

PHYLOGENETIC EVIDENCE OF A RAPID RADIATION OF PLEUROCARPOUS MOSSES (BRYOPHYTA)

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Abstract.—Pleurocarpous mosses, characterized by lateral female gametangia and highly branched, interwoven stems, comprise three orders and some 5000 species, or almost half of all moss diversity. Recent phylogenetic analyses resolve the Ptychomniales as sister to the Hypnales plus Hookeriales. Species richness is highly asymmetric with approximately 100 Ptychomniales, 750 Hookeriales, and 4400 Hypnales. Chloroplast DNA (cpDNA) sequences were obtained to compare partitioning of molecular diversity among the orders with estimates of species richness, and to test the hypothesis that either the Hookeriales or Hypnales underwent a period (or periods) of exceptionally rapid diversification. Levels of biodiversity were quantified using explicitly historical ‘‘phylogenetic diversity’’ and non-historical estimates of standing sequence diversity. Diversification rates were visualized using lineage-through-time (LTT) plots, and statistical tests of alternative diversification models were performed using the methods of Paradis (1997). The effects of incomplete sampling on the shape of LTT plots and performance of statistical tests were investigated using simulated phylogenies with incomplete sampling. Despite a much larger number of accepted species, the Hypnales contain lower levels of (cpDNA) biodiversity than their sister group, the Hookeriales, based on all molecular measures. Simulations confirm previous results that incomplete sampling yields diversification patterns that appear to reflect a decreasing rate through time, even when the true phylogenies were simulated with constant rates. Comparisons between simulated results and empirical data indicate that a constant rate of diversification cannot be rejected for the Hookeriales. The Hypnales, however, appear to have undergone a period of exceptionally rapid diversification for the earliest 20% of their history.

Key words.—Diversification, Hookeriales, Hypnales, lineages through time, phylogenetic diversity, radiation.

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There has been much recent interest in the use of molecular phylogenies for inferring rates and patterns of diversification (e.g., Nee et al. 1992, 1994a, b; Guyer and Slowinski 1993; Kirkpatrick and Slatkin 1993; Harvey et al. 1994; Sanderson and Donoghue 1996; Mooers and Heard 1997; Paradis 1997, 1998a, b; Nee 2001; Mooers and Heard 2002). Molecular phylogenies can reveal both the topology of ancestor-descendent relationships, and the tempo of descent among members of a monophyletic group. In comparison with paleontological data, molecular phylogenies have the obvious advantage of applicability to groups lacking a fossil record.

It is clear that organismal diversification rates (speciation minus extinction) have been variable both across lineages and through time. ‘‘Radiations’’ are generally defined in a way that includes rapid cladogenesis from a common ancestor (Simpson 1953). Sometimes key innovations can be identified that are associated with rapid increases in diversification rates. The unique pharyngeal jaw of African ciclids, for example, has been implicated as a key innovation that facilitated explosive radiations of diversity in rift valley lakes (Schluter 2000). A number of approaches have been developed to detect shifts in diversification rate, the choice of method to a large extent depending on the type and extent of available evidence (Sanderson and Donoghue 1996). Paradis (1997, 1998a, b) introduced statistical methods for testing hypotheses about rates of diversification within and between clades based on branching times inferred from molecular phylogenies. For a

given clade, three alternative models of diversification rate can be tested: constant through time (Paradis’s model A), gradually increasing or decreasing rates of diversification (model B), or abrupt changes in rate such that two discretely different rate estimates fit the empirical pattern most closely (model C). The method developed by Paradis (1997) draws an analogy between survival analyses and diversification, and permits maximum-likelihood-based hypothesis testing of alternative diversification patterns.

This paper describes an analysis of diversity and diversification in a major clade of mosses (Division Bryophyta). Our general goals are to assess the partitioning of biodiversity between two major lineages that have been resolved as sister groups by previous molecular analyses, and test the hypothesis that one or both lineages underwent a rapid increase in diversity during its history. As an alternative to comparing levels of biodiversity in these groups by counting numbers of species, we use two approaches that employ molecular data to objectively quantify diversity. We compare such molecular estimates to species richness and show that they yield very different inferences about the partitioning of biodiversity among these moss groups.

With approximately 10,000 species, mosses (bryophytes) comprise the second largest group of land plants, after the highly successful angiosperms. Bryophytes lack lignified vascular tissue and consequently have a very poor fossil record, but phylogenetic analyses of both morphological and molec-

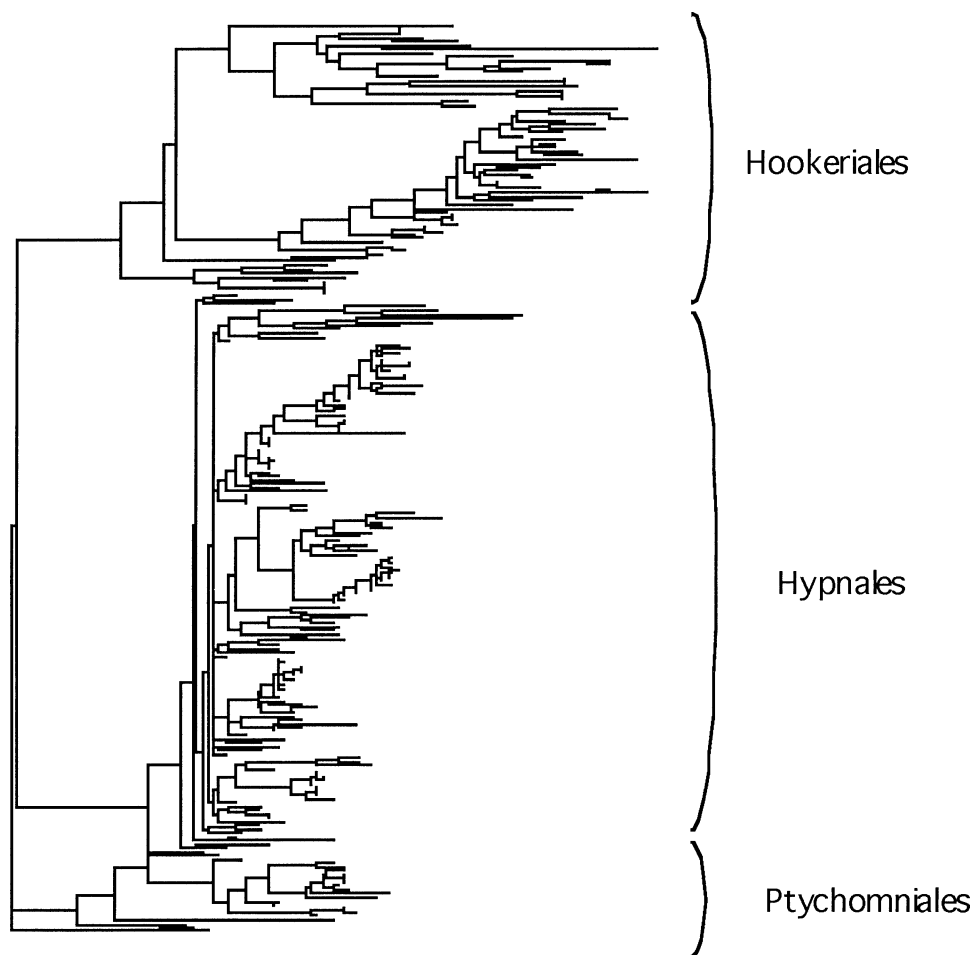


FIG. 1. Phylogram of pleurocarpous mosses based on DNA sequences from *trnL-trnF* and *rps4* (cpDNA). The analysis was constrained to the ordinal topology inferred from previous research (see text for additional details).

ular characters indicate that they are one of the earliest branching lineages of land plants (Mishler and Churchill 1984; Kenrick and Crane 1997; Hedderson et al. 1998; Beckert et al. 1999; Nickrent et al. 2000). There are four main groups of mosses, sometimes treated as classes within the Division Bryophyta: Takakiopsida, Andreaobryopsida, Sphagnopsida, and Bryopsida. The Bryopsida, or "true mosses," include over 90% of moss diversity in terms of species numbers (Schofield 1985; Shaw and Goffinet 2000; Crum 2001).

Within Bryopsida, pleurocarpous mosses are defined by lateral placement of female reproductive structures (archegonia) along gametophyte stems (Bridel 1826–1827). Monophyly of the pleurocarps is strongly supported by nuclear, chloroplast, and mitochondrial DNA sequences (De Luna et

al. 1999; Newton et al. 2000; Goffinet et al. 2001; W. R. Buck, C. J. Cox, B. Goffinet, S. Boles, and A. J. Shaw, unpubl. ms.), and the clade is consistently resolved as a relatively recent derivation within the Bryopsida. Traditionally, three orders of pleurocarpous mosses have been distinguished: Hookeriales, Leucodontales, and Hypnales. Buck et al. (2000) showed that the Leucodontales, defined primarily by erect sporophytes and reduced peristomes, are polyphyletic. These morphological features are usually associated with epiphytism, and DNA data indicate that epiphytic species with erect sporophytes and reduced peristomes have evolved repeatedly from hypnalian ancestors. Recent analyses based on nuclear (*26s* rDNA), chloroplast (*rps4*, *trnL-trnF*), and mitochondrial (*nad5*) DNA sequences (W. R. Buck, C. J. Cox, B. Goffinet, S. Boles, and A. J. Shaw, unpubl. ms.) resolve three major lineages of pleurocarpous mosses (Ptychomniales, Hypnales, and Hookeriales; Fig. 1). The Hypnales account for about 80% of all pleurocarpous mosses (Table 1), or almost 40% of all species of Bryopsida (Crosby et al. 1999).

Previous attempts at resolving family relationships within the Hypnales have been largely unsuccessful, in part because branch lengths at the base of the hypnalian clade are very short in molecular-based trees (Buck et al. 2000). Indeed,

TABLE 1. Taxonomic diversity of the three orders of pleurocarpous mosses according to the classification of Buck and Goffinet (2000).

