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Author(s): Yin-Long Qiu, Libo Li, Bin Wang, Zhiduan Chen, Olena Dombrovska, Jungho Lee, Livija Kent, Ruiqi Li, Richard W. Jobson, Tory A. Hendry, David W. Taylor, Christopher M. Testa, and Mathew Ambros

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A NONFLOWERING LAND PLANT PHYLOGENY INFERRED FROM NUCLEOTIDE SEQUENCES OF SEVEN CHLOROPLAST, MITOCHONDRIAL, AND NUCLEAR GENES

Yin-Long Qiu,[1,*,†] Libo Li,[*,†] Bin Wang,[*,†] Zhiduan Chen,[‡] Olena Dombrovska,[*,†] Jungho Lee,[2,†] Livija Kent,[†] Ruiqi Li,[*] Richard W. Jobson,[*] Tory A. Hendry,[*] David W. Taylor,[*] Christopher M. Testa,[†] and Mathew Ambros[†]

*Department of Ecology and Evolutionary Biology, University Herbarium, University of Michigan, Ann Arbor, Michigan 48109-1048, U.S.A.; †Biology Department, University of Massachusetts, Amherst, Massachusetts 01003-5810, U.S.A.; and ‡State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, People's Republic of China

Nucleotide sequences of seven chloroplast (*atpB* and *rbcL*, SSU and LSU rDNAs), mitochondrial (*atp1*, LSU rDNA), and nuclear (18S rDNA) genes from 192 land plants and their algal relatives were analyzed using maximum likelihood and maximum parsimony methods. Liverworts, mosses, hornworts, lycophytes, monilophytes (ferns), seed plants, and angiosperms all represent strongly supported monophyletic groups. Three bryophyte lineages form a paraphyletic group to vascular plants, with liverworts representing the sister to all other land plants and hornworts being sister to vascular plants. Lycophytes are sister to all other vascular plants, which are divided into two clades, one being monilophytes, which include *Equisetum*, Psilotaceae-Ophioglossaceae, Marattiaceae, and leptosporangiate ferns, and the other being seed plants. Relationships among the monilophyte lineages remain unresolved. Within seed plants, extant gymnosperms form a moderately supported clade in which Gnetales are related to conifers. This clade is sister to angiosperms. Most of the relationships among all major lineages of nonflowering land plants are supported by bootstrap values of 75% or higher, except those among basal monilophyte lineages and among some gymnosperm lineages, probably because of extinctions. The closest algal relative of land plants is Characeae, and this relationship is well supported. Several methodological issues on reconstructing large, deep phylogenies are also discussed.

Keywords: land plants, phylogeny, liverworts, hornworts, life cycle, monilophytes, Gnetales.

Introduction

The origin and subsequent diversification of land plants (embryophytes) fundamentally changed terrestrial, atmospheric, and marine environments by accelerating rock weathering, changing atmospheric CO_2 and O_2 concentrations, and increasing mineral nutrient release into oceans (Schwartzman and Volk 1989; Graham 1993; Mora et al. 1996; Algeo et al. 2001; Berner 2001; Berner et al. 2003; Beerling and Berner 2005). These events altered the course of evolution of life and had particular impact on evolution of the organisms that coevolved with plants to establish the modern terrestrial ecosystems, e.g., animals (Banks and Colthart 1993; Edwards et al. 1995; Labandeira 1998, 2002; Dilcher 2000; Tiffney 2004) and fungi (Remy et al. 1994; Taylor et al. 1995, 2005; Brundrett 2002; Wang and Qiu 2006). Our understanding of events surrounding the origin of land plants and the history of interaction between plants and their abiotic and biotic environments depends on our knowledge of the land plant phylogeny.

[1] Author for correspondence; e-mail ylqiu@umich.edu.

[2] Current address: School of Biological Sciences, Seoul National University, Shillim, Kwanak, Seoul 151-747, Korea.

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Over the past two and half decades, a large number of studies have been carried out to analyze molecular and morphological characters from both living and extinct taxa to reconstruct various parts of the nonflowering land plant phylogeny. However, three areas of this phylogeny remain controversial. First, relationships among three bryophyte lineages (liverworts, mosses, and hornworts) and vascular plants are still vigorously contested (Mishler and Churchill 1984, 1985; Garbary et al. 1993; Mishler et al. 1994; Kenrick and Crane 1997; Hedderson et al. 1998; Qiu et al. 1998; Nickrent et al. 2000; Renzaglia et al. 2000; Samigullin et al. 2002; Dombrovska and Qiu 2004; Kelch et al. 2004; Nishiyama et al. 2004; Goremykin and Hellwig 2005; Groth-Malonek et al. 2005; Wolf et al. 2005). Second, relationships among basal members of monilophytes are only weakly to moderately supported (Hasebe et al. 1995; Pryer et al. 1995, 2001, 2004). Third, relationships among five extant gymnosperm lineages (cycads, *Ginkgo*, Pinaceae, nonpinaceous conifers, and Gnetales) and angiosperms are still being debated (Crane 1985; Doyle and Donoghue 1986; Nixon et al. 1994; Rothwell and Serbet 1994; Goremykin et al. 1996; Chaw et al. 1997, 2000; Bowe et al. 2000; Frohlich and Parker 2000; Gugerli et al. 2001; Magallón and Sanderson 2002; Rydin et al. 2002; Soltis et al. 2002; Burleigh and Mathews 2004).

The difficulty in resolving these relationships might have been caused by phenomena that characterize diversification of many major clades of organisms: large evolutionary gaps between major groups; ancient rapid radiations; the occurrence of highly divergent, relic lineages; evolutionary rate heterogeneity among different characters and different lineages; and extinctions. Several other factors further exacerbate an already difficult situation: an incomplete fossil record, character state paucity in DNA sequence evolution that results in a disproportionately large number of back mutations, and the occurrence of incompletely understood molecular evolutionary phenomena such as sequence composition bias and RNA editing. These factors often create problems for character and character state homology assessment and compromise performance of most phylogenetic methods (Kenrick and Crane 1997; Qiu and Palmer 1999; Delsuc et al. 2005). Empirical and theoretical studies have provided guidelines for overcoming some of these problems, specifically, increasing both taxon and character sampling and selecting well-understood characters from diverse sources (Raubeson and Jansen 1992; Chase et al. 1993; Hillis 1996; Graybeal 1998; Qiu et al. 1998, 1999; Soltis et al. 2000; Pryer et al. 2001; Zwickl and Hillis 2002; Kelch et al. 2004; Delsuc et al. 2005; Leebens-Mack et al. 2005).

In contrast to angiosperm phylogenetics, where several large-scale analyses sampling taxa across the entire group have complemented a large number of studies focusing on individual clades, together leading to a well-reconstructed angiosperm phylogeny (Chase et al. 1993; Soltis et al. 1997, 2000; Savolainen et al. 2000; Hilu et al. 2003), reconstruction of the nonflowering land plant phylogeny has so far been limited to studies that target problems in each of the three aforementioned areas individually. Considering the magnitude of the evolutionary gaps between major clades of land plants, it is understandable why such an approach has been taken. On the other hand, one may also question whether limited taxon sampling of outgroups might have affected the capability of phylogenetic methods to resolve relationships in ingroups. There are indeed a small number of studies that took the approach of broad taxon sampling across land plants to investigate relationships among major groups (Manhart 1994; Källersjö et al. 1998; Soltis et al. 1999; Nickrent et al. 2000; Renzaglia et al. 2000; Nishiyama et al. 2004; Goremykin and Hellwig 2005; Wolf et al. 2005), but limited taxon sampling within some major lineages of the ingroups and/or use of a small number of characters has probably undermined performance of phylogenetic methods.

In this study, we take an approach of broad taxon sampling across land plants with dense sampling in species-rich clades coupled with extensive character sampling to reconstruct the nonflowering land plant phylogeny. We recently finished analyzing six genes (chloroplast *atpB* and *rbcL* as well as LSU and SSU rDNAs, mitochondrial LSU rDNA, and nuclear 18S rDNA) from 193 land plants and green algae, together with a matrix of mitochondrial group II intron insertion sites and a matrix of chloroplast genome sequences. Analyses of all three data sets strongly supported liverworts as the sister to all other land plants, and analyses of the six-gene and chloroplast genome matrices provided moderate to strong support for placement of hornworts as the sister to vascular plants (Qiu et al. 2006*b*). Here, we add a seventh gene, mitochondrial *atp1*, which still lacks data from hornworts, to the six-gene matrix and perform maximum likelihood and maximum parsimony analyses. Our specific goals are (1) to evaluate further relationships among three bryophyte lineages and vascular plants and to examine relationships within liverworts and mosses, (2) to determine relationships among basal monilophytes, and (3) to assess the phylogenetic position of Gnetales.

Material and Methods

Our basic taxon sampling strategy was to sample one species from each of most nonflowering land plant families. We followed the classification systems of Schuster (1966) and Crandall-Stotler and Stotler (2000) for liverworts and hornworts, Crum and Anderson (1981) and Goffinet and Buck (2004) for mosses, and Kramer and Green (1990) for ferns and allies as well as gymnosperms. As a result, a large number of liverworts, mosses, ferns, and gymnosperms were included. For lineages without much living diversity but occupying pivotal phylogenetic positions, e.g., hornworts, lycophytes, *Takakia*, *Sphagnum*, and several basal monilophyte families, we included more than one species from each family. Major lineages of basal angiosperms (Qiu et al. 1999) were sampled to represent angiosperms. All five charophyte lineages (Graham 1993; Karol et al. 2001) and a prasinophycean green alga, *Nephroselmis olivacea*, were used as the outgroup. We hoped that this taxon sampling scheme would allow accurate inference of ancestral states at most deep internal nodes and thus ensure reliable reconstruction of relationships among major clades of land plants because inclusion of most living major lineages should help reveal intermediate states of character evolution. A total of 192 species (congeneric species were used to represent one terminal in some cases) were included; their detailed information is provided in table A1. The liverwort *Corsinia coriandrina*, which was used in another study (Qiu et al. 2006*b*), might have been misidentified and is thus excluded from analyses here.

