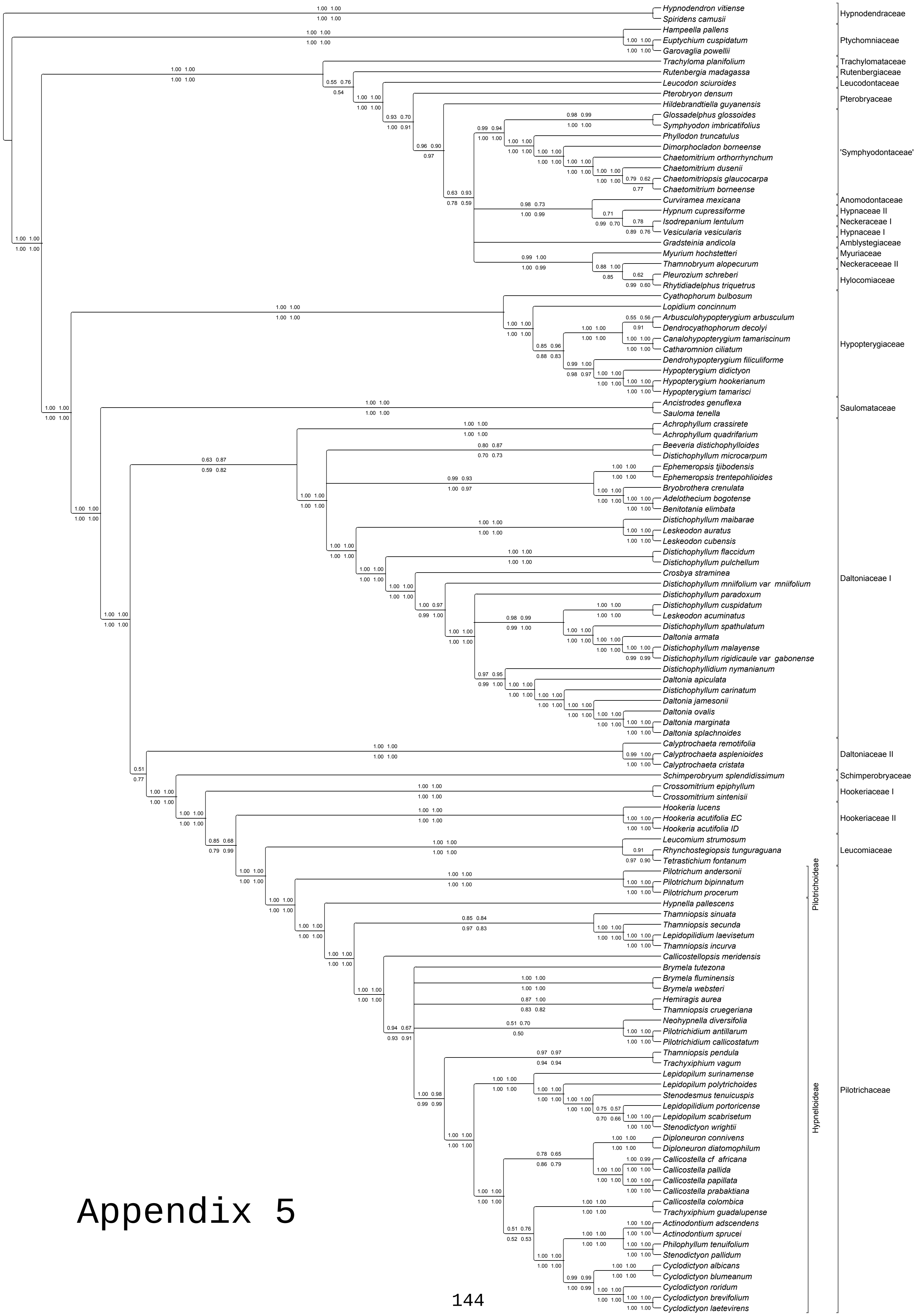
Hypnelloideae
Pilotrichaceae

Appendix 4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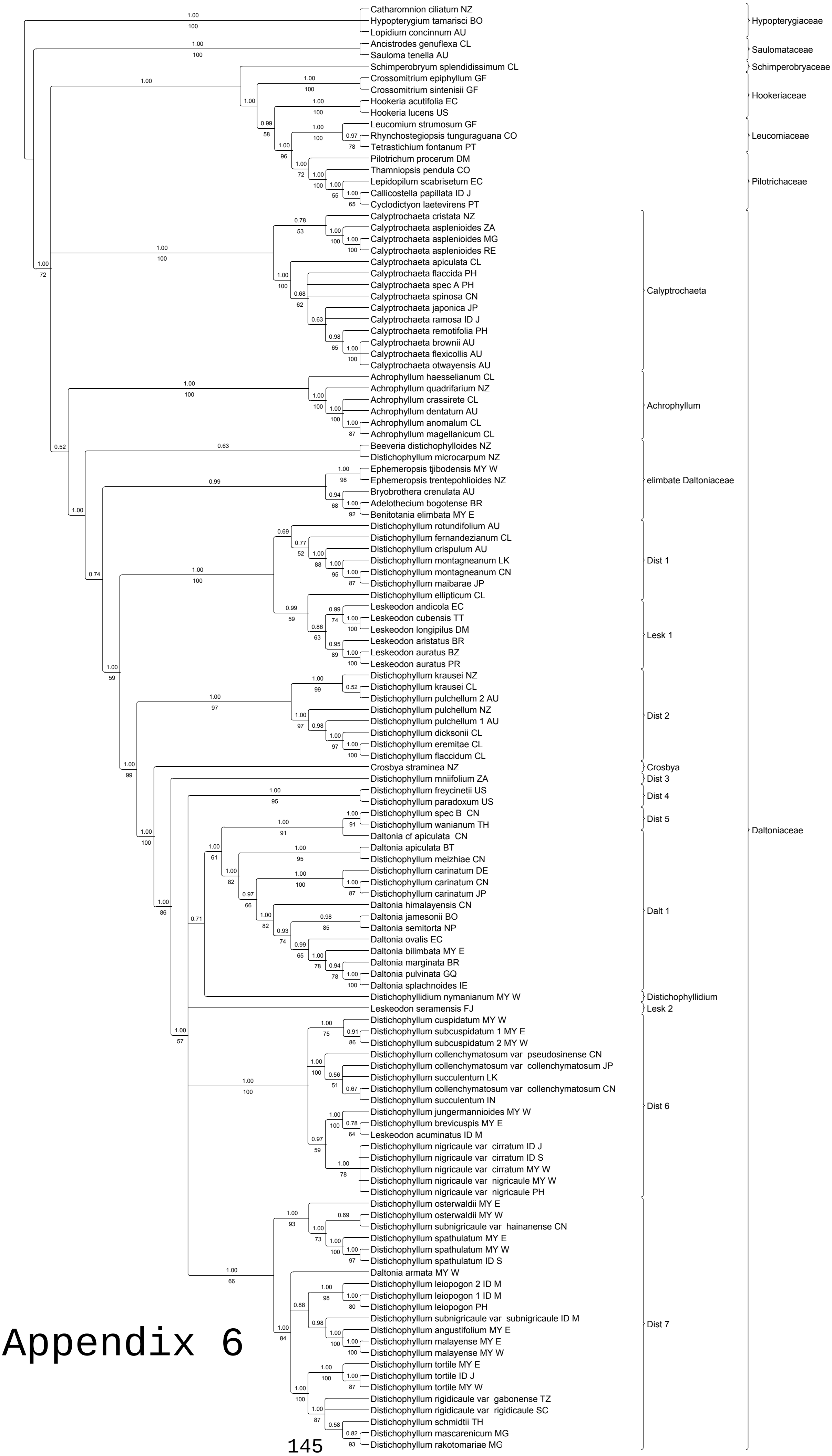
Rutenbergia madagassa
Leucodon sciuroides
Pterobryon densum
Hildebrandtiella guyanensis
Glossadelphus glossoides
Symphyodon imbricatifolius
Phyllodon truncatulus
Dimorphocladon borneense
Chaetomitrium orthorrhynchum
Chaetomitrium dusenii
Chaetomitriopsis glaucocarpa
Chaetomitrium borneense
Curviramea mexicana
Hypnum cupressiforme
Isodrepanium lentulum
Vesicularia vesicularis
Gradsteinia andicola
Myurium hochstetteri
Thamnobryum alopecurum
Pleurozium schreberi
Rhytidiadelphus triquetrus
Cyathophorum bulbosum
Lopidium concinnum
Arbusculohypopterygium arbusculum
Dendrocyathophorum decolyi
Canalohypopterygium tamariscinum
Catharomnion ciliatum
Dendrohypopterygium filiculiforme
Hypopterygium didictyon
Hypopterygium hookerianum
Hypopterygium tamarisci
Ancistrodes genuflexa
Sauloma tenella
Achrophyllum crassirete
Achrophyllum quadrifarium
Beeveria distichophylloides
Distichophyllum microcarpum
Ephemeropsis tjibodensis
Ephemeropsis trentepohlioides
Bryobrothera crenulata
Adelothecium bogotense
Benitotania elimbata
Distichophyllum maibarae
Leskeodon auratus
Leskeodon cubensis
Distichophyllum flaccidum
Distichophyllum pulchellum
Crosbya straminea
Distichophyllum mniifolium var mniifolium
Distichophyllum paradoxum
Distichophyllum cuspidatum
Leskeodon acuminatus
Distichophyllum spathulatum
Daltonia armata
Distichophyllum malayense
Distichophyllum rigidicaule var gabonense
Distichophyllidium nymanianum
Daltonia apiculata
Distichophyllum carinatum
Daltonia jamesonii
Daltonia ovalis
Daltonia marginata
