

# Global patterns in peatmoss biodiversity

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## Abstract

DNA sequence data from the nuclear ribosomal internal transcribed spacers (*ITS*) and the *trnL-trnF* chloroplast DNA regions were used to quantify geographical partitioning of global biodiversity in peatmosses (*Sphagnum*), and to compare patterns of molecular diversity with patterns of species richness. Molecular diversity was estimated for boreal, tropical, Neotropical, nonboreal (tropical plus Southern Hemisphere), Old World and New World partitions, based on a total of 436 accessions. Diversity was partitioned among geographical regions in terms of combined nuclear and chloroplast sequence data and separately for the *ITS* and *trnL-trnF* data sets. Levels of variation were estimated using phylogenetic diversity (PD), which incorporates branch lengths from a phylogenetic tree, and the number of polymorphic nucleotide sites. Estimates of species richness suggest that peatmoss diversity is higher in New World than Old World regions, and that the Neotropics constitute a 'hotspot' of diversity. Molecular estimates, in contrast, indicate that peatmoss biodiversity is almost evenly divided between New and Old World regions, and that the Neotropics account for only 20–35% of global peatmoss diversity. In general, levels of tropical and boreal peatmoss molecular diversity were comparable. Two species, *S. sericeum* from the Old World tropics and *S. lapazense* from Bolivia, are remarkably divergent in nucleotide sequences from all other *Sphagna* and together account for almost 20% of all peatmoss diversity, although they are represented by only three of the 436 accessions (0.7%). These species clearly demonstrate the nonequivalence of species biodiversity value.

*Keywords:* biodiversity, molecular ecology, Neotropical diversity, peatmosses, phylogenetic diversity, *Sphagnum*

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## Introduction

Although 'biodiversity' has become common currency among professional biologists and the public, there remains much controversy about how to estimate it, and how to use the information once obtained (Moritz 1994; Crandall *et al.* 2000; Reed & Frankham 2001; van Tienderen *et al.* 2002; Hobohm 2003). An important reason to estimate global patterns of biodiversity is to identify 'hotspots' on which to focus efforts (Myers *et al.* 2000). Analyses of biodiversity patterns in monophyletic groups of organisms can provide insight into evolutionary processes that give rise to the world's biodiversity (e.g. Young *et al.* 2002). Perhaps the simplest metric for estimating biodiversity is taxic diversity, the numbers of species, genera or higher-level taxa. Checklists and other floristic treatments are the primary source of

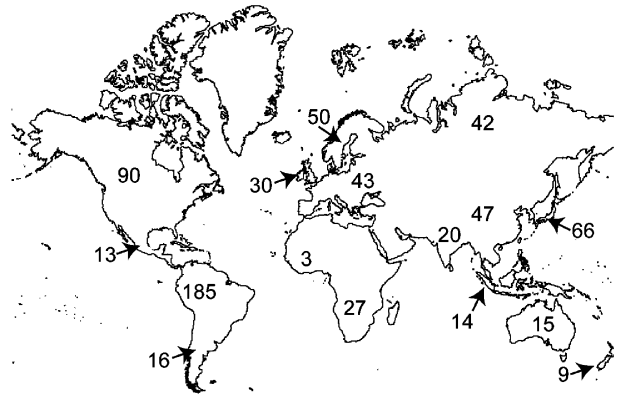
information about geographical patterns in taxic diversity. For specific areas under consideration for preservation, it is impractical to obtain complete species lists even for the better-known groups of organisms. In some cases at least, estimates of taxic diversity based on families seem to provide good proxies for numbers of species (Williams & Gaston 1994; Williams *et al.* 1994a; but see also, Prance 1994). However, the use of species numbers alone to assess biodiversity necessarily assumes that all species are equal in value. This is clearly not the case, as has been noted many times (Vane-Wright *et al.* 1991; Faith 1992; Nixon & Wheeler 1992; Harper & Hawksworth 1994; Humphries *et al.* 1995). It is intuitively clear that an area with 50 species representing 40 different families is more diverse than another area that contains 50 species all from the same family. In addition, biodiversity estimates based on species richness incorporate all the vagaries of subjective taxonomic practices. While this may not be a big problem in such well-known groups as the vertebrates, it can create

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significant ambiguity for lesser-known groups such as invertebrates and many plants.

Molecular data provide an alternative to taxonomic richness for estimating levels of biodiversity. For DNA sequences, standard genetic statistics such as the proportion of polymorphic nucleotide sites, or theta, provide estimates of standing diversity that depend neither on particular taxonomic concepts, nor on reconstructions of phylogenetic relationships. Various approaches have also been proposed to incorporate phylogenetic considerations into biodiversity estimates. In the absence of formal cladistic analyses, classifications can serve as proxies for genealogical hypotheses (Faith 1994). When cladograms are available, alternative measures of phylogenetic diversity (PD) may emphasize topology, numbers of nodes, and/or branch lengths (e.g. Vane-Wright *et al.* 1991; Faith 1992; Nixon & Wheeler 1992; Williams *et al.* 1994b). Conceptual issues that surround the choice of metric for PD estimates include the relative importance of anagenic vs. cladogenic origins for new phenotypic traits, the value of unique trait combinations vs. maximizing single-trait diversity and how to deal with evolutionary rate heterogeneity (Humphries *et al.* 1995). A molecular estimate that takes branch length into consideration may be the best available predictor of so-called feature diversity (Faith 1992) or option value (McKay & Latta 2002); i.e. variation in features that may be functionally important. The extent to which gene trees incorporating branch lengths predict diversity in other (including phenotypic) traits depends on the accurate estimation of branch lengths and patterns of evolutionary rate heterogeneity among different clades and loci.

This work describes geographical patterns in the levels of biodiversity in peatmosses (*Sphagnum*; Bryophyta). *Sphagnum* is one of two genera in the class Sphagnopsida of the division Bryophyta (mosses) (Shaw 2000). The genus has a worldwide distribution and dominates community structure and function in many habitats where it occurs, especially in the boreal zone. Because of disequilibrium between the rates of carbon fixation and decay processes, boreal and subarctic wetlands, which occupy almost 3.5 million km<sup>2</sup> of the terrestrial land surface, accumulate vast quantities of peat. It is estimated that some 455 Pg of carbon, or approximately one-third of the global carbon pool, is stored in northern peatlands, which currently function as a net sink for atmospheric carbon (Gorham 1991). The amount of carbon stored in northern peatlands is said to be two to three times that contained in tropical rain forests (O'Neill 2000). Peatlands also function as a source for atmospheric methane (CH<sub>4</sub>) and are important in the emission and consumption of other atmospheric gases including CO, N<sub>2</sub>O, NH<sub>3</sub>, H<sub>2</sub>S, COS, and DMS. Moreover, northern peatlands play a prominent role in determining patterns of regional hydrology, permafrost, and biodiversity. It has been claimed that more biomass is currently



**Fig. 1** Geographic patterns in species richness of peatmosses (*Sphagnum*). Estimates obtained from Smith (1976), Eddy (1988); Ignatov & Afonina (1992); Tan & Iwatsuki (1993), Fife (1996), O'Shea (1997), He (1998), Li & He (1999), Seppelt (2000), Flatberg (2002), and unpublished treatments of *Sphagnum* for North America by C. McQueen and R. Andrus, and an unpublished treatment for *Sphagnum* in northern South America by H. A. Crum.

accumulated in the genus *Sphagnum* than in any other single genus of vascular or nonvascular plant (Clymo & Heywood 1982).

Most people associate 'peat bogs' and *Sphagnum* with the boreal zone and while there is no question that *Sphagnum* is most abundant at high latitudes of the Northern Hemisphere (Gore 1983), it is less clear that the genus is most diverse there. Biomass accumulation in a habitat or region is not necessarily correlated with species richness in that area; *Picea* biomass is extremely high in the North American boreal zone but with only a few taxa, species diversity obviously is not.

In their unpublished revision of *Sphagnum* for the Flora of North America project, McQueen and Andrus (pers. comm.) recognize approximately 90 North American species, and 25 or more species of *Sphagnum* can occur sympatrically in some very diverse peatlands. Checklists and floras for northern areas of Europe and Asia also indicate a species-rich *Sphagnum* flora, even if less diverse than in North America (Fig. 1). Variation in species richness among Northern Hemisphere areas probably reflects both differences in taxonomic concepts among sphagnologists, and real differences in diversity.