The seven genes analyzed here show slow (all five rDNAs) to moderate (*atp1* and *rbcL*) to fast (*atpB*) evolutionary rates under this particular taxon-sampling scheme. The reason we sampled this combination of genes was to achieve a balance between maximizing signal retrieval and optimizing homoplasy assortment: slow-evolving genes would be good for resolving deep relationships but might not have sufficient signal, whereas fast-evolving genes would provide a lot of variable characters but might generate spurious groupings of certain taxa at the same time (Källersjö et al. 1999; Hilu et al. 2003; Qiu et al. 2006*b*). For 192 taxa analyzed, 188, 191, 192, 192, 177, 171, and 188 taxa had sequences for cp-*atpB*, cp-*rbcL*, cp-LSU rDNA, cp-SSU rDNA, mt-*atp1*, mt-LSU rDNA, and nu-18S rDNA, respectively. All species had data for three or more genes. Among these data, 134 new *atp1* sequences were generated in this study. Table A1 provides detailed information on all the sequences analyzed here.

The methods of DNA extraction, gene amplification, and sequencing are as described previously (Qiu et al. 1999, 2000). The primer sequence information is available upon request.

All seven genes were aligned individually using ClustalX (http://www.csc.fi/molbio/progs/clustalw/clustalw.html) and then adjusted manually. For mt-LSU rDNA, autapomorphic insertions/introns were removed in *Klebsormidium flaccidum*, liverworts, mosses, and vascular plants. The data were then concatenated to form a multigene matrix. The alignment has 14,553 nucleotide positions.

Both maximum likelihood (ML) and maximum parsimony (MP) methods were used to analyze the data. For ML analyses, an optimal model of nucleotide evolution (general time-reversible model $+ I + \Gamma$, with parameter values for the proportion of invariant sites [$I = 0.27$] and the gamma distribution [$\Gamma = 0.60$]) was selected using the Akaike Information Criterion as implemented in Modeltest, version 3.07 (Posada and Crandall 1998). The ML analyses were then implemented in PHYML, version 2.4.4 (Guindon and Gascuel 2003), under the model with all parameters as estimated by Modeltest. One hundred bootstrap (BS) replicates were used in a bootstrapping analysis to assess nodal support (Felsenstein 1985). For parsimony analyses, only bootstrapping analyses were performed, using both PAUP*, version 4.0b10 (Swofford 2003), and NONA (Goloboff 1998), as implemented in Winclada (Nixon 2001). The PAUP bootstrapping analysis was conducted with 500 replicates, using simple taxon addition, one tree held at each step during stepwise addition, tree-bisection-reconnection branch swapping, steepest descent option on, MulTree option on, and no upper limit of MaxTree set. The NONA bootstrapping analysis was performed using 1000 replicates, with five trees held per replicate and 50 characters randomly reweighed per iteration.

Results

The ML and MP analyses recovered trees with virtually identical topologies and mostly similar bootstrap values (fig. 1; table 1; additional data not shown). Liverworts, mosses, hornworts, vascular plants, lycophytes, monilophytes, seed plants, and angiosperms were all strongly supported as monophyletic groups (BS values between 90% and 100% are deemed to have strong support, and those between 75% and 90% and below 75% are considered to have moderate and weak support, respectively). The three bryophyte lineages formed serial sister groups to vascular plants. Liverworts were sister to all other land plants, with 100% and 87% ML BS values, 100% and 91% PAUP parsimony bootstrap (P-BS) values, and 100% and 93% NONA parsimony bootstrap (N-BS) values (where the first value of each pair defines the placement of liverworts within land plants and the second value separates all other land plants from liverworts). Mosses followed liverworts, with values of 87% and 87% for ML BS, 91% and 76% for P-BS, and 93% and 82% for N-BS. Hornworts were sister to vascular plants, with values of 87% and 100% for ML, 76% and 100% for P-BS, and 82% and 100% for N-BS. The most closely related charophyte algae to land plants were *Chara* and *Nitella* of Characeae, with values of 93% and 100% for ML BS, 87% and 100% for P-BS, and 89% and 100% for N-BS.

Within the liverworts, *Haplomitrium* and *Treubia* formed a moderately supported clade sister to all other taxa, with values of 100% and 92% for ML BS, 100% and <50% for P-BS, and 100% and 50% for N-BS. The rest of liverworts fell into two strongly supported monophyletic groups, which corresponded to traditionally recognized complex thalloid liverworts (node 4) and simple thalloid plus leafy liverworts (node 6). *Blasia*, which used to be classified as a simple thalloid liverwort, was sister to the complex thalloid liverworts. The simple thalloid liverworts were paraphyletic to the monophyletic leafy liverworts (node 7).

Among the mosses, *Takakia* and *Sphagnum* formed a moderately supported clade sister to the remaining taxa, with values of 100% and 100% for ML BS, 100% and 81% for P-BS, and 100% and 84% for N-BS. Several isolated, divergent lineages, *Andreaea*, *Tetraphis*, *Atrichum*, and *Polytrichum* of Polytrichaceae as well as *Buxbaumia* and *Diphyscium*, formed serial sister groups to a clade composed of "true" arthrodontous mosses (node 13). Within this clade, two strongly supported monophyletic groups were identified: one corresponding to the diplolepidous alternate peristomate mosses (node 15) and the other corresponding to the rest (node 14). *Archidium*, an eperitomate moss traditionally regarded as being distinct from "true" arthrodontous mosses, fell into this latter group. Among the diplolepidous alternate peristomate mosses, pleurocarpous mosses formed a strongly supported monophyletic group (node 16).

Within the vascular plants, lycophytes were sister to the remaining taxa, with values of 100% and 100% in all three bootstrapping analyses. Relationships among basal members of monilophytes (*Equisetum*, Marattiaceae, Psilotaceae-Ophioglossaceae, and leptosporangiate ferns) were poorly supported. Relationships within leptosporangiate ferns were generally well supported except for the placement of gleichenoid ferns (*Hymenophyllum*, *Trichomanes*, and *Gleichenia*).

Among the seed plants, gymnosperms formed a monophyletic group with values of 87% for ML BS, 68% for P-BS, and <50% for N-BS, being sister to angiosperms. Cycads and *Ginkgo* were serial sister groups to the clade containing conifers and Gnetales in the ML analyses. Gnetales were sister to Pinaceae, with values of 67% and 100% for ML BS, and together, they were sister to a strongly supported nonpinaceous conifer clade, with values of 87% and 100% for ML BS. In both parsimony bootstrapping analyses, cycads and *Ginkgo* formed a weakly supported monophyletic group, and they were sister to the clade consisting of the remaining gymnosperms in the PAUP parsimony analysis and were part of a polytomy including Gnetales, Pinaceae, other conifers, and angiosperms in the NONA parsimony analysis. Relationships among these clades were all weakly supported. Within angiosperms, *Amborella*, Nymphaeales, and Austrobaileyales formed three serial sister groups to the rest of taxa, and the relationships had weak to strong bootstrap support.

Discussion

In this study of sampling 192 diverse land plants and green algae and seven genes from all three plant genomes, likelihood and parsimony methods recovered trees with virtually identical topologies and moderate to strong bootstrap support throughout much of the trees (fig. 1). Several aspects of

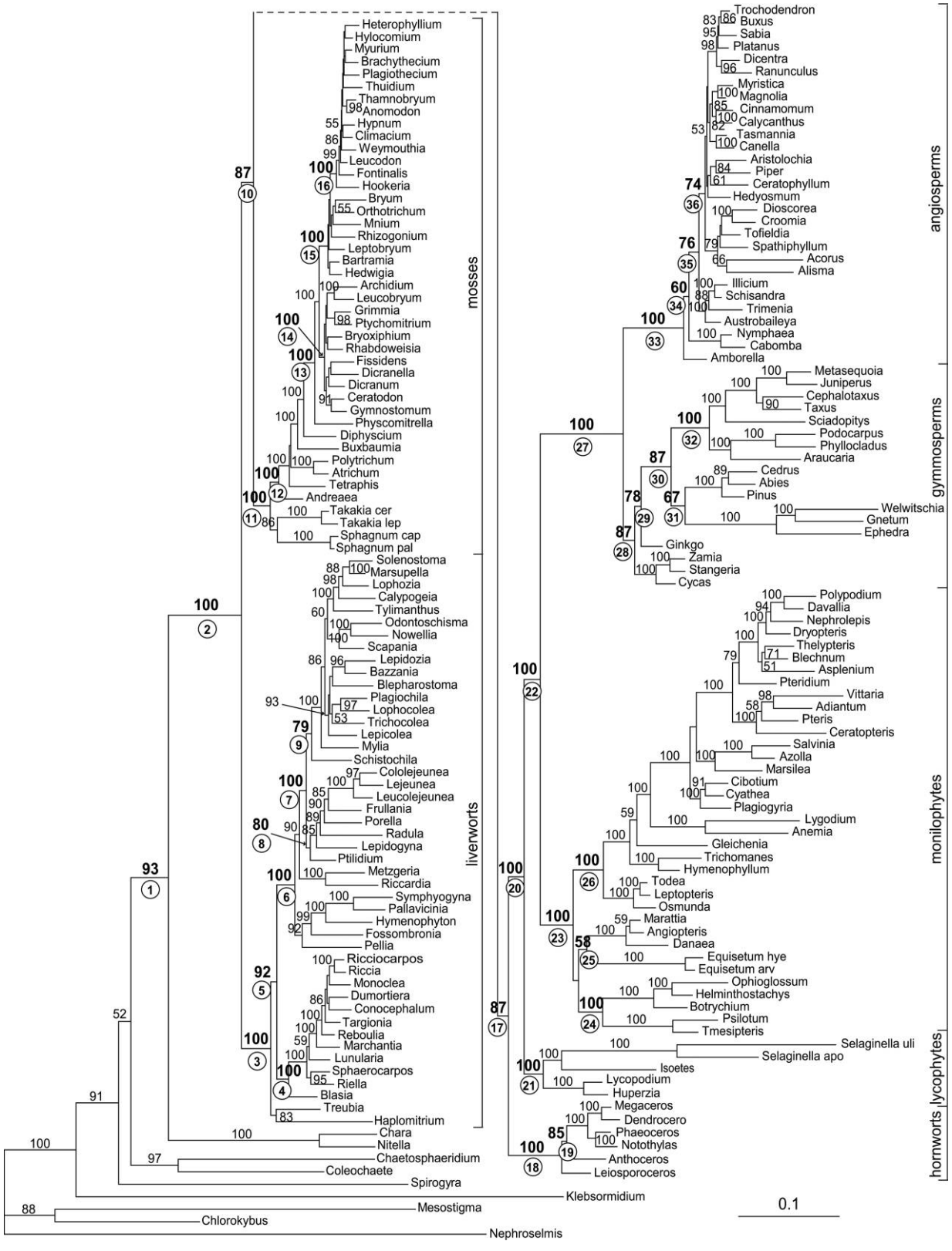

Fig. 1 Phylogram from a maximum likelihood analysis of the seven-gene, 192-taxon matrix of land plants in this study (ln likelihood = −296,341.161413). Numbers above (and occasionally to the right of) branches are bootstrap percentage values at or above 50%. Bootstrap values depicting the backbone relationships in land plants are shown in larger, boldface type. Numbers in circles indicate the nodes for which PAUP and NONA parsimony bootstrap values are presented in table 1.