	Ptychomniales	Hookeriales	Hypnales
Species	100	743	4418
Genera	9	48	408
Families	2	6	44
Species sampled	21 (21%)	71 (10%)	149 (3.4%)
Genera sampled	7 (78%)	35 (73%)	85 (21%)

molecular diversity within the Hypnales seems to be generally low in comparison to other major clades of mosses (Shaw et al. 2002). Variable regions such as the nuclear ribosomal internal transcribed spacers (ITS) are often unalignable among congeneric species of many mosses, but may be aligned across genera or even families of pleurocarps (Shaw et al. 2002; Vanderpoorten et al. 2002).

The derived phylogenetic position within mosses, the very short branches at the base of the pleurocarp clade, and the generally low level of nucleotide diversity distinguishing pleurocarpous taxa, suggest the possibility that this speciose group represents a relatively recent and rapid radiation within the mosses. Indeed, the starlike shape of pleurocarp clade resolved in previous phylogenetic analyses (e.g., Buck et al. 2000) suggests that all of the extant families may have originated almost simultaneously. The Hypnales are especially diverse in the Northern Hemisphere whereas the Hookeriales and Ptychomniales are predominantly Southern Hemisphere and tropical. The Hypnales contain almost 40 times the number of species as the Ptychomniales, and about six times the number of hookerian species (Table 1). Because sister group relationships among these clades of pleurocarps are strongly supported, we are in a position to ask questions about the partitioning of biodiversity among them, and patterns of diversification within them. Our analyses focus on the Hypnales and Hookeriales because they contain most of the species of pleurocarps and are sister groups. Specifically, this study was designed to answer the following questions. (1) Does the partitioning of molecular diversity among orders of pleurocarpous mosses parallel patterns of biodiversity inferred from species numbers? (2) Has the rate of diversification (speciation minus extinction) been constant through time in the Hookeriales, and in the Hypnales? (3) If a constant diversification rate can be rejected (in one or both orders), has the rate of diversification increased or decreased, and has the change been gradual or discontinuous?

METHODS

Taxon Sampling and DNA Sequencing

The analyses of biodiversity and diversification were based on 241 collections representing 127 genera (Appendix). Collections represent a worldwide sample without geographic bias in favor of, for example, Northern Hemisphere or North American taxa. Voucher specimens are primarily in herbaria at the Missouri Botanical Garden (MO) and the New York Botanical Garden (NY; Appendix). A total of 75 collections was included in the previous analyses published by Buck et al. (2000) and 166 were newly sequenced for this study. We obtained sequences for two chloroplast DNA regions from each specimen: the *rps4* gene (Nadot et al. 1994) and the *trnL-trnF* region (Taberlet et al. 1991). Sampling of gametophyte tissue, PCR amplification, and sequencing were accomplished according to the protocols described in Buck et al. (2000).

Phylogenetic Analyses

The conclusion that pleurocarpous mosses comprise three major clades, the Hookeriales, Ptychomniales, and Hypnales, comes from analyses of 99 pleurocarpous taxa from which

four loci were sequenced: *rps4* and *trnL-trnF* from the chloroplast genome, 26S nuclear ribosomal DNA, and *nad5* from the mitochondrial genome (W. R. Buck, C. J. Cox, B. Goffinet, S. Boles, and A. J. Shaw, unpubl. ms.). Data used in the present paper represent a larger taxon sample (241 accessions) but with sequence data from only the two chloroplast regions. Sequences from *trnL-trnF* and *rps4* alone are insufficient to completely resolve sister-group relationships at the ordinal level within pleurocarps, but parsimony analyses of our two-gene dataset do not contradict the topology shown in Figure 1. Furthermore, this topology is not in conflict with previously published analyses of phylogenetic relationships within pleurocarpous mosses (Buck et al. 2000; Goffinet et al. 2001). Nonparametric bootstrap support and Bayesian posterior probabilities for clades in the topology shown in Figure 1 are very strong with respect to the three taxonomic orders, hence the two-gene phylogenetic analyses presented here were constrained to the ordinal relationships established independently by the four-gene analyses.

The 241-taxon, two-gene dataset, constrained to the ordinal topology supported by previous research, was analyzed under equally weighted parsimony implemented in PAUP 4.0b10 (Swofford 2001). Heuristic searches were conducted, saving up to 60 most-parsimonious (MP) trees from each of 300 random sequence addition replicates with TBR branch swapping. A single arbitrarily chosen, fully resolved, most-parsimonious tree (henceforth the object tree) was used for subsequent analyses of phylogenetic diversity and diversification patterns.

Due to the size of the dataset, tree searching under maximum likelihood was not practical. Analyses of other MP trees indicate that our conclusions are robust to the relatively minor topological differences among trees, but systematic study of the effects of phylogenetic uncertainty on inferences about patterns of diversity and diversification might prove worthwhile in future studies.

Biodiversity Estimates

One estimate of the ‘‘biodiversity’’ represented by the Hookeriales and Hypnales is the total number of species in each order (Table 1). We obtained complementary estimates that do not depend on taxonomic concepts by estimating levels of molecular diversity in the two chloroplast DNA regions sampled for this study. ‘‘Phylogenetic diversity’’ (PD; Faith 1992) was estimated as the sum of branch lengths in the subtree connecting members of each taxonomic order. Phylogenetic diversity quantifies the amount of (chloroplast DNA) evolution that has occurred in each of the two orders, and was estimated using PAUP by the following procedure. Branch lengths of the object tree were estimated under maximum likelihood under a general time-reversible (GTR) model with a proportion of invariant sites and rate heterogeneity among sites specified by a gamma distribution approximated by four discrete categories. Choice of this substitution model was based on likelihood ratio tests facilitated by MrModeltest version 1.1b (Nylander 2002). The sum of all branch lengths in the object tree constitutes the total PD contained in our sample of pleurocarps. Partitioning of PD between the Hookeriales and Hypnales was estimated by deleting all taxa other than those in the clade of interest, and branch lengths were

again summed for the remaining subsample without reoptimizing branch lengths. Individual clade PD estimates were expressed as percentages of total pleurocarp PD. Stem lineages were not included in PD calculations.

Comparisons between clade estimates of PD are affected by differing taxon complements. Our sample included 149 Hypnales, 71 Hookeriales, and 29 Ptychomniales. To make direct comparisons between the Hookeriales and Hypnales, we subsampled 71 hypnalian taxa at random (using the Wichmann and Hill algorithm as implemented in Python 2.2.1 (van Rossum 2002). PD was recalculated on each of 100 subsamples so that we could estimate the mean and standard deviation of hypnalian PD based on a sample size equivalent to the hookerian sample. The effect of phylogenetic uncertainty on PD estimation was explored by repeating PD estimates on each of 20 equally parsimonious trees PD estimates were almost identical and are not presented. Estimates derived from incrementally longer trees were not conducted but this aspect of phylogenetic uncertainty may warrant exploration in the future.

Although we estimated PD in the ptychomnalian data partition, we did not attempt to estimate hookerian and hypnalian PD with equivalent sample sizes because our ptychomnalian sample was small (29 taxa), and also because the appropriate phylogenetic comparison would be Ptychomniales versus Hookeriales plus Hypnales (Fig. 1).

Nonhistorical estimates of molecular biodiversity (i.e., independent of phylogeny) in each of the three orders of pleurocarps were obtained using Arlequin (Schneider et al. 2000). Molecular diversity was estimated as the absolute numbers of polymorphic sites among haplotypes within each partition, θ_{π} , derived from the mean number of pairwise differences among haplotypes (Tajima 1983), and θ_s , based on the number of polymorphic sites and the sample size (Watterson 1975). Nucleotide diversity was also estimated on a per site basis for each partition to account for differences in sequence lengths (θ_{π}/n , where n is the number of sites).

Diversification Rates

Rates of diversification were quantified using lineage-through-time (LTT) plots, which illustrate the accumulation of lineages over time for the object tree. The object tree was significantly nonclocklike (likelihood ratio test; $df = \text{LRT} = 676.78$, $df = 239$ $P \ll 0.001$), hence substitution rates and time are confounded as causal mechanisms underlying branch lengths. We used Sanderson's (1997) nonparametric rate smoothing (NPRS), implemented in his program, r8s (ver. 1.05 beta), to tease these two factors apart. The method minimizes changes in local substitution rate on the phylogenetic tree such that rates are "smoothed" across the whole tree. It is based conceptually on the assumption that substitution rates are heritable and therefore autocorrelated, a reasonable but unconfirmed hypothesis in most cases (Sanderson 2001). Rate smoothing allows branch lengths to be used as proxies for absolute time in the absence of a molecular clock.

The following procedure was used to generate LTT plots for the Hookeriales and Hypnales. A NPRS tree for the Hookeriales plus Hypnales clade was generated by pruning Ptychomniales from the object tree and setting the root node, or

most recent common ancestor (MRCA), to 100 time units. The Powell algorithm under the NPRS model was used to optimize branch lengths with 10 random initializations, each with 10 repeated perturbations. The number of lineages through time in the NPRS tree was calculated in GENIE (Pybus and Rambaut 2002) and plotted in Gnuplot (Williams and Kelly 1999). The same methodology was used to calculate LTT plots for the Hypnales and Hookeriales clades separately by the reciprocal pruning of taxa.

The program DIVERSI version 0.20.0 (Paradis 2000) was used to investigate patterns of diversification in the Hypnales and Hookeriales. Three alternative models were tested: model A specifies a constant rate of diversification (i.e., the expected number of lineages increases at a constant exponential rate); model B specifies that diversification rate has increased or decreased gradually over time; and model C specifies that a change in diversification rate has occurred such that two different rates, distinguished by an abrupt shift at some point in the past, best fit the evidence. For model B, the parameter, β , is less than one when diversification rate increases gradually through time and is greater than one when the rate decreases through time (Paradis 1997, 2000). Alternative models are evaluated using LRT and/or the Akaike information criterion (AIC; Paradis 1997). The LRT is appropriate for evaluating models A versus B and A versus C because model A is nested within both models B and C. No such nested relationship exists between models B and C, so using a chi-square distribution to test significance of the LRT is inappropriate. Another approach for testing alternative models is the AIC, another likelihood-based metric with explicit penalties for the number of model parameters. The AIC must be used to evaluate non-nested models (Paradis 1998a, 2000). The numbers of lineages-through-time data calculated in GENIE (see above) were converted to the DIVERSI format with appropriate corrections for polytomies (see Paradis 2000).