Daltonia splachnoides
Calyptrochaeta remotifolia
Calyptrochaeta asplenioides
Calyptrochaeta cristata
Schimperobryum splendidissimum
Crossomitrium epiphyllum
Crossomitrium sintenisii
Hookeria lucens
Hookeria acutifolia EC
Hookeria acutifolia ID
Leucomium strumosum
Rhynchostegiopsis tunguraguana
Tetrastichium fontanum
Pilotrichum andersonii
Pilotrichum bipinnatum
Pilotrichum procerum
Hypnella pallescens
Thamniopsis sinuata
Thamniopsis secunda
Lepidopilidium laevisetum
Thamniopsis incurva
Callicostellopsis meridensis
Brymela tutezona
Brymela fluminensis
Brymela websteri
Hemiragis aurea
Thamniopsis cruegeriana
Neohypnella diversifolia
Pilotrichidium antillarum
Pilotrichidium callicostatum
Thamniopsis pendula
Trachyxiphium vagum
Lepidopilum surinamense
Lepidopilum polytrichoides
Stenodesmus tenuicuspis
Lepidopilidium portoricense
Lepidopilum scabrisetum
Stenodictyon wrightii
Diploneuron connivens
Diploneuron diatomophilum
Callicostella cf africana
Callicostella pallida
Callicostella papillata
Callicostella prabaktiana
Callicostella colombica
Trachyxiphium guadalupense
Actinodontium adscendens
Actinodontium sprucei
Philophyllum tenuifolium
Stenodictyon pallidum
Cyclodictyon albicans
Cyclodictyon blumeanum
Cyclodictyon roridum
Cyclodictyon brevifolium
Cyclodictyon laetevirens
Hypnodendraceae
Ptychomniaceae
Trachylomataceae
Rutenbergiaceae
Leucodontaceae
Pterobryaceae
'Symphyodontaceae'
Anomodontaceae
Hypnaceae II
Neckeraceae I
Hypnaceae I
Amblystegiaceae
Myuriaceae
Neckeraceeae II
Hylocomiaceae
Hypopterygiaceae
Saulomataceae
Daltoniaceae I
Daltoniaceae II
Schimperobryaceae
Hookeriaceae I
Hookeriaceae II
Leucomiaceae
Pilotrichoideae
Hypnelloideae
Pilotrichaceae