Table 1

Bootstrap Percentage Values for the Nodes Labeled in Figure 1

Node	P-BS	N-BS
1	87	89
2	100	100
3	100	100
4	100	100
5	<50	<50
6	100	99
7	100	98
8	73	65
9	56	<50
10	91	93
11	100	100
12	81	84
13	100	100
14	98	100
15	99	99
16	100	100
17	76	82
18	100	100
19	72	64
20	100	100
21	100	100
22	100	100
23	100	100
24	100	100
25	71	65
26	100	100
27	100	100
28	68	<50
29	...[a]	...[a]
30	69	<50
31	<50	<50
32	100	100
33	100	100
34	78	70
35	92	93
36	92	93

Note. P-BS and N-BS = bootstrap percentage values from the PAUP and NONA parsimony analyses, respectively.

[a] *Ginkgo* was sister to the cycads, with values of 63% for P-BS and 61% for N-BS.

this reconstructed phylogeny permit an optimistic interpretation that we are close to the goal of understanding the evolutionary history of nonflowering land plants. First, the backbone of the trees is supported by moderate to high bootstrap values, which are deemed to be more reliable indicators of phylogenetic reconstruction than optimality criteria such as parsimony length or likelihood of trees (Nei et al. 1998). Second, monophylies of many traditionally recognized groups, e.g., liverworts, mosses, vascular plants, and lycophytes, were confirmed, indicating a level of congruence between results of this study and classic morphological studies. Earlier molecular phylogenetic studies often yielded unconventional results and raised doubt about the naturalness of these groups (e.g., Manhart 1994; Källersjö et al. 1998; Soltis et al. 1999; see also review in Qiu and Palmer 1999). In retrospect, those results were probably artifacts caused by low information content of single genes and sparse taxon sampling (Hillis 1996). Third, relationships within all major clades recovered in this study generally agree with those reconstructed in the studies that focused on these clades individually and had more broad ingroup taxon sampling and/or extensive character sampling, e.g., liverworts (Heinrichs et al. 2005; Forrest et al. 2006; He-Nygren et al. 2006), mosses (Goffinet et al. 2001; Cox et al. 2004), hornworts (Duff et al. 2004), lycophytes (Wikstrom and Kenrick 2001), leptosporangiate ferns (Pryer et al. 2004), seed plants (Goremykin et al. 1996; Bowe et al. 2000; Chaw et al. 2000; Gugerli et al. 2001; Burleigh and Mathews 2004), and angiosperms (Qiu et al. 1999; Soltis et al. 2000). Fourth, for the relationships that were deemed to be novel from molecular phylogenetic studies conducted over the past 15 yr, namely, the sister relationship of lycophytes to all other vascular plants (Raubeson and Jansen 1992), monophyly of monilophytes, and the sister relationship between Psilotaceae and Ophioglossaceae (Pryer et al. 2001), this study obtained the same results as previous studies, with high bootstrap support. Finally, for the relationships that have been vigorously contested in recent molecular phylogenetic studies, i.e., the relationships among three bryophyte lineages and the placement of Gnetales, this study obtained resolution with moderate to strong bootstrap support, at least in the likelihood analysis. The only area where this study did not achieve its goal is in the relationship among basal members of monilophytes. One important point we want to emphasize is that besides having high bootstrap values, most of the relationships identified here conform to one of the previous hypotheses formulated based on morphology. Below we discuss these three last issues in detail and also some methodological issues.

Relationships among and within Three Bryophyte Lineages

Since the cladistic analyses of Mishler and Churchill (1984, 1985), relationships among three bryophyte lineages have been subject to intensive debate. The discussion centers around three questions: (1) Do liverworts or hornworts represent the sister group of all other land plants (Mishler and Churchill 1984; Mishler et al. 1994; Kenrick and Crane 1997; Hedderson et al. 1998; Qiu et al. 1998; Nickrent et al. 2000; Renzaglia et al. 2000; Dombrovska and Qiu 2004; Kelch et al. 2004)? (2) Are mosses or hornworts sister to vascular plants (Mishler and Churchill 1984; Kenrick and Crane 1997; Samigullin et al. 2002; Dombrovska and Qiu 2004; Kelch et al. 2004; Groth-Malonek et al. 2005)? (3) Are bryophytes mono- or paraphyletic (Garbary et al. 1993; Nishiyama et al. 2004; Goremykin and Hellwig 2005)?

In a recent study, we analyzed a six-gene, 193-species data set together with a mitochondrial group II intron insertion site matrix and a chloroplast genome sequence matrix. Analyses of all three data sets showed bryophytes to be paraphyletic to vascular plants and strongly supported liverworts as the sister group of all other land plants. Analyses of the six-gene and the chloroplast genome matrices provided moderate to strong support for placement of hornworts as the sister to vascular plants (Qiu et al. 2006*b*). Our analyses of the seven-

gene supermatrix here, which still lack *atp1* data for hornworts, obtained results similar to those of the earlier study. The taxon and character sampling in these two supermatrices represents by far the most extensive data sampling in investigation of early land plant phylogeny. An issue has been raised in the past regarding whether the divergence between charophytes and land plants is large enough to cause a rooting problem (Qiu and Palmer 1999), and this issue has not been explicitly investigated using the random sequence outgroup rooting approach as was done for the basal angiosperm relationships (Qiu et al. 2001). However, the intron matrix, which does not suffer from the kind of long-branch attraction problem that normally affects the nucleotide sequence matrices, produced the same rooting as the multigene supermatrices. This result indicates that the six- and seven-gene supermatrices contain sufficient phylogenetic signal to overcome the outgroup divergence problem, allowing appropriate rooting of the ingroup. In light of these results and of morphological, biochemical, and fossil evidence presented in previous studies (Mishler and Churchill 1984; Sztein et al. 1995; Kenrick and Crane 1997; Wellman et al. 2003), we believe that the position of liverworts as the basalmost lineage in the land plant phylogeny is secure.

The placement of hornworts as sister to vascular plants revealed in analyses of the six- and seven-gene supermatrices is somewhat novel and has been shown in a few earlier analyses of smaller data sets, which cover features from single genes to chloroplast genome sequences and chloroplast and mitochondrial genomic structural features (Lewis et al. 1997; Samigullin et al. 2002; Dombrovska and Qiu 2004; Kelch et al. 2004; Groth-Malonek et al. 2005; Wolf et al. 2005). Although the bootstrap values in our analyses for this relationship are still in the range of 76%–90% (fig. 1; table A1; Qiu et al. 2006*b*), we think this placement reflects the correct position of hornworts in the land plant phylogeny for the following reasons. First, there are morphological and physiological characters that support a close relationship between hornworts and vascular plants. These include lack of ventral slime papillae, hairs, and/or scales in prothalli (Renzaglia et al. 2000); embedded position of gametangia (Smith 1955; Schuster 1992); the intermingled/interdigitate gametophyte-sporophyte junction (Frey et al. 2001); the persistently chlorophyllous and nutritionally largely independent sporophyte (Campbell 1924; Stewart and Rodgers 1977; Schuster 1992); rhizoidlike behavior of surface cells of the sporophyte foot (Campbell 1924); the longevity and large size of the sporophyte (Campbell 1924; Schuster 1992); and xylan content in cell walls of pseudoelaters and spores (Carafa et al. 2005). Some of these similarities between hornworts and vascular plants may be controversial (Mishler and Churchill 1984; Kenrick and Crane 1997; Renzaglia et al. 2000), but our molecular phylogenetic results suggest that they should be critically reexamined to identify truly synapomorphic changes shared by these two groups. Morphological cladistic analyses by both Mishler and Churchill (1984) and Kenrick and Crane (1997) acknowledged that the position of hornworts in their studies was unstable, and sometimes hornworts came to be sister to vascular plants.

Second, the placement of hornworts as sister to vascular plants fits best with our current understanding on evolution of life cycles in land plants. When life cycles of different lineages of land plants are compared under a phylogenetic framework that has been developed over the past several decades (i.e., charophytes giving rise to land plants, bryophytes predating vascular plants, and angiosperms representing one of the youngest major land plant clades; Pickett-Heaps 1975; Stewart 1983; Gray 1993; Kenrick and Crane 1997; Wellman et al. 2003), it becomes clear that they have followed a trend of continuously expanding their sporophyte generation while at the same time reducing the gametophyte generation (Bower 1908, 1935; Stebbins 1950; Takhtajan 1976). This change is probably in response to selection pressure that plants encountered on land, where sperm locomotion is hindered by lack of water and DNA mutation rate is high because of abundant UV, since plants having a big, multicellular, and long-lived sporophyte can have numerous cells going through meiosis that will lead to production of a large number of genetically diverse gametes to ensure fertilization, mask deleterious effect of mutations, and allow a large number of alleles to persist in the gene pool through recessive and dominant allelic interactions (Bower 1935; Stebbins 1950; Graham 1993; Crum 2001). Three bryophyte lineages, although they all have a dominant gametophyte generation in their life cycles, exhibit different degrees of sporophyte nutrition independence. Liverworts have small, short-lived, and matrotrophic sporophytes (Crum 2001). Mosses have short- to long-lived, photosynthetic, yet generally matrotrophic sporophytes (Bold 1940; Stark 2002). Hornworts have short- to long-lived sporophytes that are nutritionally the most independent sporophytes among all bryophytes (Campbell 1924; Stewart and Rodgers 1977; Schuster 1992). In fact, Campbell (1924) reported that *Anthoceros fusiformis* had biennial, nearly free-living sporophytes in the wild, with the gametophytic tissues around the base of the sporophyte discolored and more or less collapsed. He also showed that excised sporophytes survived independent of the gametophyte on sterile soil for 3 mo. It should be added here that the extinct prevascular plant *Horneophyton lignieri*, shown to be positioned between bryophytes and vascular plants (Kenrick and Crane 1997), exhibits several features reminiscent of hornworts: a massive lobed rhizome (like the lobed foot of *Anthoceros*), the shoot terminating in a single sporangium, hornwortlike stem anatomy, the growth habit of sporophytes (Campbell 1924), and an unequivocal columella in the sporangium (Kenrick and Crane 1997 and references therein). The lobed foot of the hornwort sporophyte, with rhizoidlike absorbing cells on the surface (Campbell 1924), is similar, and probably homologous, to the protocorm of some lycophytes, the development of which has been interpreted as essential for establishment of a free-living sporophyte (Bower 1908). We also wish to point out that the positions of sporophytes on gametophytes in three bryophyte lineages can be informative to the discussion of alternation of generations in early land plants and the placement of hornworts as the sister to vascular plants shown here. In basal lineages of liverworts (e.g., *Haplomitrium* and many thalloid liverworts) and mosses (*Takakia* and acrocarpous mosses), the sporophytes are on elevated positions of gametophytes and high above the ground. In hornworts, however, the sporophytes grow uniformly out of thalloid gametophytes, and thus if gametophytes die, sporophytes

may be able to survive on their own because of their preadaptation to the soil environment. This was indeed what Campbell (1924) observed for *A. fusiformis* in the wild. From the evidence discussed above, it seems that hornworts, among the three extant bryophyte lineages, approach closest toward vascular plants in their sporophyte development in terms of achieving an independent, free-living sporophyte generation. Thus, the elaborate, nutritionally largely independent sporophyte generation of hornworts can perhaps be taken as evidence to support their close relationship to vascular plants.