Tests of different diversification models assume that sampling within clades is essentially exhaustive at the species level (Pybus and Harvey 2000). Our sampling within both the Hookeriales and Hypnales is very incomplete at the species level, and indeed, even at the generic level (Table 1). To test the effect of sampling on the profile of the LTT plots and the statistical tests of DIVERSI, we implemented the following simulations independently for the Hookeriales and Hypnales. Our phylogenetic sample of Hookeriales consisted of 71 taxa, or approximately 10% of the total hookerian species. We used PHYLOGEN (Rambaut 2002) to generate 100 replicate phylogenies under a constant diversification rate (birth:death = 2:1) with 743 extant taxa (the total number of species recognized in the order), then randomly pruned all but 71 taxa from the resulting trees and constructed LTT plots from these subsamples using the methodology outlined above. This was intended to simulate a constant diversification rate phylogeny for the Hookeriales, with subsequent random sampling of 10% of terminals for diversification analyses. The procedure was repeated 1000 times to generate a mean LTT curve with 95% confidence intervals. A similar procedure was conducted for the Hypnales, but in that case we generated constant birth/death phylogenies with 4418 extant taxa, and randomly pruned all but 141 taxa from the trees to generate LTT plots simulating our roughly 4% sampling of hypnalian taxa. We evaluated our

TABLE 2. Number of samples (n) included in this study (% of total in parentheses) and phylogenetic diversity (PD) based on the sum of the branch lengths of each partition, with sum expressed as percentages of total tree length, for three orders of pleurocarpous mosses. The bottom entry is the mean PD (\pm SD) for 100 replicate subsamples of 71 randomly selected Hypnales.

	n	PD
Ptychomniales	21 (9%)	12%
Hookeriales	71 (29%)	48%
Hypnales	149 (62%)	40%
Hypnales	71	$23 \pm 1.5\%$

empirical LTT plots by comparison with the simulated curves and their 95% confidence intervals. In addition, we used DIVERSI to fit the best diversification model (A, B, or C, as above) to each of the 1000 pruned, simulated phylogenies to assess the robustness of the statistical algorithms in DIVERSI to incomplete sampling.

RESULTS

Phylogenetic Reconstruction

The dataset contained 955 characters, of which 388 were parsimony informative and 141 others were autapomorphic. The heuristic maximum parsimony search yielded 6500 trees of 2427 steps, with a consistency index of 0.330 and retention index of 0.747. The phylogram of one of the MP trees (the object tree), with branch lengths estimated under maximum likelihood (Fig. 1), shows obvious differences in clade shape between the Ptychomniales, Hookeriales, and Hypnales. The hypnalian clade is almost comb-shaped; major lineages (which correspond to families) appear to have arisen simul-

taneously because the basal internodes are so short. In contrast, branch lengths near the base of the Hookeriales and Ptychomniales are obviously longer (Fig. 1).

Biodiversity

Partitioning of phylogenetic diversity among the three orders of pleurocarpous mosses, as estimated from our sample of 241 collections, is shown in Table 2. The Ptychomniales accounted for 9% of our samples and 12% of the PD. The Hookeriales accounted for only 29% of our samples, but comprised 48% of the PD, whereas the Hypnales made up 62% of the samples but only 40% of the PD. The distribution of branch lengths in the Hypnales is strongly skewed toward very short lengths, and much less so in the Hookeriales (Fig. 2). The lower PD in Hypnales compared to Hookeriales is clearly not a function of differing sample sizes since we sampled many more Hypnales than Hookeriales (149 vs. 71). On average, PD estimated from 100 replicate samples of 71 Hypnales was 23% ($\pm 1.5\%$ SD) of the total pleurocarp diversity, about half of the PD of 71 hookerialian species. These numbers indicate that, on average, branch lengths in the Hypnales are about half as long as branch lengths in the Hookeriales. The only reason we obtained roughly comparable estimates for PD for the two orders (40 vs. 48%) in our sample of DNA sequences was that we included twice as many Hypnales.

The Hookeriales had a higher number of polymorphic nucleotides than did the Hypnales despite the much larger sample size of Hypnales (Table 3). Similarly, the Hookeriales contain higher diversity than Hypnales in terms of θ_S , θ_π , and nucleotide diversity. In fact, even the smallest order, Ptychomniales, is more diverse than Hypnales as estimated by θ_π and nucleotide diversity. Standard deviations for these

Distribution of branch lengths: Hookeriales vs. Hypnales

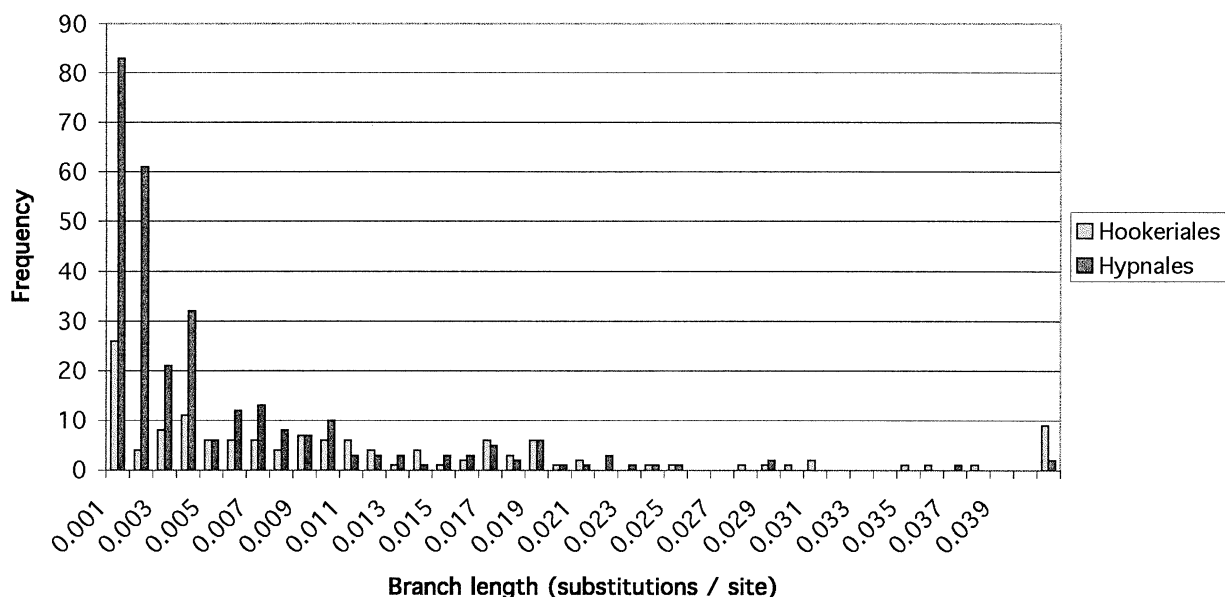


FIG. 2. Distribution of branch lengths in the Hookeriales and Hypnales, from the cpDNA tree shown in Fig. 1.

TABLE 3. Molecular diversity within three orders of pleurocarpous mosses. Numbers in parentheses after each ordinal name are sample sizes.

	Polymorphic sites	θ_s	θ_n	Nucleotide diversity
Ptychomniales (21)	183	50.87 \pm 17.22	37.27 \pm 18.85	0.040 \pm 0.021
Hookeriales (71)	360	74.47 \pm 19.40	51.14 \pm 24.81	0.056 \pm 0.027
Hypnales (149)	346	62.03 \pm 14.25	27.83 \pm 13.56	0.030 \pm 0.015

estimates are overlapping among the orders, but these trends, especially the relatively low diversity found within Hypnales, are consistent with the PD estimates. All estimates of molecular diversity are at odds with levels of biodiversity based on species richness.

Diversification Patterns and Rates

The NPRS tree is shown in Figure 3. Statistical analyses of an LTT plot for Hookeriales, derived from the NPRS tree, suggests that model B, a gradually changing rate of diversification, fits the data better than model A (constant rate; Table 4; Fig. 4). A positive value for β (1.416) indicates that the rate of diversification has decreased over time, in agreement with an apparent reduction in slope of the LTT plot (Fig. 5). The relative fit of models B versus C depends on

when during history a discrete shift in diversification rate is proposed (Fig. 4). There is some indication that model C fits the data almost as well as model B if a shift in rate is hypothesized to have occurred between 20 and 30 times units after the origin of the Hookeriales, but for no point in time is model C favored (Fig. 4).

Lineage-through-time plots from simulated phylogenies (with 10% sampling of extant taxa and constant diversification rate) indicate that the inference of a decreasing diversification rate in the Hookeriales, either gradually or with a discrete inflection point, could be an artifact of our incomplete sampling. Although diversification was simulated under a constant rate, the mean LTT curve and its 95% CI exhibit a decreasing slope and the empirical curve for Hookeriales falls almost completely within the confidence interval (Fig.