The Old World tropics are considerably less diverse than the boreal zone in terms of peatmoss species richness, while the Neotropics appear to have an exceptionally diverse *Sphagnum* flora (Fig. 1). *Sphagnum* does not form expansive peatlands at tropical latitudes but in the Andes Mountains of northern South America peatlands are abundant, although discontinuous and far less widespread compared to boreal areas. In the lowland tropics, *Sphagnum* is a minor element in terms of abundance, but recent taxonomic work suggests that peatmosses are exceptionally

diverse at the species level (e.g. Crum 1984, 1987a,b, 1989, 1990a,b, 1992a,b, 1993a,b, 1994, 1995a,b). In the subantarctic zone of Chile, Argentina and Tasmania, *Sphagnum*-dominated peatlands are extensive, but species diversity still appears to be low compared to the Northern Hemisphere boreal zone (Roivainen 1937; He 1998; Seppelt 2000).

Our goals were to compare levels of peatmoss diversity among major regions of the globe, and to assess congruence between geographical patterns inferred from estimates of species richness with molecular estimates. We sampled populations of *Sphagnum* globally and obtained DNA sequences from one chloroplast region (*trnL-trnF*; hereafter, *trnL*) and one nuclear region (*ITS1-5.8s-ITS2*; hereafter, *ITS*). Sequence data were used to obtain geographically partitioned estimates of peatmoss biodiversity. Specifically, we compared levels of diversity between the boreal, tropical and Neotropical peatmosses, and between New and Old World populations. We were further able to partition peatmoss diversity among these geographical regions separately for nuclear and chloroplast sequences. Molecular diversity was estimated using explicitly historical (phylogenetic) and nonhistorical (phenetic) metrics.

## Materials and methods

### Geographic and taxonomic sampling

The molecular data set consists of 436 accessions for which both *ITS* and *trnL* sequences were available. These include a substantial number of infraspecific samples, as well as a thorough representation of the overall generic diversity (Table 1). Approximately 75 of the sequences were included in the phylogenetic analysis of *Sphagnum* published by Shaw (2000); the remaining sequences were generated for this study. Samples from all continents were included and although the data set contains more boreal samples than from elsewhere, every attempt was made to sample haphazardly with respect to geography. Differences in sample sizes for different regions reflect the availability of recent collections because of the abundance of *Sphagnum* in those regions, and therefore represent real ecological characteristics of the genus. Moreover, bias introduced to estimates of phylogenetic diversity because of the relative abundance of boreal samples was eliminated by the random subsampling of boreal accessions we conducted for estimates of phylogenetic diversity, as described below. Numbers of samples representing the different geographical regions are provided in Tables 2, 3 and 4.

A phylogenetically random sample, as well as a geographically random sample, is essential for estimating patterns of biodiversity within *Sphagnum*. Six well-supported monophyletic lineages can be resolved in *Sphagnum* (Shaw 2000). Four large sections, *Sphagnum*, *Subsecunda*, *Cuspidata* and *Acutifolia*, with at least 30–50 species each, contain

most of the infrageneric species diversity, and two smaller sections, *Rigida* and *Squarrosa*, contain three to five species each. All six sections are well represented in the data set. The section *Inretorta* was published by Crum (1990b) when he described *S. inretortum* from Bolivia; we were unable to obtain sequences for this species. Warnstorff (1911) recognized the subsection *Sericea* for two morphologically aberrant species, *S. macrophyllum* Brid. from eastern North America and *S. sericeum* C. Muell. from the Old World tropics of Malaysia south to New Guinea. *Sphagnum macrophyllum* is nested unambiguously within the larger section, *Subsecunda*, and is not especially distinctive on a molecular level (Shaw 2000). *S. sericeum*, on the other hand, is highly isolated from other sphagna on the basis of both *ITS* and *trnL* (results presented in this paper), and also on the basis of eight other nuclear, chloroplast, and mitochondrial genes (unpubl.). In fact, phylogenetic analyses of *Sphagnum* based on 12 genes, rooted with *Takakia* and *Andraeaea*, indicate that *S. sericeum* is outside rather than nested within the main peatmoss clade (Shaw, unpubl.). Another tropical species, *S. lapazense*, described recently from Bolivia by Crum (2001), is also highly isolated and appears to be outside the major *Sphagnum* clade, as indicated by 12 genes representing all three genomic compartments (nuclear, chloroplast, mitochondrial). *ITS* and *trnL* sequences from these two taxa are included in the present study. However, *S. lapazense* and *S. sericeum* account for such a substantial proportion of peatmoss molecular diversity that all analyses were conducted with and without these taxa included in the data set. Although they are of course part of the diversity of *Sphagnum* in Australasia (*S. sericeum*) and South America (*S. lapazense*) and should therefore be included in the analyses, geographical patterns other than those produced by such highly aberrant taxa are also relevant.

### Molecular methods

DNA extraction, amplification of the *ITS* and *trnL* regions, sequencing and construction of contigs was accomplished according to the protocols modified from Baldwin (1992) and Taberlet *et al.* (1991) as described by Shaw (2000). In a few cases when unambiguous sequences could not be obtained by direct sequencing, *ITS* was cloned and sequenced as in Shaw *et al.* (in press). Identification of introns, exons, intergenic spacers, and coding regions was based on comparisons with sequences available in GenBank and with hundreds of other moss sequences in the Shaw laboratory for these regions.

### Phylogenetic analyses

*ITS* and *trnL* sequences were aligned separately and then combined for the analyses. Heuristic searches were conducted

**Table 1** Collection information for samples included in the analyses, along with GenBank Accession numbers for all DNA sequences

Species	Country	Collector	Collection no.	Herb	GenBank: <i>ITS</i>	GenBank: <i>trnL</i>
<i>S. aciphyllum</i>	Brazil	Buck	26853	MICH	AY298360	AY297993
<i>S. acutirameum</i>	Brazil	Vital & Buck	19692	NYBG	AY298361	AY297994
<i>S. affine</i>	Bhutan	Long	28884	DUKE	AY298363	AY297996
<i>S. affine</i>	India	Long	26521	DUKE	AY298362	AY297995
<i>S. affine</i>	USA	Shaw	s.n.	DUKE	AF193697	AF192573
<i>S. africanum</i>	South Africa	Stoutamire	s.n.	MICH	AY298364	AY297997
<i>S. africanum</i>	South Africa	Von Rooy	1802	DUKE	AF193674	AF192567
<i>S. alegendse</i>	Australia	Glime	7147	DUKE	AF193729	AF192579
<i>S. amoenoides</i>	Brazil	Buck	26422	MO	AF193698	AY297998
<i>S. andersonianum</i>	England	Andrus	8182	DUKE	AY298369	AY298003
<i>S. andersonianum</i>	Ireland	Andrus	8111b	DUKE	AY298368	AY298002
<i>S. andersonianum</i>	Ireland	Andrus	8164	DUKE	AY298370	AY298004
<i>S. andersonianum</i>	USA	Andrus	8358	DUKE	AY298365	AF192589
<i>S. andersonianum</i>	USA	Andrus	8466	DUKE	AY298366	AY298000
<i>S. andersonianum</i>	USA	Allen	9438	DUKE	AY298367	AY298001
<i>S. angermanicum</i>	USA	Andrus & Karlin	6995	DUKE	AY298372	AY298006
<i>S. angermanicum</i>	USA	Town	2253	DUKE	AF193747	AF192618
<i>S. angustifolium</i>	Norway	Stenoien & Flatberg	2.41	DUKE	AY298371	AF192593
<i>S. angustifolium</i>	Norway	Shaw	9639	DUKE	AF193686	AY298005
<i>S. annulatum</i>	Japan	Uchida	1024	DUKE	AY298374	AY298008
<i>S. annulatum</i>	Norway	Sastad & Flatberg	230–98	DUKE	AY298373	AY298007
<i>S. annulatum</i>	Norway	Andrus & Flatberg	7557	DUKE	AY298375	AY298009
<i>S. aongstroemii</i>	Norway	Andrus & Flatberg	7531	DUKE	AF193748	AF192619
<i>S. aongstroemii</i>	Russia	Cronberg	aongstr. 1	DUKE	AY298376	AY298010
<i>S. aongstroemii</i>	Russia	Cronberg	aongstr. 2	DUKE	AY298377	AY298011
<i>S. arcticum</i>	Canada	Scotter	76467	DUKE	AY298379	AY298013
<i>S. arcticum</i>	Norway	Flatberg <i>et al.</i>	270–00	DUKE	AY298378	AY298012
<i>S. aureum</i>	Costa Rica	McQueen	7165	NYBG	AY298524	AY298156
<i>S. aureum</i>	Panama	Dauphin	1564	MO	AF193750	AF192622
<i>S. auriculatum</i>	Norway	Flatberg	39–97	DUKE	AY298382	AY298016
<i>S. auriculatum</i>	Norway	Shaw	9667	DUKE	AY298418	AY298051
<i>S. auriculatum</i>	Spain	Infanta & Heras	VIT 16670	DUKE	AY298380	AY298014
<i>S. auriculatum</i>	Spain	Infanti & Heras	VIT 21068	DUKE	AY298381	AY298015
<i>S. austinii</i>	Canada	Andrus	6669	NYBG	AY298383	AY298017
<i>S. austinii</i>	Norway	Shaw	9730	DUKE	AF193735	AF192576
<i>S. austinii</i>	USA	Schofield	105911	DUKE	AY298384	AY298018
<i>S. austro-americanum</i>	Colombia	Churchill & Betancur	18752	MO	AF193695	AF192625
<i>S. azuayense</i>	Ecuador	Laegaard	53594E	NYBG	AY298385	AY298019
<i>S. bartlettianum</i>	USA	Andrus	7970	DUKE	AY298386	AY298020
<i>S. bartlettianum</i>	USA	Anderson	27686	DUKE	AY298387	AY298021
<i>S. bartlettianum</i>	USA	Sheridan & Underwood	3	DUKE	AY298388	AY298022
<i>S. bartlettianum</i>	USA	Shaw	9950	DUKE	AY298389	AY298023
<i>S. bartlettianum</i>	USA	Shaw	9280	DUKE	AY298390	AY298024
<i>S. bartlettianum</i>	USA	Shaw	9279	DUKE	AY298391	AF192600
<i>S. bartlettianum</i>	USA	Shaw	9282	DUKE	AY298392	AY298025
<i>S. bartlettianum</i>	USA	Anderson	27360	DUKE	AF193727	AY298026
<i>S. billbuckii</i>	Brazil	Buck	26642	NYBG	AY298393	AY298027
<i>S. boliviae</i>	Bolivia	de Luna	2097	MICH	AY298394	AY298028
<i>S. bordasii</i>	South Africa	Buck	13594	NYBG	AY298395	AF192598
<i>S. boyacanum</i>	Colombia	Escobar & Santa	497	NYBG	AY298396	AY298029
<i>S. brevirameum</i>	Brazil	Buck	26633	MO	AF193716	AF192629
<i>S. brevirameum</i>	Brazil	Buck	26844	MO	AF193715	AF192627
<i>S. buckianum</i>	Brazil	Vital & Buck	20513	NYBG	AY298397	AY298030
<i>S. calymmatophyllum</i>	Japan	Inoue	Bryophyta Selecta Exs. 700	MICH	AY298399	AY298032
<i>S. capense</i>	Malawi	Chapman & Chapman	6771	DUKE	AY298410	AY298042
<i>S. capense</i>	South Africa	Snook	7352	NYBG	AF193664	AF192563
<i>S. capillifolium</i>	England	Vanderpoorten	691	DUKE	AY298398	AY298031