Appendix 5

Appendix 6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Sauloma tenella AU
Saulomataceae
Schimperobryum splendidissimum CL
Schimperobryaceae
Crossomitrium epiphyllum GF
Crossomitrium sintenisii GF
Hookeria acutifolia EC
Hookeria lucens US
Hookeriaceae
Leucomium strumosum GF
Rhynchostegiopsis tunguraguana CO
Tetrastichium fontanum PT
Leucomiaceae
Pilotrichum procerum DM
Thamniopsis pendula CO
Lepidopilum scabrisetum EC
Callicostella papillata ID J
Cyclodictyon laetevirens PT
Pilotrichaceae
Calyptrochaeta cristata NZ
Calyptrochaeta asplenioides ZA
Calyptrochaeta asplenioides MG
Calyptrochaeta asplenioides RE
Calyptrochaeta apiculata CL
Calyptrochaeta flaccida PH
Calyptrochaeta spec A PH
Calyptrochaeta spinosa CN
Calyptrochaeta japonica JP
Calyptrochaeta ramosa ID J
Calyptrochaeta remotifolia PH
Calyptrochaeta brownii AU
Calyptrochaeta flexicollis AU
Calyptrochaeta otwayensis AU
Calyptrochaeta
Achrophyllum haesselianum CL
Achrophyllum quadrifarium NZ
Achrophyllum crassirete CL
Achrophyllum dentatum AU
Achrophyllum anomalum CL
Achrophyllum magellanicum CL
Achrophyllum
Beeveria distichophylloides NZ
Distichophyllum microcarpum NZ
Ephemeropsis tjibodensis MY W
Ephemeropsis trentepohlioides NZ
Bryobrothera crenulata AU
Adelothecium bogotense BR
Benitotania elimbata MY E
elimbate Daltoniaceae
Distichophyllum rotundifolium AU
Distichophyllum fernandezianum CL
Distichophyllum crispulum AU
Distichophyllum montagneanum LK
Distichophyllum montagneanum CN
Distichophyllum maibarae JP
Dist 1
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Leskeodon andicola EC
Leskeodon cubensis TT
Leskeodon longipilus DM
Leskeodon aristatus BR
Leskeodon auratus BZ
Leskeodon auratus PR
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Distichophyllum krausei CL
Distichophyllum pulchellum 2 AU
Distichophyllum pulchellum NZ
Distichophyllum pulchellum 1 AU
Distichophyllum dicksonii CL
Distichophyllum eremitae CL
Distichophyllum flaccidum CL
Dist 2
Crosbya straminea NZ
Crosbya
Distichophyllum mniifolium ZA
Dist 3
Distichophyllum freycinetii US
Distichophyllum paradoxum US
Dist 4
Distichophyllum spec B CN
Distichophyllum wanianum TH
Daltonia cf apiculata CN
Dist 5
Daltonia apiculata BT
Distichophyllum meizhiae CN
Distichophyllum carinatum DE
Distichophyllum carinatum CN
Distichophyllum carinatum JP
Daltonia himalayensis CN
Daltonia jamesonii BO
Daltonia semitorta NP
Daltonia ovalis EC
Daltonia bilimbata MY E
Daltonia marginata BR
Daltonia pulvinata GQ
Daltonia splachnoides IE
Dalt 1
Distichophyllidium nymanianum MY W
Distichophyllidium
Leskeodon seramensis FJ
Lesk 2
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Distichophyllum subcuspidatum 1 MY E