Finally, in molecular phylogenetic studies that either identified hornworts as sister to all other land plants (Nickrent et al. 2000; Renzaglia et al. 2000) or recovered bryophytes as a monophyletic group (Nishiyama et al. 2004; Goremykin and Hellwig 2005), there is a possibility that those two topologies were analytical artifacts caused by rooting problems. In both of those two topologies, if the root of land plant phylogeny is changed to liverworts, hornworts become sister to vascular plants. Nickrent et al. (2000) and Nishiyama et al. (2004) actually obtained the topology we produced here (i.e., liverworts sister to all other land plants and hornworts sister to vascular plants) with some of their data sets, but they claimed that those results were caused by homoplasy in the third-codon transitional changes (Nickrent et al. 2000) or by base composition bias in the chloroplast genome (Nishiyama et al. 2004). These are controversial issues, and empirical evidence tends to suggest that while the third-codon positions and transitions can be problematic when taxon sampling is sparse, they actually contain a significant amount of phylogenetic signal (Källersjö et al. 1999; Qiu et al. 2005). In analyses of the chloroplast genome sequences that differ from those of Nishiyama et al. (2004) and Goremykin and Hellwig (2005) by addition of a lycophyte (*Huperzia*), Wolf et al. (2005) found that bryophytes were paraphyletic and hornworts were associated with vascular plants in all data partitions. Qiu et al. (2006*b*) obtained the same results when analyzing a larger chloroplast genome sequence data set that included two more charophytes, one more lycophyte (*Selaginella*), and several more angiosperms. Hence, we suggest that the molecular evidence against the hypothesis of hornworts being sister to vascular plants is rather weak. To the contrary, those other studies can in fact be seen to contain evidence to support our hypothesis when the rooting issue is dissected carefully.

The relationships within liverworts are better resolved in this study than in that of Qiu et al. (2006*b*) because of addition of the moderately fast-evolving mitochondrial gene *atp1* (fig. 1; table 1). *Haplomitrium-Treubia* were shown to be sister to the remaining liverworts, with 92% ML BS support. Although *Haplomitrium* was recognized to be distinct from all other liverworts by Schuster (1966), the affinity of *Treubia* to *Haplomitrium* and the sister relationship of these two genera to all other liverworts were realized only recently (Garbary et al. 1993; Heinrichs et al. 2005; Forrest et al. 2006; He-Nygren et al. 2006). Our large-scale analyses with extensive taxon sampling both within and outside of liverworts play an instrumental role in helping identifying this deepest dichotomy within liverworts (Qiu et al. 2006*b*; this study). Similarly, our analyses provide a critical piece of evidence to support *Blasia* as the sister to complex thalloid liverworts because of the broad scope of taxon coverage. Previously, *Blasia* was suggested to be more closely related to complex thalloid liverworts than to simple thalloid liverworts (Duckett et al. 1982; Garbary et al. 1993; Heinrichs et al. 2005; Forrest et al. 2006; He-Nygren et al. 2006). The current study also produced weak to moderate support for *Ptilidium* as sister to the complex consisting of Lejeuneaceae-Frullaniaceae-Porellaceae-Radulacea-Lepidolaenaceae. Three previous studies focusing on liverworts (Heinrichs et al. 2005; Forrest et al. 2006; He-Nygren et al. 2006) as well as our earlier study (Qiu et al. 2006*b*) were unable to identify the split of leafy liverworts between this complex (node 8) and the rest (node 9); the positions of *Ptilidium* and some related taxa were unstable in those studies. This particular result demonstrates an advantage of extensive taxon sampling both within and outside of a group in resolving relationships among major lineages in the group and determining the position of some difficult isolated lineages.

The relationships within mosses inferred here are similar to those proposed by Qiu et al. (2006*b*). *Takakia*, extensively debated for its phylogenetic affinity before discovery of its sporophyte (Smith and Davison 1993), is clearly shown to be a moss, as there is strong bootstrap support for monophyly of mosses. Its sister relationship to *Sphagnum* is moderately supported (fig. 1). Compared to the results of Goffinet et al. (2001) and Cox et al. (2004), several major clades identified in our two sets of analyses have higher or significantly higher bootstrap support, all values approaching 100% (fig. 1; table 1). These include the "true" arthrodontous mosses (node 13), the Haplolepideae (*sensu* Goffinet et al. 2001; node 14), the diplolepidous alternate peristomate mosses (node 15), and the pleurocarpous mosses (node 16). The relationships within the Haplolepideae and the pleurocarpous mosses are poorly resolved, probably reflecting rapid radiations of these mosses because of their colonization of new habitats (Shaw et al. 2003).

The relationships within hornworts inferred in our two sets of analyses are congruent to those of Duff et al. (2004), who used only *rbcL*. Two particular points worth mentioning are the sister relationship of *Leiosporoceros* to all other hornworts and the embedded position of *Notothylas*, which traditionally was placed in a family separate from all other hornworts.

Relationships among Basal Lineages of Monilophytes

Since identification of monilophytes as a monophyletic group that includes the traditionally delimited ferns and their allies of *Equisetum* and Psilotaceae but not lycophytes (Kenrick and Crane 1997; Pryer et al. 2001), there has been an interest in clarifying relationships among several basal lineages in this group: *Equisetum*, Psilotaceae, Ophioglossaceae, Marattiaceae, and leptosporangiate ferns (Pryer et al. 2004; Wikstrom and Pryer 2005). In a series of analyses (Pryer et al. 2001, 2004; Wikstrom and Pryer 2005), *Equisetum*-Marattiaceae have been shown to be sister to leptosporangiate ferns, but bootstrap support for this relationship is only moderate. Further, like many novel relationships identified in molecular phylogenetic studies, the sister relationship between these two groups of free-sporing vascular plants still

lacks morphological synapomorphy to corroborate it (Pryer et al. 2004). With the extensive outgroup taxon sampling in this study, we thought relationships among the basal monilophytes might be better resolved, but we did not succeed in achieving that goal. In a comparison of the genes used by Pryer et al. (2001, 2004; chloroplast *atpB*, *rbcL*, and *rps* as well as nuclear 18S) and Wikstrom and Pryer (2005; the previous four genes plus mitochondrial *atp1*) and those used in this study (chloroplast *atpB*, *rbcL*, SSU, and LSU, mitochondrial *atp1* and LSU, and nuclear 18S), the difference between their results and ours might be explained by either lack of signal in the many slow-evolving genes we used or a possibility of long-branch attraction caused by the dominance of fast-evolving genes in their analyses (*atpB* and *rps4*). The current difficulty in resolving relationships among these basal monilophytes may be caused by the extinction these plants suffered over the past 400 million years and rapid radiation experienced by early vascular plants during the Devonian (Stewart 1983; Kenrick and Crane 1997). Future studies sampling more genes with different rates and functions and from different genomes might shed light on this ancient radiation. Genomic structural characters, such as intron distribution explored by Wikstrom and Pryer (2005), may also offer an additional source of characters for resolving these relationships.

Monophyly of Extant Gymnosperms and Affinity of Gnetales

Relationships among five extant seed plant lineages—cycads, *Ginkgo*, conifers, Gnetales, and angiosperms—have been vigorously contested in morphological and molecular phylogenetic studies over the past 2 decades. Specifically, molecular studies have often shown that the four extant gymnosperm lineages form a monophyletic group sister to angiosperms and that Gnetales are embedded among conifers (Goremykin et al. 1996; Chaw et al. 1997, 2000; Qiu et al. 1999; Bowe et al. 2000; Frohlich and Parker 2000; Gugerli et al. 2001; Magallón and Sanderson 2002; Rydin et al. 2002; Soltis et al. 2002; Burleigh and Mathews 2004). On the other hand, morphological studies have suggested that the living gymnosperms are paraphyletic to angiosperms and that Gnetales are related to angiosperms (Crane 1985; Doyle and Donoghue 1986; Nixon et al. 1994; Rothwell and Serbet 1994). In our current study, we paid particular attention to this problem in the experimental design by sampling nonseed plants extensively and choosing five slow-evolving genes (the rRNA genes from all three genomic compartments) among the seven genes analyzed so that the perceived problems of insufficient outgroup taxon sampling and extinctions of seed plants (Stewart 1983) could be remedied.

The results we obtained here are improved over those of our earlier analyses (Qiu et al. 2006*b*) in terms of resolution and bootstrap support on relationships among seed plant lineages. Both studies show that we are making progress toward solving this long-standing problem. Both monophyly of extant gymnosperms and the coniferous affinity of Gnetales suggested by the previous molecular studies were recovered here. The taxon sampling scheme and gene choices used in our analyses, very different from those employed in the earlier molecular studies, should serve as evidence of independent corroboration. In our two parsimony analyses, bootstrap values for monophyly of gymnosperms and sister relationship between Gnetales and Pinaceae decreased significantly (table 1). These were probably results of long-branch attraction between Gnetales and the nonseed plants in the data set; parsimony methods are more sensitive to such a problem than are likelihood methods (Felsenstein 1978). Consistent with this diagnosis, we observed higher bootstrap values than those shown in figure 1 for these relationships when the fast-evolving gene *atpB* was excluded from the matrix (data not shown). This observation has also been made in several earlier studies on volatility of the position of Gnetales when the third-codon positions alone or fast-evolving sites were used in analyses (Magallón and Sanderson 2002; Rydin et al. 2002; Burleigh and Mathews 2004). Hence, we think molecular evidence is accumulating to support monophyly of extant gymnosperms and the coniferous affinity of Gnetales.