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. capillifolium</i>	Finland	Shaw	9739	DUKE	AY298404	AY298036
<i>S. capillifolium</i>	Finland	Shaw	9739	DUKE	AY298408	AY298040
<i>S. capillifolium</i>	Norway	Shaw	9648	DUKE	AY298405	AY298037
<i>S. capillifolium</i>	Norway	Shaw	9650	DUKE	AY298406	AY298038
<i>S. capillifolium</i>	Norway	Shaw	9683	DUKE	AY298407	AY298039
<i>S. capillifolium</i>	USA	Redfearn <i>et al.</i>	33655	NYBG	AY298400	AY298033
<i>S. capillifolium</i>	USA	Town	s.n.	NYBG	AY298401	AY298034
<i>S. capillifolium</i>	USA	Talbot	228	DUKE	AY298403	AF192621
<i>S. carolinianum</i>	USA	Anderson	27727	DUKE	AY298411	AY298043
<i>S. carolinianum</i>	USA	Shaw	9330	DUKE	AY298412	AY298044
<i>S. centrale</i>	Romania	Heras & Infanti	VIT 21149	DUKE	AY298413	AY298045
<i>S. centrale</i>	USA	Andrus	7686	DUKE	AY298414	AY298046
<i>S. compactum</i>	Norway	Shaw	9712	DUKE	AY298416	AY298049
<i>S. compactum</i>	Russia	Forbes	91–7A	MICH	AY298415	AY298048
<i>S. compactum</i>	USA	Allen	14772	DUKE	AF193706	AY298047
<i>S. compactum</i>	USA	Eric Karlin	9308–2301	DUKE	AY298417	AY298050
<i>S. compactum</i>	USA	Shaw	9332	DUKE	AY298419	AF192578
<i>S. contortum</i>	USA	Anderson	25410	DUKE	AF193669	AF192636
<i>S. cristatum</i>	Australia	Streimann	50625	NYBG	AY298420	AF192580
<i>S. crumii</i>	Brazil	Schafer-Verwimp & Verwimp	15129	MICH	AY298421	AY298052
<i>S. cuculliforme</i>	Ecuador	Largaard	53745B	NYBG	AY298422	AY298053
<i>S. curvatulum</i>	Ecuador	Laegaard	53239A	NYBG	AY298423	AY298054
<i>S. cuspidatulum</i>	India	Long	26466	DUKE	AY298425	AY298056
<i>S. cuspidatulum</i>	India	Long	26445	DUKE	AY298426	AY298057
<i>S. cuspidatulum</i>	India	Long	22475	DUKE	AY298428	AY298059
<i>S. cuspidatulum</i>	Nepal	Long	22218	DUKE	AY298427	AY298058
<i>S. cuspidatulum</i>	Nepal	Long	22255	DUKE	AY298429	AY298060
<i>S. cuspidatum</i>	Japan	Higuchi	40863	DUKE	AY298424	AY298055
<i>S. cuspidatum</i>	Philippines	Schwartz	3771	DUKE	AY298432	AY298063
<i>S. cuspidatum</i>	USA	Shaw	9327	DUKE	AF193677	AF192633
<i>S. cyclophyllum</i>	USA	Shaw	8560	DUKE	AF193665	AF192562
<i>S. cymbifolioides</i>	Australia	Streimann	47192	NYBG	AF193713	AF192584
<i>S. davidii</i>	South Africa	Buck	13508	NYBG	AF193670	AF192566
<i>S. denticulatum</i>	Poland	Brzeg	12	POZG	AY298434	AY298065
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298435	AY298066
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298436	AY298067
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298437	AY298068
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298438	AY298069
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298439	AY298070
<i>S. denticulatum</i>	Poland	Melosik	s.n.	AMU	AY298440	AY298071
<i>S. denticulatum</i>	Poland	Melosik	43	POZG	AY298444	AY298075
<i>S. denticulatum</i>	Poland	Melosik	36	POZG	AY298445	AY298076
<i>S. denticulatum</i>	Poland	Stebel	2	POZG	AY298446	AY298077
<i>S. ecuadorensis</i>	Ecuador	Luteyn <i>et al.</i>	6554	NYBG	AY298447	AY298078
<i>S. ehyalinum</i>	Chile	Goffinet	5782	DUKE	AF193678	AY298079
<i>S. exquisitum</i>	Brazil	Schafer-Verwimp & Verwimp	15127	MICH	AY298448	AY298080
<i>S. falcatulum</i>	Tasmania	Moseal	13388	NYBG	AF193719	AF192586
<i>S. fallax</i>	USA	Schofield	99959	DUKE	AF193725	AF192595
<i>S. fimbriatum</i>	Canada	Schofield	98564	DUKE	AY298454	AY298086
<i>S. fimbriatum</i>	Canada	Shaw	10189	DUKE	AY298455	AY298087
<i>S. fimbriatum</i>	Hungary	Heras & Infanti	VIT 21165	DUKE	AY298449	AY298081
<i>S. fimbriatum</i>	Japan	Uchida	2004	DUKE	AY298450	AY298082
<i>S. fimbriatum</i>	New York	Shaw	11554	DUKE	AY298452	AY298084
<i>S. fimbriatum</i>	Norway	Flatberg <i>et al.</i>	309–00	DUKE	AY298702	AY298338
<i>S. fimbriatum</i>	Russia	Forbes	91–10C	MICH	AY298457	AY298089