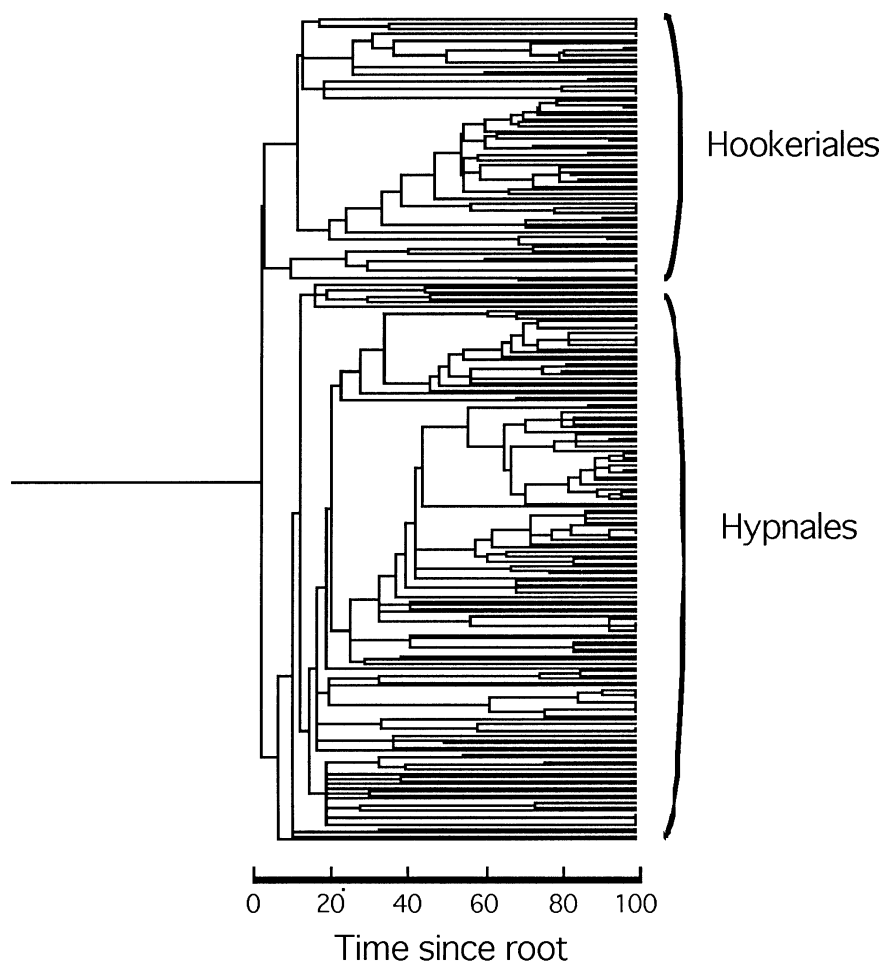


FIG. 3. Phylogenetic tree derived from nonparametric rate smoothing (Sanderson 1997) of tree shown in Fig. 1.

TABLE 4. Likelihoods associated with alternative models of diversification in the Hookeriales and Hypnales. Model B provides the best fit for Hookeriales. Model C provides the best fit for Hypnales; models A and B are not significantly different. The likelihood of model C depends on the hypothesized breakpoint so it is not compared in this table. See Figure 5.

	Hookeriales	Hypnales
Model A	-276.930	-516.417
Model B	-271.780	-516.278

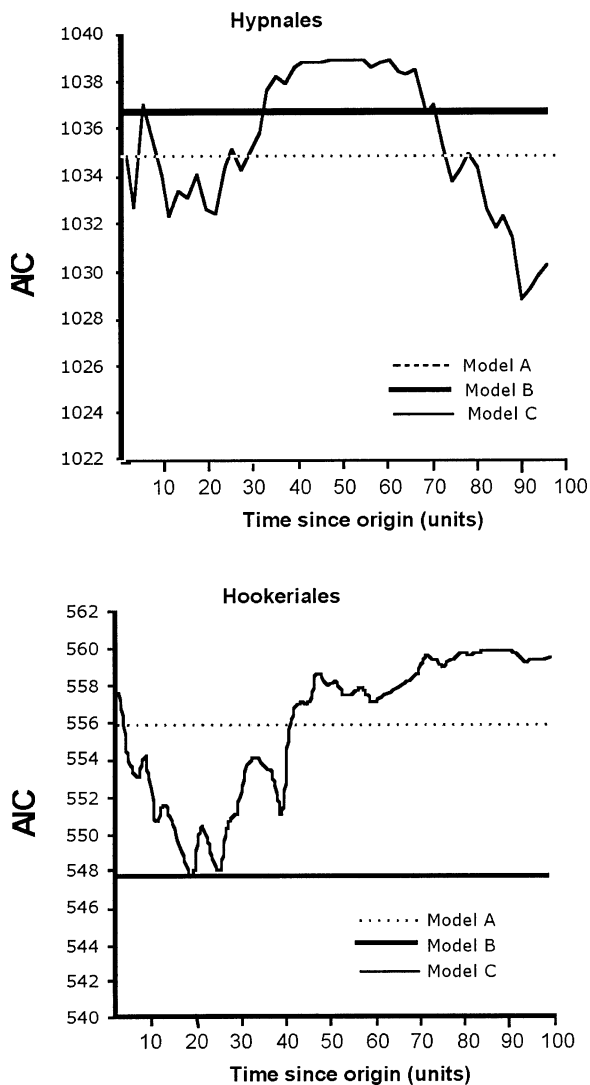


FIG. 4. Akaike information criterion (AIC) values for diversification models A, B, and C. Model A implies a constant (exponential) rate of diversification, model B a gradually changing rate, and model C a pattern with two different rates of diversification. The lowest AIC value identifies the best model. The AICs for models A and B do not depend on time and are constant through phylogenetic history (x-axis). The AIC for model C depends on the hypothesized breakpoint in diversification rate. The line for model C was smoothed from DIVERSI analyses modeling the breakpoint every five units of time.

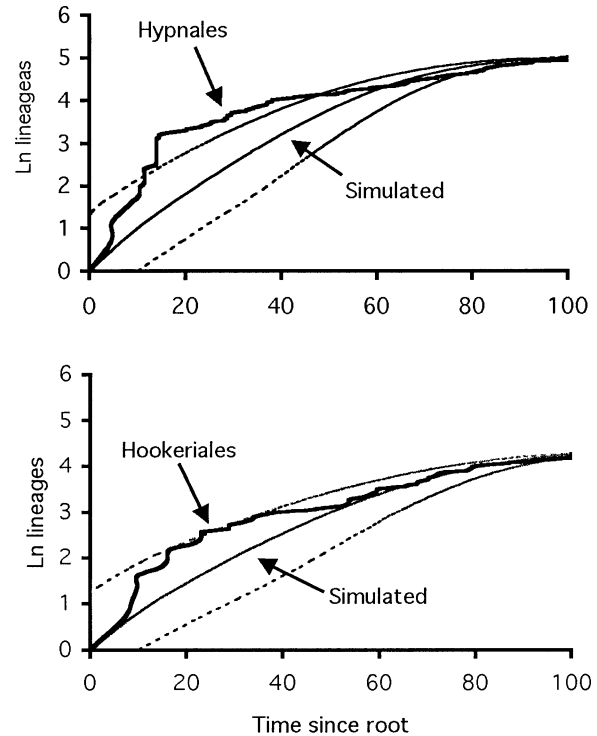


FIG. 5. Lineage-through-time (LTT) plots for the Hookeriales and Hypnales, with the results from simulated phylogenies with incomplete sampling. See text for additional explanation of the simulations and construction of LTT plots.

5). Both the LRTs and the AIC confirm that these simulated curves best fit a model of decreasing diversification rate over time (Table 5). With this level of incomplete sampling, it is not possible to reject any of the three models of diversification. The fact that the empirical LTT curve falls within the 95% CI of simulations is consistent with the interpretation that diversification of Hookeriales has been constant.

The LTT plot derived from the smoothed NPRS tree for Hypnales, in contrast, exhibits a very steep initial slope, followed by a relatively abrupt change to a much more gentle positive slope (Fig. 5). Both the LRT and AIC, implemented in DIVERSI, indicate that model C, with two discrete rates of diversification separated by an inflection point, provides a best fit for the data (Table 5). Across the whole of hypnalian history, model C provides the best fit when an inflection point is hypothesized early or late in the chronology (Fig. 4).

Lineage-through-time plots from simulated phylogenies of hypnalian diversity exhibit a gradually decreasing slope (Fig. 5), as expected based on theoretical considerations. The empirical curve falls outside the 95% CI between 15 and 40 time units after the origin, and also from 80 time units up to the present. Likelihood-ratio-tests and the AIC suggest that model B provides a best fit to the simulated data (Table 5). As only 3% of the simulated trees are best fit by model C, the fit of model C to our empirical Hypnales data is not an artifact of incomplete sampling. Even with 4% sampling of extant taxa from our simulated phylogenies, fewer than 5% of the LTT plots fit model C. Instead, as in the hookerian simulations, incomplete sampling confounds models A and B, but does not lead to falsely accepting model C.

TABLE 5. Fit of alternative diversification models to lineage-through-time (LTT) plots derived from simulated phylogenetic trees sampled to mimic the incomplete sampling employed in the sample of real taxa. All simulations were run with a constant diversification rate; speciation = 0.2, extinction = 0.1. Hookeriales—1000 trees with LTT plots derived from 71 extant (terminal) taxa sampled randomly from a clade with 743 taxa. Hypnales—1000 trees with LTT plots derived from 149 extant (terminal) taxa sampled randomly from a clade with 4418 taxa. Statistics are the percent of trees for which that model was favored.

	LRT	AIC
Hookeriales		
Model A vs. B	A: 0.8 B: 99.2	A: 0.0 B: 87.3
Model A vs. C	A: 12.6 C: 87.4	C: 12.7
Hypnales		
Model A vs. B	A: 0.0 B: 100.0	A: 0.0 B: 97.4
Model A vs. C	A: 0.0 C: 100	C: 2.6

DISCUSSION

Phylogenetic analyses support the hypothesis that the Hypnales underwent a period of relatively rapid diversification early in their history. This conclusion appears to be robust despite our incomplete taxon sampling within the Hypnales. Simulations with comparable levels of incomplete sampling showed that sampling artifacts is unlikely to produce the pattern of diversification observed in the hypnalian data. The model of diversification that provides a best fit to the data specifies an early period, approximately 20% of the total history of Hypnales, in which the increase in lineages was relatively rapid, followed by an abrupt decrease in rate and a longer period of reduced diversification. There may have been a further slow-down in rate relatively recently, but this is not nearly as obvious as the earlier change after the initial radiation. The later stages of diversification, occupying at least 80% of the history of Hypnales, appear to be characterized by a constant rate of diversification in which the number of lineages grew exponentially.

No such early period of rapid diversification is evident for the Hookeriales, which is the sister group to Hypnales and therefore of the same age. An abrupt change in diversification rate (model C) cannot be statistically rejected, but evidence for a pattern of hookerian diversification that departs from rate constancy is absent. Internodal branches are less strongly skewed toward very short lengths in the Hookeriales, and analyses of the LTT plot derived from the rate-smoothed tree best fits a model of gradually decreasing diversification rate over time. In this case, however, simulations suggest that the apparent pattern of decreasing diversification is likely an artifact of incomplete sampling.