Problems in Reconstructing the Land Plant Phylogeny and Strategies to Overcome These Problems

Reconstructing phylogeny for a group such as land plants, which encompasses more than 300,000 living species, has undergone several episodic radiations, spans an evolutionary time of more than 480 million years, and has experienced many extinction events during this period of the earth's history, faces many daunting challenges. These include large evolutionary gaps between major groups; ancient rapid radiations; the occurrence of highly divergent, relic lineages; extinctions; evolutionary rate heterogeneity among different characters and lineages; DNA sequence composition bias; and RNA editing (Kenrick and Crane 1997; Qiu and Palmer 1999).

Among all these challenges, the most difficult ones are the large evolutionary gaps among major lineages. These problems may be caused by evolutionary rate heterogeneity, extinctions, and rapid radiation during the incipient period of a major lineage when it explored a new niche. The most effective strategy for overcoming these problems is perhaps to engineer an experimental design that samples a large number of taxa to represent both the phylogenetic breadth and depth of land plants and that chooses a set of genes with well-balanced evolutionary rates as well as functional and genomic representations. The issue of taxon versus character sampling has been debated extensively (Hillis 1996; Graybeal 1998; Zwickl and Hillis 2002; Rokas et al. 2003; Delsuc et al. 2005). However, when it comes to reconstruction of a really difficult phylogeny like that of land plants, it seems that the issue is underappreciated since some studies have attempted to solve the problem with only a small number of taxa (e.g., Hedderson et al. 1998; Soltis et al. 1999; Nickrent et al. 2000; Renzaglia et al. 2000; Nishiyama et al. 2004; Goremykin and Hellwig 2005). In our study, we adopted a middle-ground approach that we have used successfully in investigating basal angiosperm relationships, namely, sampling a moderate number of taxa and a moderate number of characters rather than going to either extreme. Our dense taxon sampling in leafy liverworts, acrocarpous and pleurocarpous mosses, and leptosporangiate ferns and sparse taxon sampling in all other nonflowering land plant lineages reflect this thinking. Choosing slow- versus fast-evolving genes in reconstructing large,

deep phylogenies is also a delicate issue. An empirical study has shown that a fast-evolving gene such as *matK* can be highly informative and efficient in reconstructing a large phylogeny like that of angiosperms when an appropriate taxon sampling density is achieved (Hilu et al. 2003). However, we caution that the use of fast-evolving genes should be properly balanced with that of slow-evolving genes for the following reason. Undoubtedly, fast-evolving genes have a potential to provide a large number of variable characters for unraveling relationships in shallow parts of the phylogeny and within tightly knotted nodes, which probably arose from rapid radiations. On the other hand, if they are not properly balanced by slow-evolving genes, they can also produce a large amount of homoplasy in deep parts of the tree and parts of the phylogeny that experienced extinctions (e.g., bases of monilophytes and seed plants in this study). As a result, the homoplasy will overwhelm the signals generated by slow-evolving genes and cause long-branch attraction. Choosing likelihood over parsimony methods at the data analysis stage can help to alleviate this problem to a certain extent, but if the issue of balance between fast- and slow-evolving genes is dealt with during the experimental design, the experiment is more likely to obtain congruent results from both types of analyses. Finally, as a complementary approach, one can also try to assemble a matrix of genomic structural characters, such as those used by Kelch et al. (2004) and Qiu et al. (2006*b*) in investigating relationships among early land plant lineages, but these kinds of characters are still limited in quantity and cannot be relied on to resolve relationships at all parts of a phylogeny.

RNA editing has been shown to be more widespread in basal land plant organellar genomes than originally observed and occurs in a highly lineage- and gene-specific fashion (Steinhauser et al. 1999; Kugita et al. 2003; Dombrovska and Qiu 2004; Wolf et al. 2004; Suzuki et al. 2005). It has been suspected to influence phylogenetic reconstruction (Bowe and dePamphilis 1996; Qiu and Palmer 1999). Comparative analyses of a basal angiosperm multigene matrix with RNA editing sites removed or retained show that retention of RNA editing sites in the matrix does lead to some erroneous grouping of taxa in a single-gene analysis where editing is frequent and the gene has a low substitution rate (mitochondrial *nad5*). However, in analyses of a combined multigene matrix with RNA editing sites retained and of single gene matrices where editing is infrequent and/or the genes have high substitution rates (mitochondrial *atp1*, *matR*, and *rps3*), the effect of RNA editing on phylogenetic reconstruction is negligible (Qiu et al. 2006*a*; Y.-L. Qiu, unpublished data). In this study, we took a dual approach to curtail the effect of RNA editing on phylogenetic reconstruction by including closely related, editing-light species such as *Leiosporoceros dussii* for hornworts (Duff and Moore 2005) and by sampling multiple genes from all three plant genomes (there is no report so far of heavy, genome-wide RNA editing in all three genomes of a plant). This approach seems to have been effective.

DNA base composition bias in a genome-wide fashion can also influence performance of phylogenetic methods (Steel et al. 1993). Here again, we believe that the effective ways to overcome this problem are (1) to sample genes from different genomes of the same plant, which are unlikely to experience the same kind of base composition bias simultaneously during evolution of the organisms, and (2) to use model-based methods, which are more effective than parsimony methods in dealing with variable nucleotide frequencies throughout a data set. For both RNA editing and base composition bias, one can again resort to using genomic structural characters, which do not have the problems typically associated with DNA sequence evolution.

In conclusion, maximum likelihood and maximum parsimony analyses of seven genes from three different genomes of 192 diverse land plants and their algal relatives reconstructed trees with similar topologies and bootstrap values. The major clades of nonflowering land plants have been identified and their relationships resolved with generally strong statistical support. Liverworts represent the sister to all other land plants. Hornworts are sister to vascular plants. Lycophytes are sister to other vascular plants. *Equisetum*, Psilotaceae, eusporangiate ferns, and leptosporangiate ferns form a clade, but relationships among them are not resolved. This clade is sister to seed plants. Extant gymnosperms are likely to represent a monophyletic group. Gnetales are related to conifers but not angiosperms. The poor resolution of relationships among basal monilophyte lineages and among some seed plant lineages is perhaps caused by extinction that these groups suffered during the Permian-Triassic boundary (Erwin 1994; Stanley and Yang 1994; Becker et al. 2004) and the Cretaceous-Tertiary boundary (Vajda et al. 2001). Two lines of evidence are consistent with this idea. One is that there are many extinct lineages of early vascular plants and seed plants that are well documented in the fossil record (Stewart 1983; Kenrick and Crane 1997). The other is the low bootstrap values in the angiosperm portion of the trees we reconstructed. Here we know that there is a large living diversity of angiosperms, but the limited taxon sampling employed in this study created an "extinction" perceived by the computer. Hence, we suggest that future studies sampling more slow-evolving genes and genomic structural characters should produce better resolution of these relationships. Finally, we acknowledge that it is possible that there are still analytical artifacts in the phylogenetic hypothesis we presented but that the chance of their occurrence should be much smaller than in previous studies with limited taxon and character sampling. We believe that the prospect for achieving a complete understanding of the evolution of land plants and their interaction with the abiotic and biotic environments under a well-reconstructed phylogenetic framework is better than ever.

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Appendix

Table A1

Information on Sequences Used in This Study

Species	*atpB*	*rbcL*	cp-LSU	cp-SSU	*atp1*	mt-LSU	18S
Abies homolepis Siebold & Zucc.	DQ646115	*A. numidica* De Lannoy ex Carrière AB019827	DQ629333	DQ629445	DQ646224	DQ647865	*A. lasiocarpa* (Hook.) Nutt. X79407
Acorus calamus L.	AJ235381	M91625	DQ629345	DQ629453	AF197621	DQ008817	L24078
Adiantum raddianum Pr.	U93840	U05906	*A.* sp. DQ629311	*A. pedatum* L. AF244549	. . .	*A.* sp. DQ647885	X78889
Alisma Plantago-aquatica L.	DQ007417	L08759	DQ629348	DQ629456	AF197717	DQ008812	AF197585
Amborella trichopoda Baill.	AF235041	L12628	DQ629336	DQ629447	DQ007412	DQ008832	U42497
Andreaea rothii Web. & Mohr	DQ646054	AF231060	*A. rupestris* Roth DQ629234	DQ629541	. . .	DQ647840	X99750
Anemia phyllitidis (L.) Sw.	DQ646098	*A. mexicana* Klotzsch U05603	DQ629301	DQ629480	DQ646241	DQ647858	DQ629420
Angiopteris evecta (Forst.) Hoffm.	*A. lygodiifolia* Ros. X58429	*A. lygodiifolia* Ros. X58429	DQ629291	U24580	DQ646249	DQ647855	*A. lygodiifolia* Ros. D85301
Anomodon attenuatus (Hedw.) Hub.	DQ646083	*A. minor* (Hedw.) Furnr. AB019471	DQ629263	DQ629569	*A. viticulosus* (Hedw.) Hook. & Tayl. DQ646198	DQ648769	*A. viticulosus* (Hedw.) Hook. & Tayl. DQ629402
Anthoceros agrestis	*A. formosae* Steph. D43695	*A. formosae* Steph. D43695	*A. formosae* Steph. NC_004543	DQ629579	. . .	DQ647842	X80984
Araucaria araucana (Mol.) K. Koch	DQ646109	U96467	DQ629324	DQ629437	*A. heterophylla* (Salisb.) Franco AF209104	DQ647874	*A. excelsa* (Lamb.) R. Br. D38240
Archidium alternifolium (Hedw.) Mitt.	DQ646055	*A. stellatum* AF231066	DQ629235	DQ629542	DQ646172	DQ648744	*A. donnelli* Austin AF223025
Aristolochia macrophylla Lam.	AJ235399	L12630	DQ629354	DQ629461	AF197669	DQ008796	AF206855
Asplenium nidus L.	U93839	AB042151	DQ629313	DQ629488	DQ646217	DQ647878	*A. australasicum* Hook. D85303
Atrichum angustatum (Brid.) Bruch & Schimp.	DQ646058	DQ645986	DQ629238	DQ629545	DQ646175	DQ648747	*A. undulatum* (Hedw.) P. Beauv. X85093
Austrobaileya scandens C. T. White	AJ235403	L12632	DQ629341	DQ629585	AF197664	DQ008827	AF206858
Azolla sp.	DQ646099	*A. caroliniana* Willd. U24185	DQ629303	DQ629583	DQ646234	DQ647860	DQ629421
Bartramia pomiformis Hedw.	DQ646073	AB024620	DQ629253	DQ629559	*B. halleriana* Hedw. DQ646189	DQ648760	X96501
Bazzania trilobata (L.) Gray	DQ646026	L11056	DQ629204	DQ629513	DQ646142	DQ647833	DQ629373
Blasia pusilla L.	DQ646047	DQ645982	DQ629225	DQ629533	DQ646163	DQ647916	DQ629388
Blechnum gibbum (Lab.) Mett.	*B. occidentale* L. U93838	*B. occidentale* L. U05910	DQ629315	DQ629489	DQ646244	DQ647881	*B. occidentale* L. U18622
Blepharostoma trichophyllum (L.) Dumort.	DQ646020	DQ645964	DQ629198	DQ629507	DQ646137	DQ647832	. . .
Botrychium dissectum var. *obliqum*	*B. lunaria* (L.) Sw. U93826	*B. biternatum* (Sav.) Underw. L13474	DQ629288	*B. biternatum* (Sav.) Underw. U24581	DQ646215	DQ647853	*B. virginianum* (L.) Sw. AF313566
Brachythecium rutabulum (Hedw.) Br. Eur.	DQ646085	DQ645997	DQ629265	DQ629571	DQ646200	DQ648771	X94256
Bryoxiphium norvegicum (Brid.) Mitt.	DQ646062	AF231294	DQ629242	DQ629548	DQ646179	DQ648751	AF223008
Bryum argenteum Hedw.	DQ646070	*B. billarderi* Schwägr. AF231083	DQ629250	DQ629556	. . .	DQ648757	U18529