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. fimbriatum</i>	Russia	Cronberg	s.n.	DUKE	AY298458	AY298090
<i>S. fimbriatum</i>	Russia	Cronberg	s.n.	DUKE	AY298459	AY298091
<i>S. fimbriatum</i>	USA	Shevock	18330	DUKE	AY298451	AY298083
<i>S. fimbriatum</i>	USA	Schofield	105892	DUKE	AY298453	AY298085
<i>S. fimbriatum</i>	USA	Nelson	19541	DUKE	AY298456	AY298088
<i>S. fitzgeraldii</i>	USA	Horn	s.n.	DUKE	AF193751	AY298092
<i>S. flaccidum</i>	Colombia	Churchill	16393	MO	AF193718	AF192626
<i>S. flavicomans</i>	Canada	Schofield	101051	DUKE	AF193690	AF192571
<i>S. flavicomans</i>	Canada	Hedderson	8702	DUKE	AY298462	AY298095
<i>S. flavicomans</i>	Canada	Belland & Schofield	17174	DUKE	AY298463	AY298096
<i>S. flavicomans</i>	USA	Andrus	O2241	DUKE	AY298460	AY298093
<i>S. flavicomans</i>	USA	Allen	16775	DUKE	AY298461	AY298094
<i>S. flexuosum</i>	USA	Andrus	7169	DUKE	AY298464	AY298097
<i>S. fuscum</i>	Canada	Belland & Schofield	17956	DUKE	AY298465	AY298098
<i>S. fuscum</i>	Canada	Schofield	101020	DUKE	AY298466	AY298099
<i>S. fuscum</i>	Japan	Yamaguchi	18783	DUKE	AY298468	AY298101
<i>S. fuscum</i>	Japan	Yamaguchi	18775	DUKE	AY298469	AY298102
<i>S. fuscum</i>	Japan	Higuchi	40992	DUKE	AY298470	AY298103
<i>S. fuscum</i>	Norway	Vanderpoorten	717	DUKE	AY298471	AY298104
<i>S. fuscum</i>	Norway	Shaw	9680	DUKE	AY298474	AF192603
<i>S. fuscum</i>	Norway	Shaw	9680a	DUKE	AY298475	AY298107
<i>S. fuscum</i>	USA	Shaw	95–27–6a	DUKE	AF193730	AY297999
<i>S. fuscum</i>	USA	Risk <i>et al.</i>	6591	DUKE	AY298467	AY298100
<i>S. fuscum</i>	USA	Shevock	18333	DUKE	AY298472	AY298105
<i>S. fuscum</i>	USA	Risk	1322	DUKE	AF193736	AY298106
<i>S. fuscum</i>	USA	Bowers	24013	DUKE	AY298473	AF192601
<i>S. geraisense</i>	Brazil	Vital & Buck	11917	NYBG	AY298476	AY298108
<i>S. girgensohnii</i>	Canada	Price	694	DUKE	AY298483	AY298115
<i>S. girgensohnii</i>	Canada	Schofield	97076	DUKE	AY298484	AY298116
<i>S. girgensohnii</i>	Japan	Tsukamoto	MT-582	DUKE	AY298478	AY298110
<i>S. girgensohnii</i>	Japan	Tsukamoto	MT-473	DUKE	AY298479	AY298111
<i>S. girgensohnii</i>	Japan	Uchida	2009	DUKE	AY298480	AY298112
<i>S. girgensohnii</i>	Norway	Flatberg <i>et al.</i>	312–00	DUKE	AY298477	AY298109
<i>S. girgensohnii</i>	USA	Schofield <i>et al.</i>	101946	DUKE	AF193675	AF192604
<i>S. girgensohnii</i>	USA	Shaw	11553	DUKE	AY298481	AY298113
<i>S. girgensohnii</i>	USA	Shaw	9392	DUKE	AY298482	AY298114
<i>S. girgensohnii</i>	USA	Andreas	s.n.	DUKE	AY298485	AY298117
<i>S. graciliscens</i>	Brazil	Buck	27034	NYBG	AY298486	AY298118
<i>S. guvassanense</i>	Japan	Higuchi	41008	DUKE	AY298487	AY298119
<i>S. henryense</i>	USA	Ludwig <i>et al.</i>	1196	DUKE	AY298488	AY298120
<i>S. henryense</i>	USA	Wilbur	65925	DUKE	AF193681	AF192637
<i>S. imbricatum</i>	Japan	Higuchi	40308	DUKE	AY298505	AY298137
<i>S. inundatum</i>	England	Andrus	8244	DUKE	AY298443	AY298074
<i>S. inundatum</i>	England	Andrus	8265a	DUKE	AY298506	AY298138
<i>S. inundatum</i>	Germany	Melosik	1	AMU	AY298489	AY298121
<i>S. inundatum</i>	India	Long	26439	DUKE	AY298508	AY298140
<i>S. inundatum</i>	Norway	Andrus	7515	DUKE	AY298501	AY298133
<i>S. inundatum</i>	Norway	Flatberg	19–97	DUKE	AY298509	AY298141
<i>S. inundatum</i>	Poland	Melosik	58	POZG	AY298490	AY298122
<i>S. inundatum</i>	Poland	Stebel	3	POZG	AY298491	AY298123
<i>S. inundatum</i>	Poland	Melosik	14	POZG	AY298502	AY298134
<i>S. inundatum</i>	Poland	Melosik	46	POZG	AY298503	AY298135
<i>S. inundatum</i>	Poland	Stachnowicz	4	POZG	AY298504	AY298136
<i>S. inundatum</i>	USA	Shevock & Kellman	19661	DUKE	AY298441	AY298072
<i>S. inundatum</i>	USA	Alford	236	DUKE	AY298493	AY298125
<i>S. inundatum</i>	USA	Shaw	10301	DUKE	AY298498	AY298130
<i>S. inundatum</i>	USA	Andrus	9277	DUKE	AY298507	AY298139

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. inundatum</i>	USA	Allen	21783	DUKE	AY298633	AY298267
<i>S. inundatum</i>	USA	Shevock	21002	DUKE	AY298634	AY298268
<i>S. itatiaiae</i>	Brazil	Vital & Buck	11780	NYBG	AY298510	AY298142
<i>S. jensenii</i>	Norway	Shaw	9695	DUKE	AF193688	AF192602
<i>S. junghuhnianum</i>	Philippines	Schwartz	3768	DUKE	AY298513	AY298145
<i>S. junghuhnianum</i>	Taiwan	Shevock	14370	MO	AF193728	AF192630
<i>S. junghuhnianum</i> var. <i>pseudomolle</i>	Malaysia	Whitney	992	DUKE	AY298646	AY298282
<i>S. kenaiense</i>	USA	Andrus	8704	DUKE	AY298514	AY298146
<i>S. khasianum</i>	China	Redfern <i>et al.</i>	34401	NYBG	AF193671	AF192597
<i>S. lapazense</i>	Bolivia	Price <i>et al.</i>	1236	MICH	AY298521	AY298153
<i>S. laxirameum</i>	Colombia	Linares & Churchill	3740	MO	AF193703	AF192632
<i>S. lenense</i>	Russia	Cronberg	s.n.	DUKE	AY298528	AY298160
<i>S. leonii</i>	Brazil	Leoni	2170	MICH	AY298522	AY298154
<i>S. lescurii</i>	Belize	Vincent	6143	MICH	AY298523	AY298155
<i>S. lescurii</i>	Colombia	Churchill & Sastre-de Jesus	13086	DUKE	AY298600	AY298234
<i>S. lescurii</i>	USA	Anderson	24873	DUKE	AY298442	AY298073
<i>S. lescurii</i>	USA	Risk	7457	DUKE	AY298492	AY298124
<i>S. lescurii</i>	USA	Summers	8174	DUKE	AY298494	AY298126
<i>S. lescurii</i>	USA	Allen & Pursell	13160	DUKE	AY298495	AY298127
<i>S. lescurii</i>	USA	Andrus	8319	DUKE	AY298496	AY298128
<i>S. lescurii</i>	USA	Anderson	25421	DUKE	AY298500	AY298132
<i>S. lescurii</i>	USA	Anderson	25199	DUKE	AY298515	AY298147
<i>S. lescurii</i>	USA	Alford	1665	DUKE	AY298516	AY298148
<i>S. lescurii</i>	USA	Nelson	20863	DUKE	AY298517	AY298149
<i>S. lescurii</i>	USA	Bachmann	245	DUKE	AY298518	AY298150
<i>S. lescurii</i>	USA	Allen	20268	DUKE	AY298519	AY298151
<i>S. lescurii</i>	USA	Nelson & Robinson	18744	DUKE	AY298520	AY298152
<i>S. lescurii</i>	USA	Shaw	s.n.	DUKE	AF193667	AF192565
<i>S. limbatum</i>	Costa Rica	Dauphin	2065	MO	AF193693	AF192628
<i>S. lindbergii</i>	Canada	Hedderston	8710	DUKE	AY298525	AY298157
<i>S. lindbergii</i>	Norway	Vanderpoorten	718	DUKE	AY298527	AY298159
<i>S. longicomosum</i>	Brazil	Vital & Buck	20028	NYBG	AY298529	AY298161
<i>S. macrophyllum</i>	USA	Shaw	9336	DUKE	AF193666	AF192564
<i>S. macrophyllum</i>	USA	Risk	6856	DUKE	AY298530	AY298162
<i>S. magellanicum</i>	Chile	Goffinet	5858	DUKE	AY298534	AY298167
<i>S. magellanicum</i>	China	Koponen	36959	NYBG	AY298531	AY298163
<i>S. magellanicum</i>	Hungary	Heras & Infanti	VIT 21174	DUKE	AY298532	AY298164
<i>S. magellanicum</i>	Japan	Uchida	2011	DUKE	AY298533	AY298165
<i>S. magellanicum</i>	USA	Clampitt	1505	DUKE	AF193680	AY298166
<i>S. majus</i>	Japan	Uchida	2007	DUKE	AY298538	AY298171
<i>S. majus</i>	Norway	Flatberg	20–97	DUKE	AY298526	AY298158
<i>S. majus</i>	Norway	Shaw	9700	DUKE	AY298535	AY298168
<i>S. majus</i>	Norway	Sastad & Flatberg	229–98	DUKE	AY298537	AY298170
<i>S. majus</i>	Poland	Piotrowska & Gos	909	MICH	AY298536	AY298169
<i>S. mendocinum</i>	Canada	Schofield	98560	DUKE	AY298539	AF192620
<i>S. mendocinum</i>	USA	Andrus	7416	DUKE	AF193726	AY298172
<i>S. meridense</i>	Bolivia	Price <i>et al.</i>	1254	DUKE	AY298540	AY298174
<i>S. meridense</i>	Bolivia	Lewis	38738d-1	MO	AY298541	AF192624
<i>S. meridense</i>	Honduras	Allen	11978	DUKE	AF193692	AY298173
<i>S. meridense</i>	Mexico	LaFarge	s.n.	DUKE	AY298542	AY298175
<i>S. microcarpum</i>	USA	Reese	18337	DUKE	AY298433	AY298064
<i>S. microporum</i>	Japan	Yamaguchi	14436	DUKE	AY298543	AY298176
<i>S. microporum</i>	Japan	Higuchi	40841	DUKE	AY298544	AY298177
<i>S. molle</i>	Ireland	Andrus	8113	DUKE	AY298545	AY298179
<i>S. molle</i>	USA	Anderson	27507	DUKE	AY298431	AY298062