Taxon sampling is a crucial factor to consider in any study of diversification rates based on LTT plots derived from molecular phylogenies (Nee et al. 1994; Pybus and Harvey 2000). Two issues require consideration: completeness of sampling and randomness of sampling. Our simulations confirm previous results (Harvey and Nee 1994) that lineages with a history of constant diversification yield LTT plots that mimic a

gradually decreasing rate of diversification when taxon sampling is incomplete. Considering a constant rate of diversification as the null hypothesis, this could lead to Type I errors using the statistical approach of Paradis (1997, 1998b). In fact, the null hypothesis under a constant rate of diversification with incomplete sampling should be model B, a gradually decreasing rate. Our simulated phylogenies most commonly fit this model, as inferred from both LRTs and the AIC.

Our simulations explicitly incorporate the effects of sampling completeness, and we argue that despite extremely incomplete sampling of Hookeriales and Hypnales, we can reject constant diversification in the latter. Nevertheless, this issue of sampling completeness warrants additional study. In particular, discussions of sampling completeness have focused on species (e.g., Pybus and Harvey 2000). We question the focus on species since these units are often subjectively defined, and many (most?) species have phylogenetically structured populations comprising them. Just what does constitute “exhaustive” sampling, and to what extent (and in what ways) does infraspecific sampling affect inferences about diversification patterns?

Phylogenetic randomness of sampling is a separate issue. If taxon sampling is conducted in an overdispersed manner so that deep clades are preferentially represented, as is generally the case in molecular systematic studies, early diverging lineages will be overrepresented in the data. This could result in the *appearance* of an early period of high diversification rate, corresponding to the time when such deep lineages originated. Indeed, this criticism could be leveled against the current study. However, deep lineages that diversified early in the history of pleurocarps mostly correspond to families (and clades even more inclusive than families) rather than to genera. The latter tend to diverge closer to the tips of the phylogeny on which our analyses were based. It is apparent from the shape of the phylogenetic tree on which our pleurocarp analyses were conducted that the sudden increase in hypnalian clades occurred at the extreme base of this lineage, not at the level at which genera are resolved. Our sampling criteria did not consider the distribution of sampled families; hence, our representation of families was arbitrary. Overdispersed sampling at the generic level could not yield the relatively rapid increase in lineages so close to the base of the hypnalian clade.

Although the choice of taxa included in this study may have had some effect on the shapes of the LTT plots, we argue that this effect would have been roughly equivalent for the Hookeriales and Hypnales, and would not be substantial enough to invalidate our conclusions. Nevertheless, the effects of phylogenetically nonrandom sampling clearly warrant further study through simulations and experimental pruning of taxa from real datasets.

Despite the rapid diversification of Hypnales, the Hookeriales have undergone more chloroplast molecular evolution (higher PD) and have higher levels of standing nucleotide diversity. This pattern contrasts with the correlation between rate of *rbcL* evolution and species richness found in angiosperms (Barraclough et al. 1996). The Hypnales have almost six times the number of species as Hookeriales, yet have less diversity at the chloroplast DNA sequence level. It is unlikely that species concepts are applied in a systematically different

manner in the two orders to a degree sufficient to explain this discrepancy. Although the Hypnales form a large clade with more than 4000 species, these taxa are very closely related on a molecular level, and the pattern of dissimilar morphology coupled with homogeneity at the sequence level is striking and suggestive of adaptive radiation. This research provides a striking example of the fact that species are not all equivalent with regard to "biodiversity value." The results suggest that alternative metrics for quantifying biodiversity are useful to complement estimates based on species richness.

There has been much discussion about general patterns of diversification during the history of life, especially in the paleobiology literature (e.g., Raup 1972; Sepkoski 1984; Jablonski 1991; Benton 1997). Three generalized models describing the increase in biological diversity have been contrasted: additive, exponential, and logistic, although in reality, patterns are made more complex by events such as mass extinctions, differences in rates of speciation and extinction among lineages, and the fact that no one pattern characterizes the whole of evolutionary time (Benton 1997). Marine invertebrates, for example, appear to have undergone several more or less discrete stages of diversification (Sepkoski 1984). Both terrestrial tetrapods and vascular land plants show patterns that suggest exponential increases in diversity over time, with rapid increases in the relatively recent past (Niklas et al. 1985; Benton 1997). Such diversity-over-time curves for major heterogeneous groups of organisms of course reflect the averages of patterns characterizing many individual subgroups.

Evidence of changes in diversification rate over time within a particular lineage comes from both paleontological data and analyses of modern groups. Classic "adaptive radiations" are generally characterized by exceptionally rapid periods of diversification (Simpson 1953; Givnish and Sytsma 1997; Schluter 2000). Horses went through three phases leading to current levels of diversity: rapid radiation, stationarity, and decline (Hulbert 1993). The radiation phase, with high speciation and low extinction rates, lasted about 17% of the last 18 million years (MY) of equine history (Hulbert 1993). Cichlid fishes of Lake Victoria exhibit an excess of new lineages in the recent past, but the radiation is also borne on a long stem that implies low speciation and/or high extinction early in their history (Schluter 2000).

The California silverswords (Asteraceae) are one of the most outstanding examples of an adaptive radiation in plants. Baldwin and Sanderson (1998) estimated an age for the common ancestor of the Hawaiian silversword alliance and their sister group, the California tarweeds, as 15 MY. The silverswords occur on a long branch and the common ancestor of all living Hawaiian species was estimated to have existed 5.2 MY ago. Although Baldwin and Sanderson (1998) could not exclude the possibility that the long stem branch reflected extinction of early diverging species, it seems more likely that there really was a spurt of rapid speciation in the last five million years. The absolute diversification rate estimated for the Hawaiian silverswords (0.56 ± 0.17 species per MY) is comparable to that estimated for neogene horses. Baldwin and Sanderson (1998) did not explicitly test the hypothesis that diversification rate in the silverswords has been constant

over the last five MY, but the shape of the LTT plot they presented appears consistent with constant diversification.

There is no evidence of an initial period of slow diversification in the history of hypnalian mosses. The presence of a significant stem clade might suggest a substantial period of now-extinct ancestry prior to the radiation of extant Hypnales, but the branches separating Ptychomniales, Hookeriales, and Hypnales are very short. The radiation of Hypnales appears to have been initiated very early in history of the clade and the phase of rapid diversification continued for about 20% of their history. The base of the hypnalian clade is still phylogenetically unresolved, precisely because of the rapid diversification and consequent short branch lengths. As a result it is impossible at this point to identify the earliest diverging groups and the ecological and morphological features associated with the radiation. The pleurocarpous habit itself, including lateral gametangia and procumbent, spreading growth form, unites the Ptychomniales, Hookeriales, and Hypnales, and therefore appeared before the hypnalian radiation. Most pleurocarps are characteristic of shaded woodland habitats, but so are some acrocarpous mosses, and such forest habitats are shared by members of all three orders of pleurocarps. Such a transition is therefore unlikely to underlie the diversification of Hypnales.

The absolute time course of moss diversification is unknown, but it is well established that the pleurocarps represent a derived clade, and that the Hypnales are derived within the pleurocarps. Thus, the hypnalian radiation may have been relatively recent. Buck (1991) and Kürschner and Parolly (1999) suggested that the diversification of pleurocarps may have been temporally coincident with the rise to dominance of angiosperms, since most pleurocarp diversity occurs within angiosperm-dominated forests. Indeed, many hypnalian taxa are epiphytic on angiosperms and rarely occur on gymnosperms or other large trachophytes. It is possible that the radiation of Hypnales is related to the origin of angiosperms as host trees. This is a hypothesis that can be tested as phylogenetic resolution of the major moss lineages increases; it is not clear at present whether Hypnales at the base of the clade are terrestrial or epiphytic. Current information, however, suggests that the "angiosperm connection" applies equally well to all pleurocarps, rather than to the Hypnales alone. Clearly, the Hookeriales and Ptychomniales did not respond to the rise of angiosperms with a rapid radiation of species diversity. Moreover, host specificity is limited in epiphytic mosses. Although any key geological, ecological, or morphological innovation associated with the hypnalian radiation is currently obscure, it does seem clear that, like many major groups of organisms, the hypnalian pleurocarps underwent a relatively rapid radiation during an early stage of their history.

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APPENDIX

Specimens included in the present analyses. Those in bold were newly sequenced for this study. MO, Missouri Botanical Garden; NY, New York Botanical Garden; CHR, Christchurch, New Zealand, Dept. of Scientific and Industrial Research.