Buxbaumia aphylla Hedw.	DQ646056	AF231062	DQ629236	DQ629543	DQ646173	DQ648745	Y17603
Buxus sempervirens L.	AF092110	AF093717	DQ629363	DQ629468	AF197636	DQ008743	L54065
Cabomba sp.	*C. caroliniana* A. Gray AF187058	*C. caroliniana* A. Gray M77027	DQ629338	DQ629448	AF197641	DQ008831	*C. caroliniana* A. Gray AF206878
Calycanthus floridus L.	AJ235422	L14291	DQ629357	DQ629462	AF197678	DQ008780	U38318
Calypogeia muelleriana (Schiffn.) K. Mull.	DQ646027	U87065	DQ629205	AF244550	DQ646143	DQ647834	*C. arguta* Nees & Mont. X78439
Canella winterana (L.) Gaertn.	AJ235424	AJ131928	DQ629352	DQ629460	AF197676	DQ008804	AF206879
Cedrus deodara (D. Don.) G. Don.	DQ646114	X63662	DQ629332	DQ629444	DQ646223	DQ647864	DQ629435
Cephalotaxus harringtonia C. Koch.	DQ646112	*C. wilsoniana* Hayata AB027312	DQ629329	DQ629442	DQ646222	...	*C. wilsoniana* Hayata D38241
Ceratodon purpureus (Hedw.) Brid.	DQ646063	DQ645989	DQ629243	DQ629549	DQ646180	DQ648752	Y08989
Ceratophyllum demersum L.	AJ235430	D89473	DQ629344	DQ629452	AF197627	DQ008766	U42517
Ceratopteris sp.	DQ646102	*C. thalictroides* (L.) Brongn. U05609	DQ629309	DQ629486	...	...	DQ629426
Chaetosphaeridium globosum (Nordstedt) Klebahn	NC004115	NC004115	NC004115	NC004115	NC_004118	NC_004118	AJ250110
Chara connivens Salzm. ex A. Braun	AF408782	*C. globularis* Thuill. AF097164	*C. contraria* A. Braun ex Kutz. DQ629186	*C.* sp. AF393586	*C. contraria* A. Braun ex Kutz. DQ646124	*C. vulgaris* L. AY267353	AF408223
Chlorokybus atmophyticus Geitler	AF408805	AF408255	DQ629182	DQ629495	DQ646120	DQ647831	M95612
Cibotium sp.	DQ646100	*C. glaucum* (Sm.) Hk. & Arn. U05913	DQ629306	*C. glaucum* (Sm.) Hk. & Arn. U24582	...	DQ647880	DQ629424
Cinnamomum camphora (L.) T. Nees & Eberm.	AJ235436	L12641	DQ629358	DQ629463	AF197681	DQ008772	AF206888
Climacium americanum Brid.	DQ646089	*C. dendroides* (Hedw.) Web. & Mohr AB019442	DQ629269	DQ629575	DQ646204	DQ648742	DQ629405
Coleochaete orbicularis Pringsheim	AF408788	L13477	*C. scutata* Breb. DQ629185	*C. scutata* Breb. AF393595	*C. scutata* Breb. DQ646123	...	*C. sieminskiana* H. Szymanska AF408232
Cololejeunea biddlecomiae (Aust.) Evans.	DQ646042	DQ645980	DQ629220	DQ629528	DQ646158	DQ647912	DQ629385
Conocephalum conicum (L.) Underw.	DQ646015	U87066	DQ629192	DQ629501	*C.* sp. DQ646131	DQ647893	X80987
Croomia pauciflora Miq.	*C. japonica* Miq. AF308039	*C. japonica* Miq. AF307493	DQ629350	DQ629458	AF197708	DQ008808	AF168835
Cyathea poeppigii (Hook.) Domin	AF313553	*C. lepifera* Copel. U05616	DQ629307	DQ629484	DQ646236	...	DQ629425
Cycas revoluta Thunb.	AF313558	*C. circinalis* L. L12674	DQ629320	AF244551	AF197623	DQ008840	*C. taitungensis* C. F. Shen, K. D. Hill, C. H. Tsou & C. J. Chen D85297
Danaea elliptica Sm. in Rees	AF313578	AF313578	DQ629293	DQ629474	DQ646238	DQ647856	DQ629414
Davallia fejeensis Hk.	DQ646107	DQ646006	DQ629319	DQ629493	DQ646253	DQ647884	DQ629432
Dendroceros granulatus Mitt.	DQ646116	AY463049	DQ629276	DQ629580	...	DQ647845	...
Dicentra sp.	*D. chrysantha* Walp. AJ235454	*D. eximia* Torrey L37917	DQ629360	DQ629465	AF197649	DQ008764	*D. eximia* Torrey L37908
Dicranella heteromalla (Hedw.) Schimp.	DQ646064	AF231296	DQ629245	DQ629551	DQ646182	DQ648754	*D. staphyllina* X89873
Dicranum scoparium Hedw.	...	DQ645990	DQ629244	DQ629550	DQ646181	DQ648753	X89874
Dioscorea sp.	*D. polygonoides* Humb. & Bonpl. J235456	AF206762	DQ629349	DQ629457	AF197709	DQ008806	*D. polygonoides* Humb. & Bonpl. F206903
Diphyscium foliosum (Hedw.) Mohr	DQ646057	DQ645985	DQ629237	DQ629544	DQ646174	DQ648746	Y17765
Dryopteris wallichiana (Spreng.) Hyl.	DQ646104	*D. cristata* (L.) Gray U05923	DQ629314	DQ629490	DQ646243	...	DQ629428
Dumortiera hirsuta (Sw.) Nees.	DQ646017	U87068	DQ629194	DQ629503	DQ646133	DQ647895	DQ629368

Table A1

(*Continued*)

Species	*atpB*	*rbcL*	cp-LSU	cp-SSU	*atp1*	mt-LSU	18S
Ephedra distachya L.	*E. tweediana* C. A. Mey. AJ235463	U72821	DQ629334	*E. trifurca* Torr. ex S. Wats. U24584	DQ646225	...	*E. sinica* Stapf in Farwell D38242
Equisetum arvense L.	U93824	L11053	DQ629284	U24593	DQ646212	DQ647851	DQ629411
Equisetum hyemale L.	*E. telmateia* Erhr. AF313542	DQ646001	DQ629285	DQ629471	DQ646213	DQ647868	U18500
Fissidens dubius P. Beauv.	DQ646061	*F. adianthoides* Hedw. DQ645988	DQ629241	DQ629547	DQ646178	DQ648750	*F. taxifolius* Hedw. X95934
Fontinalis antipyretica var. *gigantea* (Sull.) Sull.	DQ646079	AB050949	DQ629259	DQ629565	DQ646194	DQ648765	AF023714
Fossombronia pusilla (L.) Dum.	DQ646046	*F. foveolata* Lindb. U87069	DQ629224	DQ629532	DQ646162	DQ647915	X78341
Frullania dilatata (L.) Dum.	DQ646041	DQ645979	DQ629219	DQ629527	DQ646157	DQ647911	DQ629384
Ginkgo biloba L.	AJ235481	D10733	DQ629323	AF244554	AF197625	DQ008838	D16448
Gleichenia dicarpa R. Br.	AF313550	AF313584	DQ629299	DQ629479	DQ646240	DQ647886	DQ629419
Gnetum gnemon L.	AF187060	L12680	AJ007508	*G. leyboldii* Tul. AF244555	AF197617	DQ008833	U42416
Grimmia alpicola Sw. ex Hedw.	DQ646068	*G. laevigata* (Brid.) Brid. AF231081	DQ629248	DQ629554	*G. ovalis* (Hedw.) Lindb. DQ646185	DQ648756	DQ629395
Gymnostomum rucurvirostrum Hedw.	DQ646067	DQ645992	DQ629247	DQ629553	DQ646184	DQ648739	DQ629394
Haplomitrium mnoides (Lindb.) R. M. Schust.	*H. hookeri* (Sm.) Nees AF313555	U87071	DQ629197	DQ629506	DQ646136	DQ647898	*H. hookeri* (Sm.) Nees U18504
Hedwigia ciliata (Hedw.) P. Beauv.	DQ646077	AF005517	DQ629257	DQ629563	DQ646192	DQ648763	X91104
Hedyosmum arborescens Sw.	AJ235491	L12649	DQ629343	DQ629451	AF197668	DQ008822	AF206925
Helminthostachys zeylandica (L.) Hk.	DQ646095	L40907	DQ629289	DQ629472	DQ646227	DQ647854	DQ629412
Heterophyllium affine (Hook.) M. Fleisch.	DQ646087	AB051218	DQ629267	DQ629573	DQ646202	DQ648773	DQ629404
Hookeria acutifolia Hook. & Grev.	DQ646082	AF158170	DQ629262	DQ629568	DQ646197	DQ648768	*H. lucens* (Hedw.) Sm. AJ275013
Huperzia lucidula (Michx.) Trevis.	U93819	*H. selago* (L.) Bernh. ex Schrank & Mart. Y07934	*H. selago* DQ629279	AF244556	*H. selago* DQ646209	DQ647848	U18505
Hylocomium splendens (Hedw.) Schimp.	DQ646088	AB024662	DQ629268	DQ629574	DQ646203	DQ648774	X95477
Hymenophyllum sp.	*H. hirsutum* (L.) Sw. AF313538	*H. fucoides* Sw. U20933	DQ629297	DQ629477	DQ646226	...	DQ629417
Hymenophyton flabellatum (Labill.) Dumort. ex. Trevis.	DQ646050	AY507406	DQ629229	DQ629537	DQ646167	...	DQ629391
Hypnum imponens Hedw.	DQ646086	DQ645998	DQ629266	DQ629572	*H. cupressiforme* Hedw. DQ646201	DQ648772	*H. cupressiforme* Hedw. X94258
Illicium floridanum Ellis	*I. parviflorum* DC. U86385	*I. parviflorum* DC. L12652	DQ629339	DQ629449	AF197663	DQ008825	*I. parviflorum* DC. L75832
Isoetes malinverniana Ces. & De Not.	*I. engelmannii* A. Braun AF313544	*I. lacustris* L. AJ010855	DQ629281	*I. melanopoda* J. Gay & Durieu U24585	DQ646242	DQ647850	*I. durieui* Bory X83521
Juniperus insida	DQ646113	*J. virginiana* L. AF119182	DQ629331	*J. virginiana* L. U24586	*J. virginiana* L. AF209106	DQ647875	*J. chinensis* L. D38243
Klebsormidium flaccidum (Kütz.) Silva	*K. subtilissimum* (Rabenh.) Silva, Mattox & Blackw. AF408802	*K.* sp. L13478	DQ629183	X75522	DQ646121	DQ647867	X75520
Leiosporoceros dussii (Steph.) Hässel	...	AY463052	DQ629277	DQ629581	...	DQ647846	DQ497432
Lejeunea cavifolia (Ehrh.) Linb.	DQ646043	AY548102	DQ629221	DQ629529	DQ646159	DQ647913	DQ629386