Distichophyllum subcuspidatum 2 MY W
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Distichophyllum collenchymatosum var collenchymatosum JP
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Distichophyllum brevicuspis MY E
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Distichophyllum osterwaldii MY W
Distichophyllum subnigricaule var hainanense CN
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Distichophyllum angustifolium MY E
Distichophyllum malayense MY E
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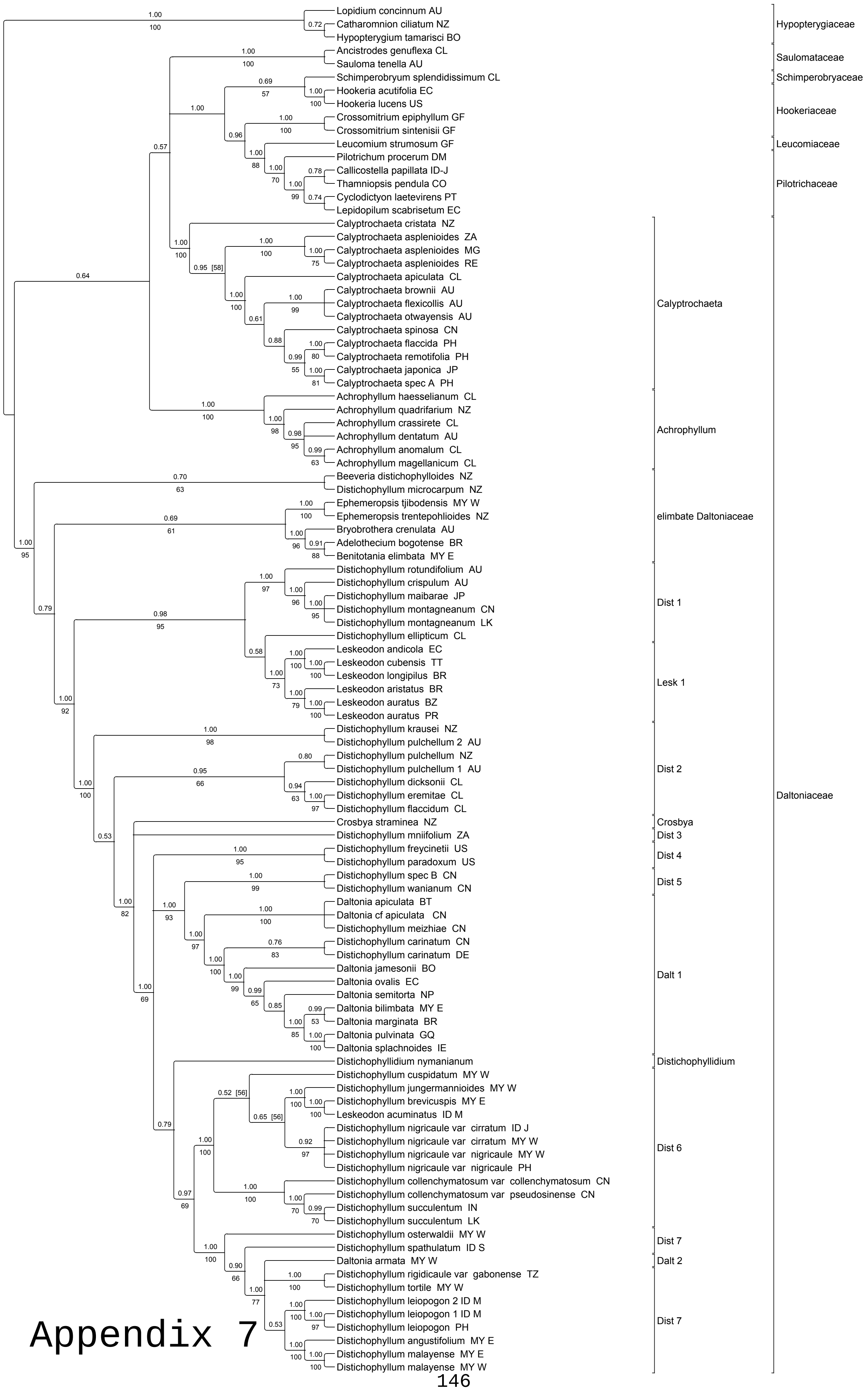
Daltoniaceae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Hookeria lucens US
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Leucomium strumosum GF
Pilotrichum procerum DM
Callicostella papillata ID-J
Thamniopsis pendula CO
Cyclodictyon laetevirens PT
Lepidopilum scabrisetum EC
Calyptrochaeta cristata NZ
Calyptrochaeta asplenioides ZA
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Calyptrochaeta asplenioides RE
Calyptrochaeta apiculata CL
Calyptrochaeta brownii AU
Calyptrochaeta flexicollis AU
Calyptrochaeta otwayensis AU
Calyptrochaeta spinosa CN
Calyptrochaeta flaccida PH
Calyptrochaeta remotifolia PH
Calyptrochaeta japonica JP
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Achrophyllum haesselianum CL
Achrophyllum quadrifarium NZ
Achrophyllum crassirete CL
Achrophyllum dentatum AU
Achrophyllum anomalum CL
Achrophyllum magellanicum CL
Beeveria distichophylloides NZ
Distichophyllum microcarpum NZ
Ephemeropsis tjibodensis MY W
Ephemeropsis trentepohlioides NZ
Bryobrothera crenulata AU
Adelothecium bogotense BR
Benitotania elimbata MY E
Distichophyllum rotundifolium AU
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Distichophyllum dicksonii CL
Distichophyllum eremitae CL
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Crosbya straminea NZ
Distichophyllum mniifolium ZA
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Daltonia marginata BR
Daltonia pulvinata GQ
Daltonia splachnoides IE
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Distichophyllum cuspidatum MY W
Distichophyllum jungermannioides MY W
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Distichophyllum malayense MY E
Distichophyllum malayense MY W
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Saulomataceae
Schimperobryaceae
Hookeriaceae
Leucomiaceae
Pilotrichaceae
Calyptrochaeta
Achrophyllum
elimbate Daltoniaceae
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Dist 2
Crosbya
Dist 3
Dist 4
Dist 5
Dalt 1
Distichophyllidium
Dist 6
Dist 7
Dalt 2
Dist 7
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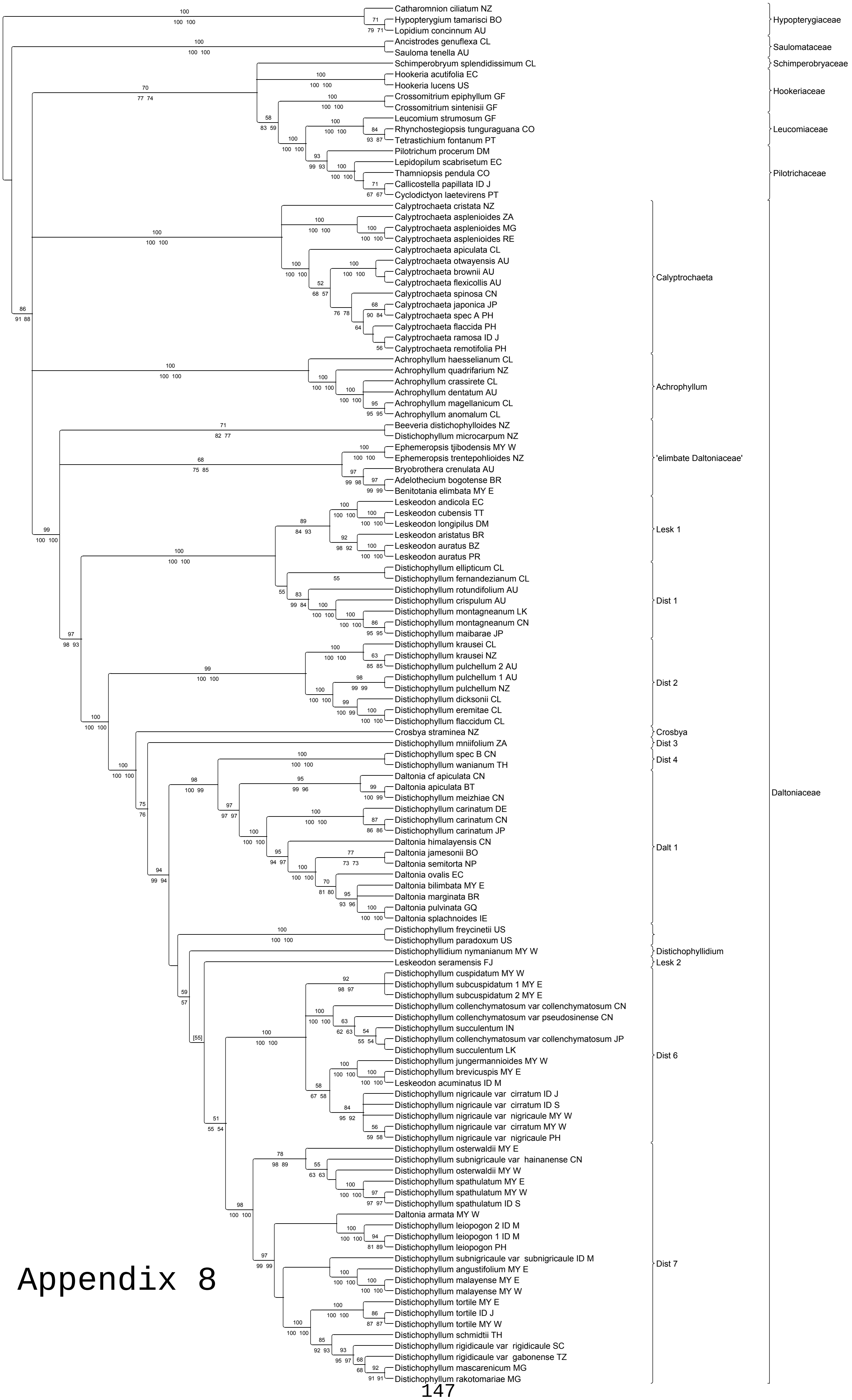
Appendix 7