Genus	Species	Country	Collector	Collection no.	Herbarium	ips4 GenBank no.	trnL GenBank no.
<i>Achrophyllum</i>	<i>dentatum</i>	Australia	Streimann	61075	NY	AY306853	AY306687
<i>Acrocladium</i>	<i>aureiculatum</i>	New Zealand	Kantak and Churchill	166	NY	AY306854	AY306688
<i>Acroporium</i>	<i>pungens</i>	French Guiana	Buck	33028	NY	AF143028	AF161121
<i>Actinodontium</i>	<i>sprucei</i>	French Guiana	Buck	37977	NY	AY306855	AY306689
<i>Adelothecium</i>	<i>bogotense</i>	Brazil	Buck	26301	NY	AF143073	AF161166
<i>Adelothecium</i>	<i>bogotense</i>	Brazil	Vital and Buck	19649	NY	AY306856	AY306690
<i>Aerobryidium</i>	<i>aureo-nitens</i>	China	Redfearn	2270	MO	AY306857	AY306691
<i>Aerobryopsis</i>	<i>capensis</i>	South Africa	Perold	908	MO	AY306858	AY306692
<i>Aerobryopsis</i>	<i>longissima</i>	Australia	Streimann	57914	MO	AY306859	AY306693
<i>Aerobryopsis</i>	<i>wallichii</i>	Australia	Streimann	54022	MO	AY306860	AY306694
<i>Aerobryum</i>	<i>speciosum</i>	China	Allen	6642	MO	AY306861	AY306695
<i>Aerolindigia</i>	<i>capillacea</i>	Colombia	Linares	3721	MO	AY306862	AY306696
<i>Anacamptodon</i>	<i>splachnoides</i>	USA	Buck	32568	NY	AF143031	AF161124
<i>Ancistrodes</i>	<i>geniiflexa</i>	Chile	Holz and Franzaring	CH 00-154	NY	AY306863	AY306697
<i>Ancistrodes</i>	<i>geniiflexa</i>	Chile	Schafer-Verwimp	8114	NY	AY306864	AY306698
<i>Anomodon</i>	<i>rugelii</i>	USA	Buck	32519	NY	AF143023	AF161116
<i>Barbella</i>	<i>pendula</i>	USA	Reese	13833	MO	AY306865	AY306699
<i>Barbellopsis</i>	<i>trichophora</i>	Dominican Republic	Buck	14076	NY	AY306866	AY306700
<i>Beeveria</i>	<i>distichophylloides</i>	New Zealand	Fife	11150	NY	AY306867	AY306701
<i>Brachythecium</i>	<i>austro-glareosum</i>	Falkland Islands	Anderson	27702	NY	AF143026	AF161119
<i>Brachythecium</i>	<i>laetum</i>	USA	Buck	32504	NY	AF143025	AF161118
<i>Brachythecium</i>	<i>plumosum</i>	USA	Buck	33463	NY	AF143078	AF161171
<i>Brachythecium</i>	<i>salebrosum</i>	Germany	Goffinet	4723	NY	AF143027	AF161120
<i>Bryhnia</i>	<i>novae-angliae</i>	USA	Buck	32561	NY	AF143029	AF161122
<i>Brymela</i>	<i>websteri</i>	Dominica	Schafer-Verwimp	17861	NY	AY306868	AY306702
<i>Bryobrothera</i>	<i>crenulata</i>	Australia	Streimann	57716	NY	AY306869	AY306703
<i>Callicostella</i>	<i>diatomophila</i>	Cuba	Buck	23312	NY	AY306870	AY306704
<i>Callicostella</i>	<i>pallida</i>	French Guiana	Holz	FG 00-14	NY	AY306872	AY306706
<i>Callicostellopsis</i>	<i>meridensis</i>	Venezuela	Griffin	PV-898	NY	AY306871	AY306705
<i>Calyptrochaeta</i>	<i>brownii</i>	Australia	Streimann	60613	NY	AY306873	AY306707
<i>Calyptrochaeta</i>	<i>japonica</i>	China	Redfearn	35826	NY	AY306874	AY306708
<i>Campochaete</i>	<i>pulvinata</i>	New Zealand	Streimann	51117	MO	AY306876	AY306710
<i>Campochaete</i>	<i>vaga</i>	Australia	Vitt	28145	MO	AY306877	AY306711
<i>Campochaete</i>	<i>aciphyllo</i>	New Zealand	Bartlett	22089	NY	AY306875	AY306709
<i>Campyllum</i>	<i>chrysophyllum</i>	USA	Buck	32532	NY	AF143048	AF161141
<i>Canalohypopterygium</i>	<i>tamariscinum</i>	New Zealand	Frey and Pfeiffer	98-T10C	CHR	AY306878	AY306712
<i>Catharomnion</i>	<i>ciliatum</i>	New Zealand	Streimann	51423	NY	AY306879	AY306713
<i>Chaetomitrium</i>	<i>borneense</i>	Brunei	Tan	95-1116	NY	AY306880	AY306714
<i>Chaetomitrium</i>	<i>duisenii</i>	Equatorial Guinea	Heras	499/94	NY	AY306881	AY306715
<i>Chrysocladium</i>	<i>flammeum</i> spp. <i>flammeum?</i>	China	Wang	860698	NY	AY306882	AY306716
<i>Cladomnion</i>	<i>ericoides</i>	New Zealand	Streimann	51478	NY	AY306884	AY306718
<i>Cladomniopsis</i>	<i>crenato-obtusa</i>	Chile	Buck	41360	NY	AY306883	AY306717
<i>Clasmatodon</i>	<i>parvulus</i>	USA	Buck	33446	NY	AF143032	AF161125
<i>Climacium</i>	<i>americanum</i>	USA	Buck	20951	NY	AF143065	AF161158
<i>Crosbya</i>	<i>straminea</i>	New Zealand	Fife	10379	NY	AY306887	AY306721
<i>Crossomitrium</i>	<i>epiphyllum</i>	French Guiana	Buck	33259	NY	AY306885	AY306719
<i>Crossomitrium</i>	<i>rotundifolium</i>	French Guiana	Buck	33042	NY	AY306886	AY306720

APPENDIX. Continued.

Genus	Species	Country	Collector	Collection no.	Herbarium	ips4 GenBank no.	trnL GenBank no.
<i>Crossomitrium</i>	<i>rotundifolium</i>	French Guiana	Buck	33043	NY	AF143070	AF161163
<i>Cryphaea</i>	<i>glomerata</i>	USA	Buck	31329	NY	AF143007	AF161100
<i>Cryptopapillaria</i>	<i>penicillata</i>	Dominican Republic	Buck	8287	NY	AY306888	AY306722
<i>Ctenidium</i>	<i>malacodes</i>	USA	Buck	33458	NY	AF143036	AF161129
<i>Curviramea</i>	<i>mexicana</i>	Mexico	Buck	28242	NY	AF143062	AF161155
<i>Cyatophorella</i>	<i>hookeriana</i>	Thailand	Akiyama	Th-39	NY	AY306890	AY306724
<i>Cyatophorella</i>	<i>tonkinensis</i>	Japan	Yamaguchi	Bryophytes of Asia fasc. 6 no. 128	NY	AY306891	AY306725
<i>Cyatophorum</i>	<i>bulbosum</i>	Australia	Streitmann	55638	NY	AY306889	AY306723
<i>Cyclodictyon</i>	<i>albicans</i>	Colombia	Churchill et al.	18795	NY	AY306892	AY306726
<i>Cyclodictyon</i>	<i>roridum</i>	Ecuador	Buck	39563	NY	AY306893	AY306727
<i>Daltonia</i>	<i>gracilis</i>	Ecuador	Buck	39508A	NY	AY306894	AY306728
<i>Daltonia</i>	<i>longifolia</i>	Ecuador	Buck	39508	NY	AY306895	AY306729
<i>Dendrocyclophorum</i>	<i>decolyi</i>	Japan	Matsui	7264	NY	AY306896	AY306730
<i>Diaphanodon</i>	<i>procumbens</i>	India	Topal	504	MO	AY306897	AY306731
<i>Dichelodontium</i>	<i>nitidum</i>	New Zealand	Fife	7332	NY	AY306917	AY306751
<i>Dimorphocladon</i>	<i>borneense</i>	Brunei	Tan	95-1060	NY	AY306898	AY306732
<i>Diploneuron</i>	<i>convivens</i>	Jamaica	Crosby	13732	NY	AY306899	AY306733
<i>Distichophyllidium</i>	<i>nymanianum</i>	Malaysia	Mohamed and Damanhuri	1118 Musci Malaysiani Exsiccati fasc. 2 no. 29	NY	AY306901	AY306735
<i>Distichophyllum</i>	<i>freycinetii</i>	USA	Flynn	5151	NY	AY306900	AY306734
<i>Distichophyllum</i>	<i>pulchellum</i>	New Zealand	Streitmann	51380	NY	AY306902	AY306736
<i>Duthiella</i>	<i>declinata</i>	China	Redfearn	1848	MO	AY306903	AY306737
<i>Duthiella</i>	<i>flaccida</i>	China	Hu	H0852	MO	AY306904	AY306738
<i>Duthiella</i>	<i>formosa</i>	China	Shevock	14453	MO	AY306905	AY306739
<i>Echinodium</i>	<i>umbrosum</i> var. <i>glaucoviride</i>	Australia	Streitmann	49668	NY	AF143044	AF161137
<i>Entodon</i>	<i>brevisetus</i>	USA	Buck	32483	NY	AF143057	AF161150
<i>Entodontopsis</i>	<i>leucostega</i>	Trinidad	Djan-Chékar	94-726	NY	AF143060	AF161153
<i>Ephemeropsis</i>	<i>trentepohlioides</i>	New Zealand	Macmillan	95/94	NY	AY306906	AY306740
<i>Eupychium</i>	<i>robustum</i>	Australia	Streitmann	56137	NY	AY306907	AY306741
<i>Eupychium</i>	<i>setigerum</i>	Australia	Streitmann	45332	NY	AY306908	AY306742
<i>Eupychium</i>	<i>viitense</i>	Fiji	Buck	7255	NY	AY306909	AY306743
<i>Floribundaria</i>	<i>aurea</i>	Japan	Mizutani	15715	MO	AY306910	AY306744
<i>Floribundaria</i>	<i>floribunda</i>	Comoros	Magill and Pocs	11641	MO	AY306911	AY306745
<i>Floribundaria</i>	<i>sparsa</i> var. <i>pilifer</i>	China	Redfearn et al.	33904	MO	AY306912	AY306746
<i>Fontinalis</i>	<i>dalecarlica</i>	USA	Allen	20153	MO	AF143064	AF161157
<i>Forsstroemia</i>	<i>trichomitria</i>	USA	Buck	32619	NY	AF143006	AF161099
<i>Garovaglia</i>	<i>binsteadii</i> var. <i>mirabilis</i>	Papua New Guinea	Iserentant	B-73	NY	AY306913	AY306747
<i>Garovaglia</i>	<i>compressa</i>	Indonesia	Akiyama	C-16340	NY	AY306914	AY306748
<i>Garovaglia</i>	<i>elegans</i>	Papua New Guinea	Streitmann	40482	NY	AF143017	AF161110
<i>Garovaglia</i>	<i>elegans</i>	Papua New Guinea	Hoffman	89-476	NY	AY306915	AY306749
<i>Garovaglia</i>	<i>Powellii</i> var. <i>brevifolia</i>	Papua New Guinea	Iserentant	B-81	NY	AY306916	AY306750
<i>Garovaglia</i>	<i>subelegans</i>	Papua New Guinea	Hoffmann	89-505	NY	AY306918	AY306752
<i>Glyphothecium</i>	<i>sciuroides</i>	Australia	Streitmann	55558	NY	AF143016	AF161109
<i>Glyphothecium</i>	<i>sciuroides</i>	Australia	Streitmann	59969	NY	AY306919	AY306753
<i>Hampeella</i>	<i>alaris</i>	New Zealand	Buck	6865	NY	AY306920	AY306754
<i>Hampeella</i>	<i>pallens</i>	Australia	Streitmann	44664	NY	AY306921	AY306755
<i>Haplodactium</i>	<i>virginianum</i>	USA	Buck	32482	NY	AF143040	AF161133

APPENDIX. Continued.