Lepicolea attenuata (Mitt.) Steph.	DQ646022	DQ645966	DQ629200	DQ629509	...	...	...
Lepidogyna hodgsoniae Grolle	DQ646024	DQ645968	DQ629202	DQ629511	DQ646140	DQ647900	DQ629371
Lepidozia reptans (L.) Dumort.	DQ646025	U87075	DQ629203	DQ629512	DQ646141	...	DQ629372
Leptobryum pyriforme (Hedw.) Wils.	DQ646072	AF231072	DQ629252	DQ629558	DQ646188	DQ648759	X80980
Leptopteris superba (Col.) Pr.	DQ646096	DQ646004	DQ629294	DQ629475	DQ646251	...	DQ629415
Leucobryum glaucum (Hedw.) Angstr.	DQ646066	*L. albidum* (Brid.) Lindb. DQ645991	DQ629246	DQ629552	*L. albidum* (Brid.) Lindb. DQ646183	DQ648755	*L. albidum* (Brid.) Lindb. DQ629393
Leucodon julaceus (Hedw.) Sull.	DQ646078	*L. temperatus* Akiyama AB019456	DQ629258	DQ629564	DQ646193	DQ648764	*L. sciuroides* (Hedw.) Schwaegr. Y15481
Leucolejeunea clypeata (Schwein.) Evans.	DQ646044	...	DQ629222	DQ629530	DQ646160	...	DQ629387
Lophocolea heterophylla (Schrad.) Dum.	DQ646034	U87076	DQ629212	DQ629520	DQ646150	DQ647906	X89872
Lophozia gillmani (Aust.) R. M. Schust.	DQ646028	DQ645969	DQ629206	DQ629514	DQ646144	DQ647901	DQ629374
Lunularia cruciata (L.) Dumort. ex Lindb.	DQ646016	DQ645962	DQ629193	DQ629502	DQ646132	DQ647894	DQ629367
Lycopodium clavatum var. *clavatum* L.	DQ646094	Y07936	DQ629280	*L. digitatum* Dill. ex A. Braun U24587	DQ646210	DQ647849	DQ629409
Lygodium japonicum (Thunb.) Sw.	AF313549	U05632	*L. circinatum* Sw. DQ629300	U24588	*L. circinatum* Sw. DQ646232	*L. circinatum* Sw. DQ647857	AB001538
Magnolia tripetala L.	AJ235526	AJ131927	DQ629355	*M.* × *soulangeana* Hort. AF244557	AF197691	DQ008741	AF206956
Marattia attenuata Labill.	AF313546	DQ646003	DQ629292	DQ629473	DQ646250	DQ647869	DQ629413
Marchantia polymorpha L.	X04465	NC_001319	X04465	X04465	M68929	M68929	X75521
Marsilea mutica Mett.	*M. drummondii* A. Braun AF313551	*M. polycarpa* Hk. & Grev. AF104213	DQ629304	DQ629483	DQ646228	DQ647861	DQ629422
Marsupella emarginata (Ehrh.) Dumort.	DQ646031	DQ645972	DQ629209	DQ629517	DQ646147	DQ647904	DQ629377
Megaceros tosanus Steph.	DQ646117	*M. aenigmaticus* R. M. Schust. L13481	DQ629274	*M. aenigmaticus* R. M. Schust. AF244558	...	DQ647843	AF244559
Mesostigma viride Lauterborn	NC002186	NC002186	AF166114	NC_002186	AF353999	AF353999	AJ250108
Metasequoia glyptostroboides Hu. & Cheng	AJ235534	AJ235805	DQ629330	DQ629443	AF197619	DQ008836	L00970
Metzgeria conjugata Lindb.	DQ646052	*M. furcata* (L.) Dum. U87081	DQ629231	DQ629539	DQ646169	*M. temperata* Kuwah. DQ647921	DQ629392
Mnium hornum Hedw.	DQ646071	AF226820	DQ629251	DQ629557	*M.* sp. DQ646187	*M.* sp. DQ648758	*M.* sp. DQ629396
Monoclea forsteri Hook.	DQ646012	*M. gottschei* Lindb. U87083	DQ629189	DQ629498	DQ646128	DQ647890	AJ239054
Mylia anomala (Hook.) S. Gray	DQ646030	DQ645971	DQ629208	DQ629516	DQ646146	DQ647903	DQ629376
Myristica fragrans Houtt.	AF209636	AF206798	DQ629356	*M. yunnanensis* Y. H. Li DQ629588	AF197698	DQ008789	AF206968
Myurium hochstetteri (Schimp.) Kindb.	DQ646091	DQ645999	DQ629271	DQ629577	DQ646206	DQ648775	DQ629406
Nephrolepis biserrata var *frucans* L. H. Bailey	DQ646105	*N. cordifolia* (L.) Pr. U05933	DQ629317	DQ629584	DQ646246	DQ647883	DQ629430
Nephroselmis olivacea Stein	AF137379	AF137379	NC_000927	AF137379	AF110138	AF110138	X74754
Nitella sp.	*N. opaca* (Bruz.) Ag. AF408786	*N. spiciformis* Morioka AB076068	AF393603	AF393604	*N. mucronata* (A. Braun) Miquel DQ646125	...	*N. flexilis* (L.) Ag. U05261
Notothylas breutelii (Gottsche) Gottsche	DQ646118	DQ646008	DQ629278	DQ629582	...	DQ647847	DQ629408
Nowellia curvifolia (Dicks.) Mitt.	DQ646037	DQ645976	DQ629215	DQ629523	DQ646153	DQ647836	DQ629380
Nymphaea odorata Aiton	AJ235544	M77034	*N.* sp. DQ629337	*N. tuberosa* Paine AF244560	*N.* sp. AF197639	*N.* sp. DQ008828	AF206973
Odontoschisma denudatum (Nees) Dumort.	DQ646038	DQ645977	DQ629216	DQ629524	DQ646154	DQ647837	DQ629381
Ophioglossum lusitanicum L.	*O. reticulatum* L. U93825	DQ646002	DQ629290	*O. engelmannii* Prantl. U24589	DQ646216	DQ647870	*O. petiolatum* Hook. U18515
Orthotrichum sordidum Sull. & Lesq. in Aust.	DQ646076	*O. pumilum* Sw. AF226819	DQ629256	DQ629562	DQ646191	DQ648762	DQ629399

Table A1

(*Continued*)