Appendix 8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Hookeria lucens US
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Crossomitrium sintenisii GF
Leucomium strumosum GF
Rhynchostegiopsis tunguraguana CO
Tetrastichium fontanum PT
Pilotrichum procerum DM
Lepidopilum scabrisetum EC
Thamniopsis pendula CO
Callicostella papillata ID J
Cyclodictyon laetevirens PT
Calyptrochaeta cristata NZ
Calyptrochaeta asplenioides ZA
Calyptrochaeta asplenioides MG
Calyptrochaeta asplenioides RE
Calyptrochaeta apiculata CL
Calyptrochaeta otwayensis AU
Calyptrochaeta brownii AU
Calyptrochaeta flexicollis AU
Calyptrochaeta spinosa CN
Calyptrochaeta japonica JP
Calyptrochaeta spec A PH
Calyptrochaeta flaccida PH
Calyptrochaeta ramosa ID J
Calyptrochaeta remotifolia PH
Achrophyllum haesselianum CL
Achrophyllum quadrifarium NZ
Achrophyllum crassirete CL
Achrophyllum dentatum AU
Achrophyllum magellanicum CL
Achrophyllum anomalum CL
Beeveria distichophylloides NZ
Distichophyllum microcarpum NZ
Ephemeropsis tjibodensis MY W
Ephemeropsis trentepohlioides NZ
Bryobrothera crenulata AU
Adelothecium bogotense BR
Benitotania elimbata MY E
Leskeodon andicola EC
Leskeodon cubensis TT
Leskeodon longipilus DM
Leskeodon aristatus BR
Leskeodon auratus BZ
Leskeodon auratus PR
Distichophyllum ellipticum CL
Distichophyllum fernandezianum CL
Distichophyllum rotundifolium AU
Distichophyllum crispulum AU
Distichophyllum montagneanum LK
Distichophyllum montagneanum CN
Distichophyllum maibarae JP
Distichophyllum krausei CL
Distichophyllum krausei NZ
Distichophyllum pulchellum 2 AU
Distichophyllum pulchellum 1 AU
Distichophyllum pulchellum NZ
Distichophyllum dicksonii CL
Distichophyllum eremitae CL
Distichophyllum flaccidum CL
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Distichophyllum mniifolium ZA
Distichophyllum spec B CN
Distichophyllum wanianum TH
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Daltonia apiculata BT
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Distichophyllum carinatum CN
Distichophyllum carinatum JP
Daltonia himalayensis CN
Daltonia jamesonii BO
Daltonia semitorta NP
Daltonia ovalis EC
Daltonia bilimbata MY E
Daltonia marginata BR
Daltonia pulvinata GQ
Daltonia splachnoides IE
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Distichophyllum paradoxum US
Distichophyllidium nymanianum MY W
Leskeodon seramensis FJ
Distichophyllum cuspidatum MY W
Distichophyllum subcuspidatum 1 MY E
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Distichophyllum succulentum IN
Distichophyllum collenchymatosum var collenchymatosum JP
Distichophyllum succulentum LK
Distichophyllum jungermannioides MY W
Distichophyllum brevicuspis MY E
Leskeodon acuminatus ID M
Distichophyllum nigricaule var cirratum ID J
Distichophyllum nigricaule var cirratum ID S
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Distichophyllum nigricaule var cirratum MY W