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. molle</i>	USA	Shaw	8729	DUKE	AF193723	AY298178
<i>S. molle</i>	USA	Anderson	27323	DUKE	AY298546	AY298180
<i>S. molle</i>	USA	Risk & Kiser	7025	DUKE	AY298547	AY298181
<i>S. molle</i>	USA	Risk	6629	DUKE	AY298548	AF192599
<i>S. molle</i>	USA	MacDonald	3923	DUKE	AY298549	AY298182
<i>S. monzonense</i>	Bolivia	Price <i>et al.</i>	1277	MICH	AY298550	AY298183
<i>S. moryungasense</i>	Bolivia	Price <i>et al.</i>	1237	MICH	AY298551	AY298184
<i>S. nemoreum</i>	Japan	Higuchi	41004	DUKE	AY298402	AY298035
<i>S. novo-zealandicum</i>	Australia	Wynne	s.n.	MICH	AY298562	AY298195
<i>S. novo-zealandicum</i>	Australia	Seppelt	20349	MICH	AY298563	AY298196
<i>S. obtusum</i>	China	Vitt	34902	MICH	AY298566	AY298199
<i>S. obtusum</i>	Japan	Uchida	2008	DUKE	AY298565	AY298198
<i>S. obtusum</i>	USA	Talbot & Talbot	6–40–32	DUKE	AY298564	AY298197
<i>S. olafii</i>	Norway	Flatberg <i>et al.</i>	288–00	DUKE	AY298567	AY298200
<i>S. orientale</i>	Russia	Afonina	exsicc.	MO	AF193717	AF192631
<i>S. ovatum</i>	Bhutan	Long	28677	DUKE	AY298568	AY298201
<i>S. oxyphyllum</i>	Bolivia	Lewis	89–953d-3	MO	AF193685	AF192623
<i>S. pacificum</i>	USA	Talbot & Talbot	s.n.	NYBG	AY298569	AY298202
<i>S. pacificum</i>	USA	Andrus	7978	NYBG	AY298570	AY298203
<i>S. palustre</i>	Bhutan	Long	28678	DUKE	AY298571	AY298204
<i>S. palustre</i>	Bhutan	Long	28667	DUKE	AY298572	AY298205
<i>S. palustre</i>	USA	Shaw	9391	DUKE	AF193679	AF192634
<i>S. papillosum</i>	Japan	Uchida	2005	DUKE	AY298574	AY298207
<i>S. papillosum</i>	USA	Anderson	27582	DUKE	AY298573	AY298206
<i>S. patens</i>	Mauritius	Lorence	7474	NYBG	AY298575	AY298208
<i>S. perfoliatum</i>	Canada	Belland <i>et al.</i>	14552	MICH	AY298580	AY298213
<i>S. perfoliatum</i>	USA	Murray	76–78	NYBG	AY298579	AY298212
<i>S. perichaetiale</i>	Malaysia	Tan	95–1004	NYBG	AY298576	AY298209
<i>S. perichaetiale</i>	Malaysia	Yamaguchi	18883	DUKE	AY298581	AY298214
<i>S. perichaetiale</i>	Paraguay	Buck	12391	NYBG	AY298577	AY298210
<i>S. perichaetiale</i>	Trinidad	Djan-Chekar	94–716	NYBG	AY298578	AY298211
<i>S. perichaetiale</i>	USA	Shaw	9213	DUKE	AF193700	AF192575
<i>S. planifolium</i>	Equatorial Guinea	Heras	VIT 20735	DUKE	AY298583	AY298216
<i>S. planifolium</i>	Kenya	Chuah-Petiot	A6604	NYBG	AY298582	AY298215
<i>S. platyphylloides</i>	Brazil	Vital & Buck	19813	NYBG	AY298584	AY298217
<i>S. platyphyllum</i>	USA	Schofield	111483	DUKE	AY298585	AY298218
<i>S. platyphyllum</i>	USA	Schofield	105816	DUKE	AY298586	AY298219
<i>S. platyphyllum</i>	USA	Andrus & Talbot	8573	DUKE	AF193668	AF192635
<i>S. portoricense</i>	USA	Anderson	26770	DUKE	AF193705	AF192577
<i>S. priceae</i>	Bolivia	Price <i>et al.</i>	1268	MICH	AY298587	AY298220
<i>S. pulchricoma</i>	Bolivia	Price	1273	MICH	AY298589	AY298222
<i>S. pulchricoma</i>	Bolivia	Price	1255	DUKE	AY298590	AY298223
<i>S. pulchrum</i>	Finland	Shaw	9796	DUKE	AY298591	AY298224
<i>S. pulchrum</i>	Japan	Uchida	2013	DUKE	AY298588	AY298221
<i>S. pulchrum</i>	Norway	Shaw	9707	DUKE	AF193687	AF192607
<i>S. pycnocladulum</i>	Malawi	Chapman	6573	MICH	AF193696	AY298225
<i>S. pylaesii</i>	Bolivia	Lewis	87449	MICH	AY298593	AY298227
<i>S. pylaesii</i>	Canada	Belland & Schofield	16525	MICH	AY298592	AY298226
<i>S. pylaesii</i>	Canada	Schofield	101031	DUKE	AF193691	AF192572
<i>S. pylaesii</i>	Colombia	Arzeni & McKnight	327	DUKE	AY298595	AY298229
<i>S. pylaesii</i>	Ecuador	Laegaard & Steere	27865	MICH	AY298594	AY298228
<i>S. pylaisii</i>	France	Durfort	3.28.02	DUKE	AY298601	AY298235
<i>S. pylaisii</i>	France	Durfort	3.29.02	DUKE	AY298602	AY298236
<i>S. pylaisii</i>	France	Durfort	3.28.02	DUKE	AY298603	AY298237
<i>S. pylaisii</i>	Spain	Franco & Oubina	3324	DUKE	AY298596	AY298230
<i>S. pylaisii</i>	Spain	Franco & Oubina	3190	DUKE	AY298597	AY298231