Species	*atpB*	*rbcL*	cp-LSU	cp-SSU	*atp1*	mt-LSU	18S
Osmunda cinnamomea L.	U93827	*O. regalis* L. AB024948	*O. regalis* L. DQ629295	U24594	*O. regalis* L. DQ646239	...	U18516
Pallavicinia lyellii (Hook.) Gray	DQ646049	DQ645983	DQ629227	DQ629535	DQ646165	DQ647918	DQ629389
Pellia epiphylla (L.) Corda.	DQ646048	AY688787	DQ629226	DQ629534	*P.* sp. DQ646164	DQ647917	X80210
Phaeoceros carolinianus (Michx.) Prosk.	DQ646119	DQ646009	DQ629275	*P. laevis* (L.) Prosk. AF244561	...	DQ647844	*P. laevis* (L.) Prosk. U18491
Phyllocladus aspleniifolius (Labill.) Hook. f.	DQ646110	*P. trichomanoides* D. Don AB027315	DQ629326	DQ629439	DQ646219	DQ647873	DQ629434
Physcomitrella patens (Hedw.) Bruch & Schimp	DQ646069	X74156	DQ629249	DQ629555	DQ646186	DQ648738	X80986
Pinus thunbergii Parl.	D17510	NC001631	D17510	NC001631	*P.* sp. AF197626	*P.* sp. DQ008835	*P. elliottii* Engelm. D38245
Piper betle L.	AJ235560	L12660	DQ629353	*P. nigrum* L. DQ629587	AF197630	DQ008795	AF206992
Plagiochila porelloides (Torrey ex Nees) Lindb.	DQ646035	*P. asplenioides* (L.) Dum. DQ645974	DQ629213	DQ629521	*P. asplenioides* (L.) Dum. DQ646151	DQ647907	*P. adiantoides* (Sw.) Lindb. X96499
Plagiogyria stenoptera (Hance) Diels	*P. japonica* Nakai AF313547	*P. japonica* Nakai U05643	DQ629305	DQ629482	DQ646235	DQ647877	DQ629423
Plagiothecium laetum Schimp. in BSG	DQ646090	*P. undulatum* (Hedw.) BSG AB024634	DQ629270	DQ629576	DQ646205	DQ648743	*P. undulatum* (Hedw.) BSG X94259
Platanus occidentalis L.	U86386	L01943	DQ629361	DQ629466	AF197655	DQ008752	U42794.
Podocarpus macrophyllus (Thunb.) Sweet	*P. milanjianus* AJ235567	AF249616	DQ629325	DQ629438	AF197620	DQ008837	*P. costalis* D38473
Polypodium polycarpon Cav.	DQ646106	*P. plesiosorum* Kunze U21144	DQ629318	DQ629492	DQ646229	DQ647879	DQ629431
Polytrichum juniperinum Hedw.	DQ646059	DQ645987	DQ629239	*P. commune* Hedw. AF244563	DQ646176	DQ648748	*P. formosum* Hedw. X80982
Porella pinnata L.	DQ646040	U87088	DQ629218	DQ629525	DQ646156	DQ647910	DQ629383
Psilotum nudum (L.) P. Beauv.	U93822	NC_003386	DQ629286	U24590	DQ646214	DQ647852	X81963
Pteridium aquilinum (L.) Kuhn	U93835	U05939	DQ629312	Z81323	DQ646237	DQ647887	U18628
Pteris ensiformis Burm.	DQ646101	*P. vittata* L. U05941	DQ629308	DQ629485	DQ646248	DQ647876	*P. vittata* L. AF126291
Ptilidium pulcherrimum (F. Weber) Hampe	DQ646021	DQ645965	DQ629199	DQ629508	DQ646138	DQ647899	DQ629369
Ptychomitrium incurvum (Schwaegr.) Spruce.	DQ646075	*P. gardneri* Lesq. AF005549	DQ629255	DQ629561	DQ646190	DQ648761	DQ629398
Radula complanata (L.) Dum.	DQ646039	DQ645978	DQ629217	DQ629526	DQ646155	DQ647909	DQ629382
Ranunculus sp.	DQ401327	*R. trichophyllus* Chaix L08766	DQ629359	DQ629464	AF197714	DQ008756	*R. taisanensis* Hayata D29780
Reboulia hemisphaerica (L.) Raddi	DQ646014	DQ645961	DQ629191	DQ629500	DQ646130	DQ647892	DQ629366
Rhabdoweisia fugax (Hedw.) BSG	DQ646065	*R. crenulata* (Mitt.) Jameson. AF005544	...	...	...	DQ648741	...
Rhizogonium paramattense (C. Müll.) Reichardt	DQ646074	DQ645993	DQ629254	DQ629560	DQ646231	DQ648740	DQ629397
Riccardia latifrons (Lindb.) Lindb.	DQ646051	...	DQ629230	DQ629538	DQ646168	DQ647920	*R. pinguis* (L.) Gray X85095
Riccia sorocarpa Bisch.	DQ646019	*R.* sp. DQ645963	DQ629196	DQ629505	DQ646135	DQ647896	*R. fluitans* L. 78441
Ricciocarpos natans (L.) Corda.	DQ646018	U87089	DQ629195	DQ629504	DQ646134	DQ647897	X89871
Riella helicophylla (Mont.) Hook.	DQ646010	DQ645959	DQ629187	DQ629496	DQ646126	DQ647888	X89868
Sabia sp.	*S. swinhoei* emsl. AF093395	L12662	DQ629362	DQ629467	AF197657	DQ008747	*S. swinhoei* Hemsl. L75840
Salvinia sp.	*S. molesta* D. Mitch. AF313552	*S. cucullata* Roxb. ex Bory U05649	DQ629302	DQ629481	DQ646233	DQ647859	*S. natans* (L.) All. X90413

Scapania nemorosa (L.) Dumort.	DQ646032	*S. nemorea* (L.) Dumort. DQ645973	DQ629210	DQ629518	*S. nemorea* (L.) Dumort. DQ646148	DQ647835	*S. nemorea* (L.) Dumort. X80983
Schisandra sphenanthera Rehd. & Wils.	*S. chinensis* (Turcz.) Baill. AF239790	L12665	DQ629340	DQ629450	AF197662	DQ008824	*S. chinensis* (Turcz.) Baill. L75842
Schistochila nobilis (Hook.) Trev.	DQ646033	*S. laminigera* (Hook. & Tayl.) Evans AY462329	DQ629211	DQ629519	DQ646149	DQ647905	DQ629378
Sciadopitys verticillata Siebold & Zucc.	DQ646111	L25753	DQ629327	DQ629440	DQ646220	DQ647872	D85292
Selaginella apoda Fernald	...	AJ010854	DQ629283	U24591	...	...	*S. umbrosa* Lem. ex Hieron. X83520
Selaginella uliginosa (Labill.) Spring	*S. wildenowii* (Desv. ex Poir) Baker AF313554	AJ010843	DQ629282	DQ629470	DQ646211	...	*S. wildenowii* (Desv. ex Poir) Baker DQ629410
Solenostoma hyalinum (Lyell) Mitt.	DQ646029	DQ645970	DQ629207	DQ629515	DQ646145	DQ647902	DQ629375
Spathiphyllum clevelandii	*S. wallisii* Hort. AJ235606	AJ005626	DQ629347	DQ629455	AF197706	DQ647866	*S. wallisii* Hort. AF207023
Sphaerocarpos donnellii Austin	DQ646011	*S. texanus* Austin U87090	DQ629188	DQ629497	DQ646127	DQ647889	X85094
Sphagnum capillifolium (Erhr) Hedw.	DQ646053	*S. fallax* (Klinggr.) Klinggr. AB013673	DQ629233	DQ629540	DQ646171	DQ647838	*S. fallax* (Klinggr.) Klinggr. X78468
Sphagnum palustre L.	AF313557	AF231887	DQ629232	U24592	*S. recurvum* P. de Beauv. DQ646170	*S. recurvum* P. de Beauv. DQ647839	Y11370
Spirogyra maxima (Hassall) Wittrock	AF408797	L11057	*S. communis* (Hassall) Kütz. DQ629184	AF393611	*S. communis* (Hassall) Kütz. DQ646122	...	AF408236
Stangeria eriopus (Kunze) Baill.	DQ646108	DQ646007	DQ629321	DQ629494	DQ646218	DQ647863	DQ629433
Symphyogyna circinata Nees. & Mont.	*S. undulata* Colenso. AY688825	DQ645984	DQ629228	DQ629536	DQ646166	DQ647919	DQ629390
Takakia ceratophylla (Mitt.) Grolle	DQ646093	DQ646000	DQ629272	DQ629578	DQ646207	DQ647841	DQ629407
Takakia lepidozioides Hatt. & Inoue.	DQ646092	AF244565	DQ629273	AF058678	DQ646208	...	AJ269686
Targionia hypophylla L.	DQ646013	DQ645960	DQ629190	DQ629499	DQ646129	DQ647891	DQ629365
Tasmannia insipida DC	AF093424	L01957	DQ629351	DQ629459	AF197674	DQ008802	AF207035
Taxus media var. *hicksii* Rehder	*T. baccata* L. AJ235619	*T. brevifolia* Nutt. AF249666	DQ629328	DQ629441	DQ646221	...	*T. mairei* (Lemee & H. Lév.) S. Y. Hu D16445
Tetraphis pellucida Hedw.	DQ646060	U87091	DQ629240	DQ629546	DQ646177	DQ648749	U18527
Thamnobryum alleghaniense	DQ646080	DQ645994	DQ629260	DQ629566	DQ646195	DQ648766	DQ629400
Thelypteris navarrensis (Christ) Proctor	*T. palustris* Schott AY612713	*T. palustris* Schott U05947	DQ629316	DQ629491	DQ646245	DQ647882	DQ629429
Thuidium recognitum (Hedw.) Lindb.	DQ646084	DQ645996	DQ629264	DQ629570	DQ646199	DQ648770	DQ629403
Tmesipteris billardierei Endl.	*T. tannensis* (Spreng.) Bernh. U93823	*T. oblanceolata* Copel. U30836	DQ629287	*T. oblanceolata* Copel. U24595	DQ646247	DQ647871	*T. tannensis* (Spreng.) Bernh. U18103
Todea barbara (L.) Moore	DQ646097	DQ646005	DQ629296	DQ629476	DQ646252	...	DQ629416
Tofieldia calyculata (L.) Wahlenb.	AJ235627	AJ235798	DQ629346	DQ629454	AF197704	DQ008816	AF207043
Treubia lacunosa (Colenso) Prosk.	DQ646045	DQ645981	DQ629223	DQ629531	DQ646161	DQ647914	AJ239055
Trichocolea tomentella (Erhr.) Dum.	DQ646023	DQ645967	DQ629201	DQ629510	DQ646139	...	DQ629370
Trichomanes radicans Sw.	AY612715	Y09201	*T.* sp. DQ629298	DQ629478	*T.* sp. DQ646230	...	*T.* sp. DQ629418
Trimenia moorei W. R. Philipson	Zanis et al. 2002	AF121367	DQ629342	DQ629586	DQ007415	DQ008826	Zanis et al. 2002
Trochodendron aralioides Sieb. & Zucc.	AF093423	L01958	DQ629364	DQ629469	AF197648	DQ008746	U42816
Tylimanthus saccatus (Hook.) Mitt.	DQ646036	DQ645975	DQ629214	DQ629522	DQ646152	DQ647908	DQ629379
Vittaria lineata (L.) Sm.	DQ646103	U20937	DQ629310	DQ629487	...	DQ647862	DQ629427
Welwitschia mirabilis Hook. F.	AF239795	AJ235814	DQ629335	DQ629446	AF197618	DQ008834	D85299
Weymouthia cochlearifolia (Sw.) Dix	DQ646081	DQ645995	DQ629261	DQ629567	DQ646196	DQ648767	DQ629401
Zamia floridana A. DC	*Z. furfuracea* Aiton AF188845	D10736	DQ629322	DQ629436	AF197624	*Z. integrifolia* L.f. DQ008839	*Z. pumila* L. M20017

Note. Sequences produced in this study are shown with underlined accession numbers; all other sequences are from the GenBank. Ellipses indicate missing data.

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