Genus	Species	Country	Collector	Collection no.	Herbarium	ips4 GenBank no.	trnL GenBank no.
<i>Haplohypnum</i>	<i>triste</i>	USA	Buck	32601	NY	AF143022	AF161115
<i>Helicodontium</i>	<i>capillare</i>	Nevis	Buck	29550	NY	AF143043	AF161136
<i>Hemiragis</i>	<i>aurea</i>	Costa Rica	Dauphin	2949	NY	AY306922	AY306756
<i>Henicodum</i>	<i>geniculatum</i>	French Guiana	Buck	33024	NY	AF143011	AF161104
<i>Hildebrandtiella</i>	<i>cuspidans</i>	Comoros	Magill and Pocs	11637	MO	AY306923	AY306757
<i>Hildebrandtiella</i>	<i>endorrhelloides</i>	Comoros	Magill and Pocs	11020	MO	AY306924	AY306758
<i>Hildebrandtiella</i>	<i>guyanense</i>	Comoros	Magill and Pocs	11732	MO	AY306925	AY306759
<i>Hildebrandtiella</i>	<i>guyanense</i>	Ecuador	Laegaard and Lozano	18909B	MO	AY306926	AY306760
<i>Hildebrandtiella</i>	<i>pachyclada</i>	Honduras	Allen	17684	MO	AY306927	AY306761
<i>Hildebrandtiella</i>	<i>subcapitata</i>	Comoros	Magill and Pocs	11234	MO	AY306928	AY306762
<i>Homalotheciella</i>	<i>acutifolia</i>	USA	Buck	32517	NY	AF143061	AF161154
<i>Hookeria</i>	<i>acutifolia</i>	Ecuador	Buck	39558	NY	AY306929	AY306763
<i>Hookeria</i>	<i>lucens</i>	USA	Allen	20123	MO	AF143071	AF161164
<i>Hookeria</i>	<i>lucens</i>	USA	Buck	37714	NY	AY306930	AY306764
<i>Hygroamblystegium</i>	<i>tenax</i>	USA	Buck	33464	NY	AF143047	AF161140
<i>Hypnella</i>	<i>diversifolia</i>	Ecuador	Buck	39277	NY	AY306931	AY306765
<i>Hypnella</i>	<i>pallescens</i>	French Guiana	Buck	37840	NY	AY306932	AY306766
<i>Hypnum</i>	<i>imponens</i>	USA	Buck	32496	NY	AF143034	AF161127
<i>Hypnum</i>	<i>lindbergii</i>	USA	Buck	33459	NY	AF143035	AF161128
<i>Hypopterygium</i>	<i>tamarisci</i>	Colombia	Churchill and Betancur	18102	NY	AF143077	AF161170
<i>Isopterygium</i>	<i>tenerum</i>	USA	Buck	33462	NY	AF143037	AF161130
<i>Isoetium</i>	<i>myosuroides</i>	USA	Schofield	105739	NY	AY306933	AY306767
<i>Lembophyllum</i>	<i>arbuscula</i>	Australia	Streimann	47425	MO	AY306934	AY306768
<i>Lembophyllum</i>	<i>divulsum</i>	Australia	Streimann	50840	NY	AF143045	AF161138
<i>Lembophyllum</i>	<i>divulsum</i>	Australia	Streimann	58549	MO	AY306935	AY306769
<i>Lembophyllum</i>	<i>divulsum</i>	New Zealand	Frahm	8-25	MO	AY306936	AY306770
<i>Lepidopilidium</i>	<i>laevisetum</i>	Brazil	Schafer-Verwimp	9237	NY	AY306937	AY306771
<i>Lepidopilidium</i>	<i>portoricense</i>	French Guiana	Buck	37825	NY	AY306939	AY306773
<i>Lepidopilidium</i>	<i>polytrichoides</i>	French Guiana	Buck	33307	NY	AY306938	AY306772
<i>Lepidopilium</i>	<i>scabrissetum</i>	Ecuador	Buck	39436	NY	AY306940	AY306774
<i>Lepidopilium</i>	<i>scabrissetum</i>	French Guiana	Buck	33081	NY	AF143066	AF161159
<i>Lepidopilium</i>	<i>surinamense</i>	French Guiana	Buck	33082	NY	AF143067	AF161160
<i>Lepyrodon</i>	<i>pseudolagarus</i>	New Zealand	Streimann	51300	NY	AF143014	AF161107
<i>Lepyrodontopsis</i>	<i>trichophylla</i>	Puerto Rico	Streimann	21117	NY	AY306941	AY306775
<i>Leskea</i>	<i>gracilescens</i>	USA	Buck	30102	NY	AF143042	AF161135
<i>Leskeodon</i>	<i>auratus</i>	Puerto Rico	Buck	18286	NY	AY306942	AY306776
<i>Leskeodon</i>	<i>cubensis</i>	St. Kitts	Buck	29474	NY	AF143072	AF161165
<i>Leucodon</i>	<i>andrewsianus</i>	USA	Buck	32502	NY	AF143005	AF161098
<i>Leucodon</i>	<i>brachypus</i>	USA	Buck	32510	NY	AF143004	AF161097
<i>Leucomium</i>	<i>strumosum</i>	French Guiana	Buck	33077	NY	AF143068	AF161161
<i>Leucomium</i>	<i>strumosum</i>	French Guiana	Holz	FG 00-268	NY	AY306943	AY306777
<i>Lindigia</i>	<i>debilis</i>	Ecuador	Churchill and Sastre	13553	MO	AY306944	AY306778
<i>Loeskeobryum</i>	<i>brevirostre</i>	USA	Buck	32522	NY	AF143079	AF161172
<i>Lopidium</i>	<i>concinnum</i>	Australia	Streimann	43706	NY	AY306945	AY306779
<i>Lopidium</i>	<i>concinnum</i>	Chile	Holz and Franzaring	20001	NY	AY306946	AY306780
<i>Lopidium</i>	<i>plumarium</i>	Brazil	Vital and Buck	20563	NY	AY306947	AY306781
<i>Meteoriidium</i>	<i>remotifolium</i>	Suriname	Allen	14337	MO	AY306949	AY306783
<i>Meteoriella</i>	<i>soluta</i>	China	Shevock	6695	MO	AY306950	AY306784
<i>Meteoriopsis</i>	<i>reclinata</i>	China	Allen	14422	MO	AY306948	AY306782
<i>Meteoriopsis</i>	<i>reclinata</i>	China	Shevock	14422	MO	AY306953	AY306787

APPENDIX. Continued.