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. pylaisii</i>	Spain	Franco & Oubina	3435	DUKE	AY298598	AY298232
<i>S. pylaisii</i>	Spain	Franco & Oubina	3436	DUKE	AY298599	AY298233
<i>S. quinquefarium</i>	Norway	Shaw	9682	DUKE	AF193743	AF192608
<i>S. quinquefarium</i>	USA	Musselman	99153	DUKE	AY298604	AY298238
<i>S. quinquefarium</i>	USA	Buck	31503	DUKE	AY298605	AY298239
<i>S. quinquefarium</i>	USA	Clampitt	0967	DUKE	AY298606	AY298240
<i>S. quinquefarium</i>	USA	Andrus	8355	DUKE	AY298607	AY298241
<i>S. quinquefarium</i>	USA	Buck	30639	DUKE	AY298608	AY298242
<i>S. quinquefarium</i>	USA	Allen	15813	DUKE	AY298609	AY298243
<i>S. reclinatum</i>	Venezuela	Buck	12751	NYBG	AY298612	AY298246
<i>S. recurvum</i>	Japan	Uchida	1029	DUKE	AY298610	AY298244
<i>S. recurvum</i>	Japan	Uchida	2014	DUKE	AY298611	AY298245
<i>S. recurvum</i>	USA	Shaw	9196	DUKE	AF193682	AF192569
<i>S. riparium</i>	Belgium	Sotiaux	19310	DUKE	AY298613	AY298247
<i>S. riparium</i>	Japan	Uchida	2012	DUKE	AY298614	AY298248
<i>S. riparium</i>	Norway	Flatberg	72–97	DUKE	AY298618	AY298252
<i>S. ripense</i>	Brazil	Buck	2544	NYBG	AY298615	AY298249
<i>S. rotundatum</i>	Brazil	Schafer-Verwimp & Verwimp	15219	MICH	AY298616	AY298250
<i>S. rotundatum</i>	Brazil	Vital & Buck	19825	NYBG	AY298617	AY298251
<i>S. rubellum</i>	Finland	Shaw	9842	DUKE	AY298619	AF192614
<i>S. rubellum</i>	Finland	Shaw	9842	DUKE	AY298624	AY298257
<i>S. rubellum</i>	Norway	Shaw	9643	DUKE	AY298620	AY298253
<i>S. rubellum</i>	Norway	Shaw	9646	DUKE	AY298621	AY298254
<i>S. rubellum</i>	Norway	Shaw	9646	DUKE	AY298622	AY298255
<i>S. rubellum</i>	Norway	Shaw	9647	DUKE	AY298623	AY298256
<i>S. rubellum</i>	Norway	Shaw	9733	DUKE	AF193742	AY298258
<i>S. rubellum</i>	Russia	Cronberg	s.n.	DUKE	AY298409	AY298041
<i>S. rubellum</i>	Russia	Cronberg	s.n.	DUKE	AY298718	AY298353
<i>S. rubiginosum</i>	Norway	Shaw	9630	DUKE	AF193745	AF192609
<i>S. rubroflexuosum</i>	USA	Andrus	7719	NYBG	AY298625	AY298259
<i>S. russowii</i>	Norway	Shaw	9681	DUKE	AY298626	AY298261
<i>S. russowii</i>	Russia	Cronberg	s.n.	DUKE	AY298628	AY298262
<i>S. russowii</i>	USA	Anderson	27411	DUKE	AY298627	AF192610
<i>S. sancto-josephense</i>	Colombia	Linares & Churchill	3978	NYBG	AF193684	AF192570
<i>S. sancto-josephense</i>	Ecuador	Madsen	s.n.	MICH	AY298643	AY298277
<i>S. santanderense</i>	Colombia	Lewis	88–1440	MO	AF193704	AY298278
<i>S. schofieldii</i>	Canada	Schofield	64344	DUKE	AF193733	AY298279
<i>S. sericeum</i>	Malaysia	Tan & Harrison	s.n.	DUKE	AY298430	AY298061
<i>S. sericeum</i>	Malaysia	Yamaguchi	18926	DUKE	AY298644	AY298280
<i>S. skyense</i>	Scotland	Flatberg	s.n.	H	AF193737	AF192611
<i>S. sonsonense</i>	Colombia	Churchill & Betancur	18703	MICH	AY298645	AY298281
<i>S. sp.</i>	Ecuador	Shaw	11015	DUKE	AY298552	AY298185
<i>S. sp.</i>	Ecuador	Shaw	10990	DUKE	AY298553	AY298186
<i>S. sp.</i>	Ecuador	Shaw	11215	DUKE	AY298554	AY298187
<i>S. sp.</i>	Ecuador	Shaw	11235	DUKE	AY298555	AY298188
<i>S. sp.</i>	Ecuador	Shaw	11468	DUKE	AY298556	AY298189
<i>S. sp.</i>	Ecuador	Shaw	11195	DUKE	AY298557	AY298190
<i>S. sp.</i>	Ecuador	Shaw	11267	DUKE	AY298558	AY298191
<i>S. sp.</i>	Ecuador	Shaw	11365	DUKE	AY298559	AY298192
<i>S. sp.</i>	Ecuador	Shaw	11390	DUKE	AY298560	AY298193
<i>S. sp.</i>	Ecuador	Shaw	11313	DUKE	AY298561	AY298194
<i>S. sp.</i>	Papua New Guinea	De Sloover	42750	H	AY298511	AY298143
<i>S. sp.</i>	Papua New Guinea	Iserentant	B-22	H	AY298512	AY298144
<i>S. sp.</i>	Uganda	Miehe & Miehe	U80–11017	DUKE	AY298671	AY298307

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. sp.</i>	Uganda	Miehe & Miehe	U71-10970	DUKE	AY298672	AY298308
<i>S. sparsum</i>	Bolivia	Price <i>et al.</i>	1457	DUKE	AY298647	AY298283
<i>S. sparsum</i>	Colombia	Linares & Churchill	3957	MO	AY298648	AF192592
<i>S. sparsum</i>	Costa Rica	McQueen	7172	MO	AF193694	AY298284
<i>S. squarrosom</i>	Canada	Belland & Schofield	17919	DUKE	AF193708	AF192581
<i>S. squarrosom</i>	India	Long	26424	DUKE	AY298649	AY298285
<i>S. squarrosom</i>	Japan	Tsukamoto	MT-467	DUKE	AY298650	AY298286
<i>S. squarrosom</i>	Japan	Higuchi	40888	DUKE	AY298651	AY298287
<i>S. strictum</i>	Colombia	Churchill, Franco & Parra	18865	MICH	AY298653	AY298289
<i>S. strictum</i>	Cuba	Buck	7623	MICH	AY298652	AY298288
<i>S. strictum</i>	Uganda	Miehe & Miehe	U74-10993	DUKE	AY298654	AY298290
<i>S. strictum</i>	Uganda	Wesche	1468-163	DUKE	AY298655	AY298291
<i>S. strictum</i>	Uganda	Wesche	9126-T	DUKE	AY298656	AY298292
<i>S. strictum</i>	USA	Shaw	9406	DUKE	AF193714	AF192585
<i>S. subditivum</i>	New Zealand	Fife	8011	MICH	AY298657	AY298294
<i>S. subfulvum</i>	Finland	Shaw	9824	DUKE	AY298661	AF192612
<i>S. subfulvum</i>	Japan	Higuchi	40898	DUKE	AY298658	AY298295
<i>S. subfulvum</i>	Norway	Shaw	9719	DUKE	AF193734	AY298293
<i>S. subfulvum</i>	USA	Andrus	8578	DUKE	AY298659	AY298296
<i>S. subfulvum</i>	USA	Shaw	10236	DUKE	AY298660	AY298297
<i>S. subhomophyllum</i>	Brazil	Schafer-Verwimp & Verwimp	8323	MICH	AY298662	AY298298
<i>S. subnitens</i>	Canada	Belland	14186	DUKE	AY298665	AY298301
<i>S. subnitens</i>	Luxembourg	Vanderpoorten	49	DUKE	AY298666	AY298302
<i>S. subnitens</i>	Norway	Shaw	9723	DUKE	AY298667	AY298303
<i>S. subnitens</i>	Norway	Shaw	9658	DUKE	AF193741	AF192613
<i>S. subnitens</i>	USA	Schofield	106106	DUKE	AY298663	AY298299
<i>S. subnitens</i>	USA	Schofield	109532	DUKE	AY298664	AY298300
<i>S. subobesum</i>	Japan	Higuchi	40307	DUKE	AY298669	AY298305
<i>S. subobesum</i>	USA	Andrus	s.n.	NYBG	AY298668	AY298304
<i>S. subsecundum</i>	Belgium	Vanderpoorten	464	DUKE	AY298637	AY298271
<i>S. subsecundum</i>	Canada	Schofield <i>et al.</i>	97577	DUKE	AY298497	AY298129
<i>S. subsecundum</i>	Canada	Kutchka	s.n.	DUKE	AY298499	AY298131
<i>S. subsecundum</i>	Canada	Schofield	101087	DUKE	AY298670	AY298306
<i>S. subsecundum</i>	Colombia	Churchill & Sastre-De Jesus	13091-b	DUKE	AY298674	AY298310
<i>S. subsecundum</i>	Finland	Karttolnen & Hyvönen	9809	DUKE	AY298638	AY298272
<i>S. subsecundum</i>	Finland	Shaw	9780	DUKE	AY298639	AY298273
<i>S. subsecundum</i>	Japan	Anderson	24276	DUKE	AY298636	AY298270
<i>S. subsecundum</i>	Japan	Uchida	2015	DUKE	AY298676	AY298312
<i>S. subsecundum</i>	Netherlands	van Tienhoven	20116	DUKE	AY298679	AY298315
<i>S. subsecundum</i>	Netherlands	Heidestein	201032	DUKE	AY298680	AY298316
<i>S. subsecundum</i>	New Zealand	Buck	6817	NYBG	AY298681	AY298317
<i>S. subsecundum</i>	Norway	Andrus & Flatberg	7514	DUKE	AY298640	AY298274
<i>S. subsecundum</i>	Poland	Melosik	21	POZG	AY298629	AY298263
<i>S. subsecundum</i>	Poland	Melosik	4	POZG	AY298630	AY298264
<i>S. subsecundum</i>	Poland	Melosik	5	POZG	AY298641	AY298275
<i>S. subsecundum</i>	Poland	Melosik	18	POZG	AY298642	AY298276
<i>S. subsecundum</i>	Russia	Ignatov	00/1011	DUKE	AY298677	AY298313
<i>S. subsecundum</i>	Russia	Ignatov	18.9. 1999	DUKE	AY298678	AY298314
<i>S. subsecundum</i>	Spain	Heras	VIT 19348	DUKE	AY298675	AY298311
<i>S. subsecundum</i>	USA	Shaw	10275	DUKE	AY298631	AY298265
<i>S. subsecundum</i>	USA	Shevock & York	18317	DUKE	AY298632	AY298266
<i>S. subsecundum</i>	USA	Allen	22474	DUKE	AY298635	AY298269
<i>S. subsecundum</i>	USA	Andrus	7246	DUKE	AY298673	AY298309
<i>S. subtile</i>	Canada	Price	10/27/05	DUKE	AY298688	AY298324