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Distichophyllum subnigricaule var hainanense CN
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Distichophyllum spathulatum MY E
Distichophyllum spathulatum MY W
Distichophyllum spathulatum ID S
Daltonia armata MY W
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Distichophyllum leiopogon 1 ID M
Distichophyllum leiopogon PH
Distichophyllum subnigricaule var subnigricaule ID M
Distichophyllum angustifolium MY E
Distichophyllum malayense MY E
Distichophyllum malayense MY W
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Distichophyllum tortile ID J
Distichophyllum tortile MY W
Distichophyllum schmidtii TH
Distichophyllum rigidicaule var rigidicaule SC
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Distichophyllum mascarenicum MG
Distichophyllum rakotomariae MG
Hypopterygiaceae
Saulomataceae
Schimperobryaceae
Hookeriaceae
Leucomiaceae
Pilotrichaceae
Calyptrochaeta
Achrophyllum
'elimbate Daltoniaceae'
Lesk 1
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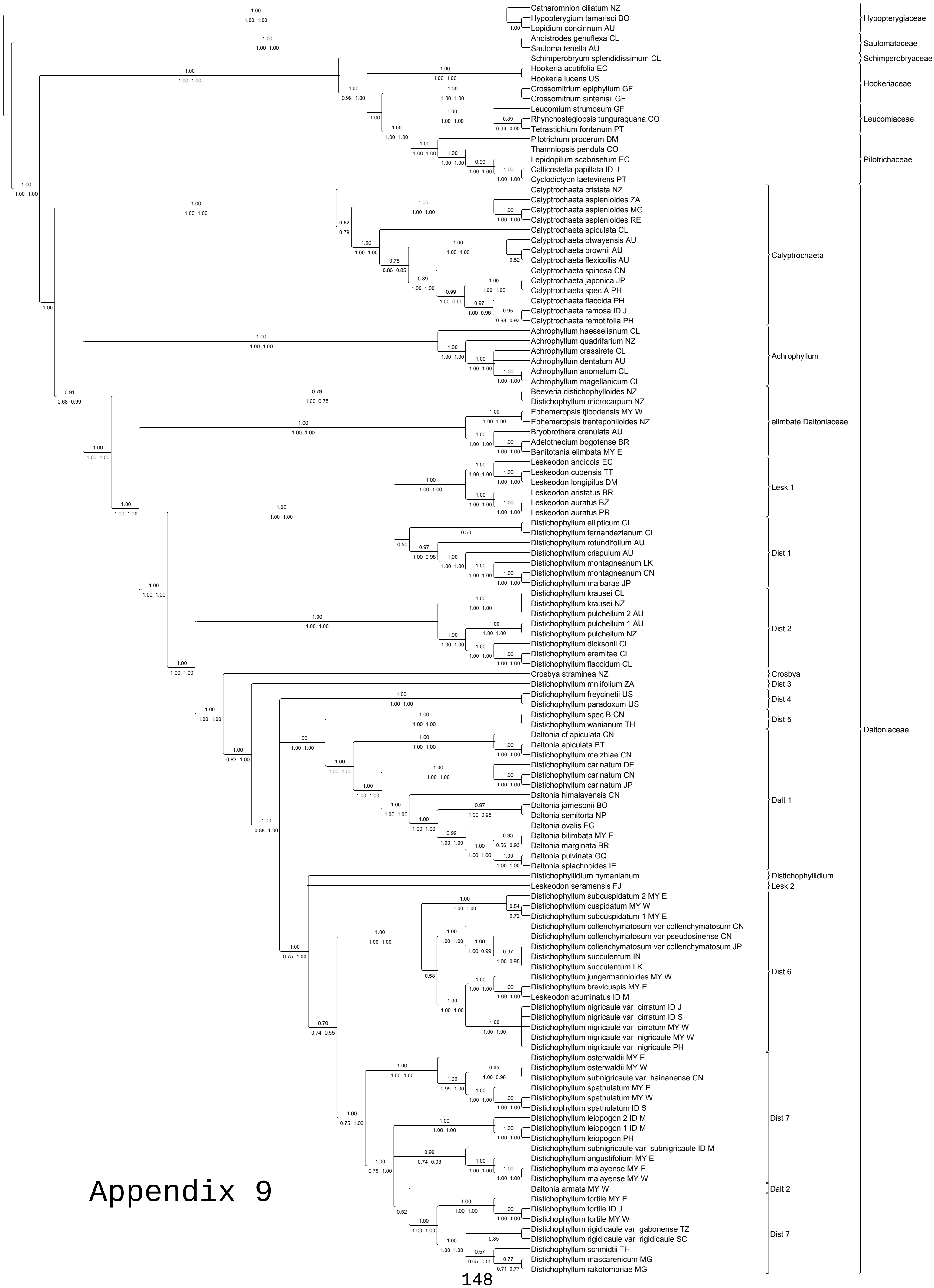
Dist 2
Crosbya
Dist 3
Dist 4
Dalt 1
Distichophyllidium
Lesk 2
Dist 6
Dist 7
Daltoniaceae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Dist 1
Distichophyllum krausei CL
Distichophyllum krausei NZ
Distichophyllum pulchellum 2 AU
Distichophyllum pulchellum 1 AU
Distichophyllum pulchellum NZ
Distichophyllum dicksonii CL
Distichophyllum eremitae CL
Distichophyllum flaccidum CL
Dist 2
Crosbya straminea NZ
Crosbya
Distichophyllum mniifolium ZA
Dist 3
Distichophyllum freycinetii US
Distichophyllum paradoxum US
Dist 4
Distichophyllum spec B CN
Distichophyllum wanianum TH
Dist 5
Daltonia cf apiculata CN
Daltonia apiculata BT
Distichophyllum meizhiae CN
Distichophyllum carinatum DE
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Daltonia himalayensis CN
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Daltonia semitorta NP
Daltonia ovalis EC
Daltonia bilimbata MY E
Daltonia marginata BR
Daltonia pulvinata GQ
Daltonia splachnoides IE
Dalt 1
Daltoniaceae
Distichophyllidium nymanianum
Distichophyllidium
Leskeodon seramensis FJ
Lesk 2
Distichophyllum subcuspidatum 2 MY E
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Distichophyllum spathulatum ID S
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Distichophyllum leiopogon 1 ID M
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Distichophyllum subnigricaule var subnigricaule ID M
Distichophyllum angustifolium MY E
Distichophyllum malayense MY E
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Dist 7
Daltonia armata MY W
Dalt 2
Distichophyllum tortile MY E
Distichophyllum tortile ID J
Distichophyllum tortile MY W
Distichophyllum rigidicaule var gabonense TZ
Distichophyllum rigidicaule var rigidicaule SC
Distichophyllum schmidtii TH
Distichophyllum mascarenicum MG
Distichophyllum rakotomariae MG
Dist 7