Genus	Species	Country	Collector	Collection no.	Herbarium	ips4 GenBank no.	trnL GenBank no.
<i>Meteorium</i>	<i>buchananii</i>	Russia	Magill	12354	MO	AY306951	AY306785
<i>Meteorium</i>	<i>illicebrum</i>	Belize	Allen	18697	MO	AY306952	AY306786
<i>Myurium</i>	<i>hochstetteri</i>	Canary Islands	O'Shea	90B3	NY	AF143018	AF161111
<i>Neckera</i>	<i>pennata</i>	USA	Buck	32503	NY	AF143008	AF161101
<i>Neckeropsis</i>	<i>distica</i>	French Guiana	Buck	33041	NY	AF143010	AF161103
<i>Neobarbella</i>	<i>comes</i>	China	Yung-ge	3417	MO	AY306954	AY306788
<i>Neocladia</i>	<i>pendula</i>	China	Shevock	14451	MO	AY306955	AY306789
<i>Neorutenbergia</i>	<i>usagarae</i>	Tanzania	Pócs et al.	88110/A	NY	AF143019	AF161112
<i>Orthostichella</i>	<i>pentasticha</i>	Colombia	Ramirez P.	10764	MO	AY306957	AY306791
<i>Orthostichella</i>	<i>pentasticha</i>	Ecuador	Laegaard	18475B	MO	AY306956	AY306790
<i>Orthostichidium</i>	<i>involutum</i>	Gabon	Magill and Crosby	8474	MO	AY306958	AY306792
<i>Orthostichidium</i>	<i>pentagonum</i>	Puerto Rico	Allen	6393	MO	AY306959	AY306793
<i>Orthostichopsis</i>	<i>praetermissa</i>	Suriname	Allen	208000	MO	AY306960	AY306794
<i>Orthostichopsis</i>	<i>tetragona</i>	French Guiana	Buck	33036	NY	AF143012	AF161105
<i>Orthostichopsis</i>	<i>tetragona</i>	Suriname	Munoz	98-3	MO	AY306961	AY306795
<i>Papillaria</i>	<i>imponderosa</i>	Colombia	Churchill	19088	MO	AY306963	AY306797
<i>Papillaria</i>	<i>imponderosa</i>	Ecuador	Laegaard	18749B	MO	AY306962	AY306796
<i>Papillaria</i>	<i>imponderosa</i>	Ecuador	Laegaard	18749B	MO	AY306971	AY306805
<i>Papillaria</i>	<i>imponderosa</i>	Honduras	Allen	12360	MO	AY306964	AY306798
<i>Papillaria</i>	<i>imponderosa</i>	Honduras	Allen	14418	MO	AY306965	AY306799
<i>Papillaria</i>	<i>nigrescens</i>	Belize	Mann	32	NY	AF143051	AF161144
<i>Papillaria</i>	<i>nigrescens</i>	Belize	Allen	18060	MO	AY306967	AY306801
<i>Papillaria</i>	<i>nigrescens</i>	Belize	Allen	18647	MO	AY306968	AY306802
<i>Papillaria</i>	<i>nigrescens</i>	Honduras	Allen	17187	MO	AY306966	AY306800
<i>Papillaria</i>	<i>penicillata</i>	Colombia	Churchill et al.	18838	MO	AY306969	AY306803
<i>Papillaria</i>	<i>penicillata</i>	Honduras	Allen	12424	MO	AY306970	AY306804
<i>Penzigella</i>	<i>cordata</i>	Nepal	Weber	B-99381	NY	AY306972	AY306806
<i>Phyllogonium</i>	<i>tenuifolium</i>	Brazil	Schafer-Verwimp	14548	NY	AY306973	AY306807
<i>Phyllogonium</i>	<i>viride</i>	Brazil	Buck	26430	NY	AF143020	AF161113
<i>Pilosium</i>	<i>chlorophyllum</i>	French Guiana	Buck	32979	NY	AF143059	AF161152
<i>Pilotrichella</i>	<i>flexilis</i>	Belize	Allen	19009	MO	AY306979	AY306813
<i>Pilotrichella</i>	<i>flexilis</i>	Brazil	Buck	26385	NY	AF143046	AF161139
<i>Pilotrichella</i>	<i>panduraefolia</i>	South Africa	Smook	7346	MO	AY306980	AY306814
<i>Pilotrichidium</i>	<i>antillarum</i>	Puerto Rico	Buck	16127	NY	AY306975	AY306809
<i>Pilotrichidium</i>	<i>callicostatum</i>	Colombia	Buck	4725	NY	AY306977	AY306811
<i>Pilotrichium</i>	<i>andersonii</i>	Trinidad and Tobago	Betancur et al.	94-678	NY	AY306974	AY306808
<i>Pilotrichium</i>	<i>bipinnatum</i>	French Guiana	Djan-Chekar	FG 00-33	NY	AY306976	AY306810
<i>Pilotrichium</i>	<i>fendleri</i>	French Guiana	Holz	32966	NY	AF143069	AF161162
<i>Pilotrichium</i>	<i>procerum</i>	Dominica	Schafer-Verwimp	17941	NY	AY306978	AY306812
<i>Pilotrichium</i>	<i>cavifolium</i>	USA	Buck	32520	NY	AF143080	AF161173
<i>Plagiothecium</i>	<i>laetum</i>	Germany	Goffinet	4721	NY	AF143058	AF161151
<i>Platygyrium</i>	<i>repens</i>	USA	Buck	33448	NY	AF143038	AF161131
<i>Prionodon</i>	<i>densus</i>	Colombia	Churchill et al.	19068	NY	AF143076	AF161169
<i>Pseudocryphaea</i>	<i>domingensis</i>	Trinidad	Djan-Chekar	94-96	NY	AF143063	AF161156
<i>Pseudoscleropodium</i>	<i>purum</i>	Germany	Goffinet	4720	NY	AF143030	AF161123
<i>Pseudospidentopsis</i>	<i>horrida</i>	Viet Nam	Averyanov	B115	MO	AY306981	AY306815
<i>Pseudotrachypus</i>	<i>martincensis</i>	Dominican Republic	Buck	8207	NY	AY306982	AY306816
<i>Pterobryon</i>	<i>densum</i>	Colombia	Linares and Churchill	3649	NY	AF143013	AF161106

APPENDIX. Continued.

Genus	Species	Country	Collector	Collection no.	Herbarium	GenBank no.	trnL
<i>Psychomnion</i>	<i>aciculare</i>	Australia	Hiscox	3	NY	AF143015	AF161108
<i>Psychomnion</i>	<i>aciculare</i>	Australia	Streimann	43623	NY	AY306983	AY306817
<i>Psychomnion</i>	<i>cygnisetum</i>	Chile	Holz and Franzaring	CH 00-72	NY	AY306984	AY306818
<i>Psychomnion</i>	<i>psychocharpon</i>	Chile	Holz and Franzaring	CH 00-53	NY	AY306985	AY306819
<i>Pylaisiadelphina</i>	<i>tenuirostris</i>	USA	Buck	32500	NY	AF143053	AF161146
<i>Rhynchossteigiopsis</i>	<i>tunguraguana</i>	Colombia	Ramirez	7690	NY	AY306986	AY306820
<i>Rhytidadelphus</i>	<i>squarrosus</i>	Germany	Goffinet	4719	NY	AF143033	AF161126
<i>Santonia</i>	<i>georgico-uncinata</i>	Antarctica	Anderson	27704	NY	AF143049	AF161142
<i>Sauloma</i>	<i>tentella</i>	Australia	Streimann	59726	NY	AY306987	AY306821
<i>Schimperobryum</i>	<i>splendissimum</i>	Chile	Holz and Franzaring	Ch 00-156	NY	AY306988	AY306822
<i>Schwetschkeopsis</i>				Bryotheca Gottingensis fasc. I no. 20			
<i>Scleropodium</i>	<i>fabronia</i>	USA	Buck	33461	NY	AF143041	AF161134
<i>Scleropodium</i>	<i>obtusifolium</i>	USA	Shevock	17142	NY	AY306989	AY306823
<i>Sematophyllum</i>	<i>demissum</i>	USA	Buck	32607	NY	AF143055	AF161148
<i>Squamidium</i>	<i>brasiliense</i>	Brazil	Visnadi	5349	MO	AY306991	AY306825
<i>Squamidium</i>	<i>brasiliense</i>	Comoros	Pocs	9159/CL	MO	AY306990	AY306824
<i>Squamidium</i>	<i>leucostrichum</i>	Honduras	Allen	17416	MO	AY306992	AY306826
<i>Squamidium</i>	<i>leucostrichum</i>	Suriname	Allen	20670	MO	AY306993	AY306827
<i>Squamidium</i>	<i>macrocarpum</i>	Belize	Allen	18646	MO	AY306994	AY306828
<i>Squamidium</i>	<i>macrocarpum</i>	Belize	Allen	18885	MO	AY306995	AY306829
<i>Squamidium</i>	<i>nigricans</i>	Colombia	Ramirez	10763	MO	AY306996	AY306830
<i>Stenodictyon</i>	<i>pallidum</i>	Dominican Republic	Buck	7940	NY	AY306997	AY306831
<i>Stenodictyon</i>	<i>wrightii</i>	Ecuador	Buck	10014	NY	AY306998	AY306832
<i>Symphiodon</i>	<i>imbricatifolius</i>	Brazil	Schafer-Verwimp	14747	NY	AY306999	AY306833
<i>Taxithelium</i>	<i>planum</i>	French Guiana	Buck	33094	NY	AF143054	AF161147
<i>Tetraphidopsis</i>	<i>pusilla</i>	New Zealand	Fife	11592	NY	AY307001	AY306835
<i>Tetrastichium</i>	<i>fontanum</i>	Portugal	Dull	Bryophyta Exsiccata Madeira 69 94-652	NY	AY307000	AY306834
<i>Thamniopsis</i>	<i>cruegeriana</i>	Trinidad and Tobago	Djan-Chekar	18434	NY	AY307002	AY306836
<i>Thamniopsis</i>	<i>pendula</i>	Colombia	Churchill and Lineares		NY	AY307003	AY306837
<i>Thamniopsis</i>	<i>sinuata</i>	Colombia	Callejas et al.	2792	NY	AY307004	AY306838
<i>Thamniobryum</i>	<i>allegghanense</i>	USA	Buck	32721	NY	AF143009	AF161102
<i>Thelia</i>	<i>lescouri</i>	USA	Buck	32864	NY	AF143024	AF161132
<i>Thuidium</i>	<i>delicatulum</i>	USA	Buck	32594	NY	AF143039	AF161132
<i>Trachyloma</i>	<i>diversinerve</i>	Australia	Streimann	53949	NY	AF143021	AF161114
<i>Trachypodopsis</i>	<i>formosana</i>	China	Wang	860193	MO	AY307007	AY306841
<i>Trachypodopsis</i>	<i>serrulata</i>	Comoros	Pocs	9150/L	MO	AY307008	AY306842
<i>Trachypus</i>	<i>bicolor</i>	China	Buck	23918	NY	AF143052	AF161145
<i>Trachypus</i>	<i>bicolor</i>	South Africa	Burrows and Burrows	5984	MO	AY307010	AY306844
<i>Trachypus</i>	<i>bicolor var. viridulus</i>	Colombia	Ramirez	9775	MO	AY307009	AY306843
<i>Trachyxiophium</i>	<i>drepanophyllum</i>	Brazil	Vital and Buck	20012	NY	AY307005	AY306839
<i>Trachyxiophium</i>	<i>vagum</i>	Ecuador	Buck	39564	NY	AY307006	AY306840
<i>Trichosteleum</i>	<i>papillosum</i>	French Guiana	Buck	33002	NY	AF143056	AF161149
<i>Weymouthia</i>	<i>cochlearifolia</i>	Chile	Mahu	22751	MO	AY307012	AY306846
<i>Weymouthia</i>	<i>mollis</i>	Australia	Streimann	58584	MO	AY307011	AY306845
<i>Weymouthia</i>	<i>mollis</i>	Chile	Labbe	22746	MO	AY307014	AY306848
<i>Weymouthia</i>	<i>mollis</i>	New Zealand	Streimann	58094	MO	AY307013	AY306847
<i>Zelometeorium</i>	<i>patulum</i>	Belize	Allen	18606	MO	AY307015	AY306849
<i>Zelometeorium</i>	<i>patulum</i>	Colombia	Ramirez	11348	MO	AY307016	AY306850
<i>Zelometeorium</i>	<i>patulum</i>	French Guiana	Buck	33046	NY	AF143050	AF161143
<i>Zelometeorium</i>	<i>patulum</i>	Suriname	Allen	19462	MO	AY307017	AY306851
<i>Zelometeorium</i>	<i>recurvifolium</i>	Belize	Allen	15426	MO	AY307018	AY306852