Table 1 Continued

Species	Country	Collector	Collection no.	Herb	GenBank: ITS	GenBank: trnL
<i>S. subtile</i>	USA	Shaw	9266	DUKE	AF193731	AY298260
<i>S. subtile</i>	USA	Shaw	10266	DUKE	AY298682	AY298318
<i>S. subtile</i>	USA	Summers	7913	DUKE	AY298683	AY298319
<i>S. subtile</i>	USA	Musselman	99157	DUKE	AY298684	AY298320
<i>S. subtile</i>	USA	Allen	22485	DUKE	AY298685	AY298321
<i>S. subtile</i>	USA	Pedano	476	DUKE	AY298686	AY298322
<i>S. subtile</i>	USA	Risk <i>et al.</i>	6875	DUKE	AY298687	AY298323
<i>S. subtile</i>	USA	Karlin	9510-0723	DUKE	AY298689	AY298325
<i>S. sucrei</i>	Brazil	Costa & Caruso Gomez	939	MICH	AY298690	AY298326
<i>S. tenellum</i>	Finland	Shaw	9792	DUKE	AF193746	AY298336
<i>S. tenellum</i>	Japan	Yamaguchi <i>et al.</i>	19209	DUKE	AY298698	AY298334
<i>S. tenellum</i>	Japan	Higuchi	41000	DUKE	AY298699	AY298335
<i>S. tenellum</i>	Norway	Shaw	9696	DUKE	AY298700	AF192617
<i>S. tenerum</i>	Colombia	Churchill	18330	MO	AY298697	AY298333
<i>S. tenerum</i>	USA	Andrus & Karlin	7080	NYBG	AY298691	AY298327
<i>S. tenerum</i>	USA	Buck	30560	DUKE	AY298692	AY298328
<i>S. tenerum</i>	USA	Shaw	10217	DUKE	AY298693	AY298329
<i>S. tenerum</i>	USA	Ludwig <i>et al.</i>	1111	DUKE	AY298694	AY298330
<i>S. tenerum</i>	USA	Shaw	9271	DUKE	AY298695	AY298331
<i>S. tenerum</i>	USA	Shaw	9283	DUKE	AY298696	AY298332
<i>S. tenerum</i>	USA	Shaw	9335	DUKE	AF193672	AF192588
<i>S. teres</i>	Canada	Hedderson	7928	DUKE	AF193720	AF192596
<i>S. teres</i>	Norway	Flatberg	161833	DUKE	AY298701	AY298337
<i>S. torreyanum</i>	Canada	Schofield & Belland	97183	DUKE	AY298703	AY298339
<i>S. torreyanum</i>	USA	Shaw	s.n.	DUKE	AF193676	AF192568
<i>S. triparum</i>	Brazil	Frahm	1834	NYBG	AY298704	AY298340
<i>S. trirameum</i>	Belize	Allen	18212	NYBG	AY298705	AY298341
<i>S. troendelagicum</i>	Norway	Andrus & Flatberg	7503	DUKE	AF193710	AF192582
<i>S. truncatum</i>	South Africa	Stoutamire	s.n.	MICH	AY298706	AY298342
<i>S. truncatum</i>	South Africa	Buck	13599	NYBG	AF193711	AF192583
<i>S. tundrae</i>	Norway	Flatberg	s.n.	NYBG	AY298707	AY298343
<i>S. tundrae</i>	Norway	Flatberg	161883	DUKE	AY298708	AY298344
<i>S. uleanum</i>	Brazil	Schafer-Verwimp & Verwimp	10616	MICH	AY298709	AY298345
<i>S. viridum</i>	Ireland	Andrus <i>et al.</i>	4098	DUKE	AY298710	AF192615
<i>S. vitjianum</i>	USA	Beitel & Daniel	80083	MICH	AY298711	AY298346
<i>S. warnstorffii</i>	Canada	Shaw	10173	DUKE	AY298714	AY298349
<i>S. warnstorffii</i>	China	Vitt	34808	MO	AY298717	AY298352
<i>S. warnstorffii</i>	USA	Schofield	98518	DUKE	AY298712	AY298347
<i>S. warnstorffii</i>	USA	Spaulding	79	DUKE	AY298713	AY298348
<i>S. warnstorffii</i>	USA	Nelson	17459	DUKE	AY298715	AY298350
<i>S. warnstorffii</i>	USA	Schofield	99947	DUKE	AY298716	AY298351
<i>S. wheeleri</i>	USA	Oppenheimer & Loomis	H110040	DUKE	AY298719	AY298354
<i>S. wilfii</i>	Canada	Schofield	83645	DUKE	AF193744	AY298355
<i>S. wulfianum</i>	Canada	Ireland <i>et al.</i>	23753	DUKE	AY298723	AY298358
<i>S. wulfianum</i>	Finland	Shaw	9855	DUKE	AY298722	AY298357
<i>S. wulfianum</i>	USA	Bowers	22665	NYBG	AY298720	AF192587
<i>S. wulfianum</i>	USA	Taub	96	DUKE	AY298721	AY298356
<i>S. wulfianum</i>	USA	Bowers	22980	DUKE	AF193712	AY298359

in PAUP 4.0b8 (Swofford 2001), saving up to 60 most-parsimonious trees from each of 300 random sequence addition replicates with tree-bisection and reconnection (TBR) branch-swapping. The 'steepest descent' option was

turned off but the 'collapse branches when maximum length is equal to zero' option was invoked. A single, arbitrarily chosen, fully resolved, most-parsimonious tree (henceforth the object tree) was utilized for subsequent analyses

**Table 2** Phylogenetic diversity (PD) estimates for peatmosses (*Sphagnum*) partitioned among geographical regions. Values represent percentages of total PD (tree length). The total data set includes 436 accessions. Values in parentheses following the regions are sample sizes. Mean values ( $\pm$  SD) for subsamples are based on 100 random samples of the size indicated parenthetically

	Combined	nrDNA	cpDNA
Boreal (313)	56	58	54
Nonboreal (123)	64	58	56
Boreal (subsampling: 123)	37 ( $\pm$ 2)	40 ( $\pm$ 2)	35 ( $\pm$ 3)
Tropical (113)	55	57	53
Boreal (subsampling: 113)	37 ( $\pm$ 2)	39 ( $\pm$ 2)	33 ( $\pm$ 3)
Neotropical (75)	37	40	32
Boreal (subsampling: 75)	31 ( $\pm$ 2)	32 ( $\pm$ 2)	27 ( $\pm$ 3)
New World (238)	66	70	61
Old World (198)	65	64	67
New World (subsampling: 198)	60 ( $\pm$ 5)	65 ( $\pm$ 4)	54 ( $\pm$ 6)

of biodiversity patterns. Alternative substitution models were compared for the object tree using hierarchical likelihood ratio tests as implemented by MRMODELTEST 1.1b (Nylander 2002). Branch lengths were estimated for phylogenetic diversity calculations (see below) under a general time-reversible model (GTR) with a proportion of invariant sites and rate heterogeneity among sites specified by a gamma distribution approximated by four discrete categories. Branch lengths were estimated for the combined *ITS* and *trnL* data sets, and also separately for the two data partitions. *ITS* and *trnL* branch lengths were optimized separately on the object tree using likelihood models identified using MRMODELTEST comparisons within each data set.