Appendix 9

Curriculum Vitae

ACADEMIC QUALIFICATIONS

since April 2007	pursuing a Ph.D. at Nees-Institut für Biodiversität der Pflanzen Rheinische Friedrich-Wilhelms-Universität Bonn, Germany Scholarship from the DAAD. Supervised by Prof. Dr. Jan-Peter Frahm & Prof. Dr. Dietmar Quandt
Jan 2003 – July 2004	M.Sc. in Biology — Plant Biodiversity and Natural Products, Faculty of Mathematics and Natural Sciences, Leiden University, The Netherlands. ECTS: 8.0 on a 10.0 scale Scholarship from the former ARCBC (currently the ACB) Thesis (minor): *Oleandra sibbaldii* (Polypodiopsida) species complex from East Malesia and the Pacific Islands (Apr – July 2003) Supervised by Dr. Peter Hovenkamp Research project (major): Taxonomy of the genus *Calyptrochaeta* (Daltoniaceae, Bryopsida) in Malesia and adjacent areas (Aug 2003 – Jul 2004)

	Supervised by Dr. Peter Hovenkamp, Dr. Andries Touw & Dr. Hans (J.D.) Kruijer
July 1998 – June 2002	B.Sc. in Biology with Honours (second class lower) National University of Singapore Major: Biology; Minor: Agrotechnology; Concentration: Plant Biology Overall CAP: 4.14 on a 5.00 scale Honour's thesis (final year): A comparative study of moss biodiversity in selected lowland rain forests in Johor (Malaysia) and Singapore (June – Oct 2001) Supervised by Assoc. Prof. Dr. Benito C. Tan
1994 – 1995	GCE 'A' Level at Jurong Junior College
1990 – 1993	GCE 'O' Level at Monk's Hill Secondary School
1984 – 1989	PSLE at Princess Elisabeth Primary School

OTHER TRAINING EXPERIENCES

6–16 Sep 2005	Third Regional Training Course on Biodiversity and Conservation of Bryophytes and Lichens, organised by the Southeast Asian Regional Center for Tropical Biology (SEAMEO BIOTROP); held at Bogor, Indonesia
7 July to 17 Aug 2002	ASEAN Regional Centre for Biodiversity Conservation (ARCBC), Research Center for Biology the Indonesian Institute of Sciences (LIPI), Nationaal Herbarium Nederland, Leiden University; held at Bogor, Indonesia

SYMPOSIA ATTENDED AND POSTER /PAPER PRESENTED

22–26 June, 2009	Hennig XXVIII Conference, organised by National University of Singapore and the Singapore Botanic Gardens (National Parks Board); held at Singapore Botanic Gardens

	Poster: Backbone Phylogeny of the Moss order Hookeriales (Bryopsida) [by L. Pokorny M., B.C. Ho, J.-P. Frahm, D. Quandt & A.J. Shaw]
28 Feb –2 Mar 2008	First regional Conference on Endangered Asian Bryophytes organised by IUCN & International Association of Bryology (IAB); held at Singapore Botanic Gardens
23–27 July 2007	World Conference of Bryology 2007: Bryology in Asia in the New Millennium, organised by IAB & University of Malaya, Kuala Lumpur, Malaysia; held at Kuala Lumpur Poster 1: New, Important Morpho-Anatomical Characters for Delimitation and Identification of Malesian *Calyptrochaeta* Species [by B.C. Ho & Hans Kruijer]; **Received the “Best Poster Award”** Poster 2: The Moss Diversity of Mount Kerinci and Mount Tujuh in Sumatra, Indonesia [by Hernawati & B.C. Ho]
17–22 Jun 2007	7th International Flora Malesiana Symposium, organised by Hortus Botanicus & Leiden University, Leiden, The Netherlands Paper: Taxonomy of the Genus *Calyptrochaeta* (Daltoniaceae, Musci) in Malesia and adjacent areas [by B.C. Ho & Hans Kruijer]
6–8 Sep 2004	Pleurocarpous Mosses: Systematics and Evolution, organised by Department of Biodiversity and Systematic Biology, National Museum and Gallery, Cardiff, Wales, United Kingdom; held in Cardiff. Poster: Growth Patterns in *Calyptrochaeta* Desv. [by B.C. Ho & Hans Kruijer]
9 Mar 2004	Ancient DNA organised by Leiden University, The Netherlands
16–17 Feb 2004	Plants in Health and Culture organised Leiden University, The Netherlands

WORK EXPERIENCES

25 Feb –3 Mar 2008	Secretary for the First regional Conference on Endangered Asian Bryophytes; Singapore Botanic Gardens, National Parks Board, Singapore
28–31 Jul 2007	Guide for post-IAB-conference fieldtrip to Cibodas & Bogor Botanical Gardens, Java; International Association of Bryology (IAB) & University of Malaya, Kuala Lumpur, Malaysia
Dec 2005 – Aug 2006	Secretariat for the 4th International Symposium on the Family Zingiberaceae; Singapore Botanic Gardens, National Parks Board, Singapore
Jan 2005 – Jul 2006	Part-time teaching assistant; National University Singapore, Dept Biological Sciences
Sep – Oct 2004	Part-time curatorial assistant; Singapore Herbarium (SING)
Sep – Nov 2002	Part-time student assistant; National Parks Board, Singapore
Sep – Nov 2002	Computer entry manager for Interactive Malesian Moss Database; ASEAN Regional Centre for Biodiversity Conservation (ARCBC)

PUBLICATIONS

Ho, B.-C. & J.D. (Hans) Kruijer. Taxonomy of the Genus *Calyptrochaeta* (Daltoniaceae, Musci) from Malesia and adjacent areas. *Blumea* (in prep.)

Ho, B.-C., B.C. Tan & J.-P. Frahm. Proposal to conserve the name *Distichophyllum* Dozy & Molk. (Daltoniaceae) with a conserved type. *Taxon* (submitted)

Frahm, J.-P. & B.C. Ho. 2010. Discovery of a natural hybrid between *Bruchia vogesiaca* Schwägr. and *Trematodon ambiguus* (Hedw.) Hornsch. (Musci, Bruchiaceae). *Cryptogamie Bryologie* (in press)

Ho. B.-C., B.C. Tan & Y. Nathi. 2010. New and Noteworthy records of *Distichophyllum* (Daltoniaceae, Bryopsida) and allied genera in Asia and Australasia. *Tropical Bryology* 31: 106–122.

Frahm, J.-P., B.J. O'Shea & B.C. Ho. 2009. The Moss Flora of Mauritius. *Archive for Bryology* 51: 1–26.

Ho, B.-C. & B.C. Tan. 2009. Does the Moss Genus *Lepidopilum* (Brid.) Brid. (Pilotrichaceae) Occur in Asia? *Gardens Bulletin Singapore* 60(2): 177–181.

Frahm, J.-P. & B.-C. Ho. 2009. A new contribution to the moss flora of the Inner Seychelles. *Archive for Bryology* 38: 1–16.

Frahm, J.-P. & B.-C. Ho. 2009. Die Moose in den Gewächshäusern des Botanischen Gartens Bonn. (in German: “The Bryophytes in the greenhouses of the Botanic Garden Bonn”). *Archive for Bryology* 37: 1–17.

Tan, B.C. & B.-C. Ho. 2008. *A guide to the mosses of Singapore*. Science Centre Singapore, 149 pp.

Tan, B.C. & B.-C. Ho. 2008. Bryophytes. In: G.W.H. Davison, P.K.L. Ng & H.C. Ho (eds.), *The Singapore Red Data Book — Threatened Plants & Animals of Singapore, 2nd ed*. , pp. 17–19, 209. The Nature Society (Singapore).

Ho, B.-C. & J.D. (Hans) Kruijer. 2007. Growth Patterns in *Calyptrochaeta* Desv. (Daltoniaceae). In: A.E. Newton & R. Tangney (eds.), *Pleurocarpous mosses: Systematics and Evolution*. Systematics Association Special Volume Series 71, Chapter 5: 111–115. CRC Press, Boca Raton

Tan, B.C., B.-C. Ho, V. Linis, E.A.P. Iskandar, I. Nurhasanah, L. Damayanti, S. Mulyati & I. Haerida. 2006. Mosses of Gunung Halimun National Park, West Java, Indonesia. *Reinwardtia*, 12: 205–214.

Ho, B.-C., B.C. Tan & N.S. Hernawati. 2006. A Checklist of Mosses of Sumatra, Indonesia. *Journal of the Hattori Botanical Laboratory* 100: 143–190.

Tan, B.C. & B.-C. Ho. 2005. Ridley and Mosses. *Gardenwise* (newsletter) 25:16–17.

Gradstein, S.R., B.C. Tan, R.-L. Zhu, B.-C. Ho, C.S.-H. King, C. Drübert, R. Pitopang. 2005. A catalogue of the bryophytes of Sulawesi, Indonesia. *Journal of the Hattori Botanical laboratory,* 98: 213–257.

Tan, B.C., B.-C. Ho & B. Seah K.-B. 2004. Two new moss species, *Trichosteleum fleischeri* and *Splachnobyrum temasekensis*, from Singapore. *Journal of the Hattori Botanical laboratory,* 96: 1–7.

Tan, B.C., V.T.T. Huong & B.C. Ho. 2003. *Trachycarpidium echinatum* and *Weissia platystegia*, new to Vietnam and Continental SE Asia. *Cryptogamie Bryologie*, 24(1): 43–47.

Wilde, W.J.J.O. De, B.E.E. Duyfjes, B. Gravendeel, R.W.J.M. Van der Ham, B.C. Ho, Rugayah & G.T.P. Vo. 2003. *Callitriche nana* (Callitrichaceae), a New Species from Java, Indonesia. *Floribunda*, 2(3): 57–87.

Ho, B.C. & B.C. Tan. 2002. Additions to the moss Flora of Endau Rompin National Park, Johore, Peninsular Malaysia. *Tropical Bryology*, 22: 67–76.

OFFICIAL INSTITUTIONAL VISITS

12 – 17 Dec 2009	University of Turku (Dr. Sanna Huttunen) and Botanical Museum, University of Helsinki, in the frame of PPP Finland 2009
7 Sep –17 Sep 2009	Bryological Lab, Duke University (Prof. Dr. A.J. Shaw)
24 – 28 May 2004	Herbier Cryptogamique, Muséum National d’Histoire Naturelle de Paris (P)