#### Molecular biodiversity estimates

Biodiversity estimates were partitioned among the following regions: boreal, nonboreal, tropical, Neotropical, Old World and New World. Boreal accessions were defined as those collected north of 30° north latitude. The boreal partition includes sites that would not be considered ecologically 'boreal' (e.g. collections from the eastern United States),

	Combined		nrDNA		cpDNA	
	Complete	Pruned	Complete	Pruned	Complete	Pruned
Boreal (313/313)	332	332	210	210	122	122
Nonboreal (123/120)	376	245	224	166	152	79
Tropical (113/110)	372	241	222	163	150	78
Neotropical (75/74)	276	179	164	121	112	58
Old World (198/196)	379	315	216	188	163	127
New World (238/237)	391	327	233	207	158	120

**Table 3** Phylogenetic diversity (PD) estimates for peatmosses (*Sphagnum*) partitioned among geographical regions. Three highly divergent accessions of *S. lapazense* (South America) and *S. sericeum* (Malaysia and Borneo) were not included in the analyses. Values represent percentages of total PD (tree length). The total data set includes 436 accessions. Values in parentheses following the regions are sample sizes. Mean values ( $\pm$  SD) for subsamples are based on 100 random samples of the size indicated parenthetically

	Combined	nrDNA	cpDNA
<i>S. lapazense</i> & <i>S. sericeum</i>	16	14	19
Boreal (313)	72	72	73
Nonboreal (120)	44	47	40
Boreal (subsampling: 120)	48 ( $\pm$ 3)	49 ( $\pm$ 3)	47 ( $\pm$ 4)
Tropical (110)	44	46	36
Boreal (subsampling: 110)	46 ( $\pm$ 3)	48 ( $\pm$ 3)	44 ( $\pm$ 4)
Neotropical (74)	30	35	23
Boreal (subsampling: 74)	39 ( $\pm$ 2)	40 ( $\pm$ 3)	38 ( $\pm$ 3)
New World (237)	67	73	61
Old World (196)	64	62	68
New World (subsampling: 196)	62 ( $\pm$ 2)	67 ( $\pm$ 2)	55 ( $\pm$ 2)

but this definition provided an unambiguous partitioning of the data; characterizing each site climatically or vegetationally was neither possible in all cases, nor fully objective. The 'boreal' partition is more accurately described as boreal-temperate. Tropical accessions were collected between 30° N and 30° S; South American accessions within this latitudinal range were classified as Neotropical. The Neotropical partition thus contains a subset of the populations included in the tropical zone. Nonboreal accessions include all those plants collected outside the boreal zone (as defined above). This partition therefore includes both tropical and Southern Hemisphere accessions. There were too few high latitude Southern Hemisphere accessions to make it worthwhile defining a 'subantarctic' partition; the nonboreal partition permitted a conservative test of the hypothesis that most peatmoss biodiversity exists in the boreal zone, where *Sphagnum* abundance is by far the highest. New World (the Americas) and Old World (Europe, Australasia, Africa) partitions each included accessions from the arctic to the subantarctic.

**Table 4** Numbers of polymorphic nucleotide sites in peatmoss samples partitioned among geographical regions. The 'complete' data set includes *Sphagnum lapazense* and *S. sericeum*; these taxa are excluded from the 'pruned' data set. Numbers of accessions per geographical partition are shown in parentheses (complete/pruned)

Geographic patterns in species richness were obtained from recent floras and checklists (see Fig. 1 and references provided in the legend). Phylogenetic diversity (PD; Faith 1992) utilizes information about inferred phylogenetic relationships among accessions included in the data set. PDs for each geographical region were estimated as the total length of the minimum-spanning subtree connecting all accessions representing that region. The sum of all branch lengths on the object tree (which was unrooted) constitutes the total PD contained in our sample of peatmosses. Partitioning of PD among regions was estimated by deleting all taxa other than those in the region of interest, and branch lengths were again summed for the remaining subsample. PD for each region is expressed as a percentage of the total PD (i.e. total tree length). Across the whole genus, plants from different geographical regions do not form monophyletic groups, so subtrees connecting accessions from different regions overlap; PD estimates for different geographical partitions therefore add up to greater than 100% because some branches are included in more than one partition. PD was estimated for each region based on the combined *ITS* and *trnL* data set, and separately for *ITS* and *trnL*.

Because PD is based on total (i.e. cumulative) branch length for each geographical region, estimates are affected by sample sizes. While extensive sampling is likely to include all major clades of peatmosses represented within a region, adding samples, unless they are identical to previous accessions, will continually add branch length to PD estimates. The difference in sample size between the boreal partition (the largest sample; 313 accessions) and the Neotropical partition (75 accessions) makes the potential effect of sample size significant. In order to correct for differing sample sizes among geographical regions and make direct comparisons possible, PDs were summed for randomly sampled subsets of the boreal partition. PD was recalculated for each of 100 subsamples so that we could estimate the mean and standard deviation of the boreal PD based on sample sizes equivalent to the less extensively sampled regions. A similar subsampling procedure was employed in order to make direct comparisons between Old World (198 accessions) and New World (238 accessions) partitions. PD estimates derived from differing sampling sizes for the extensively sampled regions are included in Tables 2 and 3 so that the effects of sampling can be evaluated explicitly.

Molecular diversity was also estimated for each region as the number of segregating sites ( $P$ ) among haplotypes within each partition.  $\theta$ , based on the number of pairwise differences among haplotypes (Tajima 1983) and  $\pi$ , calculated from the number of segregating sites (Watterson 1975), were also estimated for each geographical region, but the standard deviations were so large that patterns were ambiguous and these statistics are not presented.

Like PD estimates,  $P$  was calculated for the combined data, and for *ITS* and *trnL* sequences separately.

## Results

### *Taxic diversity*

Aside from South America, recent floristic treatments suggest that there are generally more species of *Sphagnum* in the Northern than the Southern Hemisphere (Fig. 1). North America appears to have a higher number of species than do northern Asia or Europe. These differences may reflect both real differences in species richness among Northern Hemisphere regions and different taxonomic concepts used in floristic treatments. There are a few distinctive species endemic to the southeastern United States, but in addition, some species included in the North American tally are subsumed in more broadly defined taxa by many European authors. Old World tropical and Southern Hemisphere areas of both the New and Old World are relatively poor in species, although *Sphagnum* is abundant (in terms of biomass) in Chile, Tasmania (included in the Australian estimate of 15 species) and New Zealand. At the extreme, the extensive peatlands of southern Chile and Argentina appear to be remarkably species-poor. The outlier in terms of species richness is clearly northern South America (Fig. 1). Many species have been described recently from cloud forests of Brazil and Venezuela, and the genus is also represented abundantly in the Andes Mountains of Columbia, Peru and Ecuador.

### *Phylogenetic analyses*

The combined *ITS* and *trnL* data set contained 1599 aligned sites, of which 1002 were constant, 364 were parsimony informative and 233 additional sites were autapomorphic. Of the informative sites, 215 were from *ITS* and 149 were from *trnL*. The heuristic search yielded 6600 most parsimonious trees of 1248 steps with CI of 0.6106, an RI of 0.9311 and an RC of 0.5685. Many more trees of this length would have been found had the heuristic search been conducted with no limit on the numbers of trees saved per replicate. The randomly selected object tree utilized for biodiversity estimates is shown as Fig. 2. Two taxa, *S. sericeum* from the Old World tropics and *S. lapazense* from tropical South America, are extremely isolated from all remaining species of *Sphagnum*. In maximum likelihood analyses of a 12-gene data set (unpublished), *S. sericeum* and *S. lapazense* do not form a monophyletic group, although this larger data set supports their extreme genetic divergence from all other species of *Sphagnum*. These two species are far more distinct in terms of DNA sequences than are the well-supported sections of *Sphagnum*, which are resolved (but not labelled in Fig. 2) by *ITS* and *trnL* sequences.

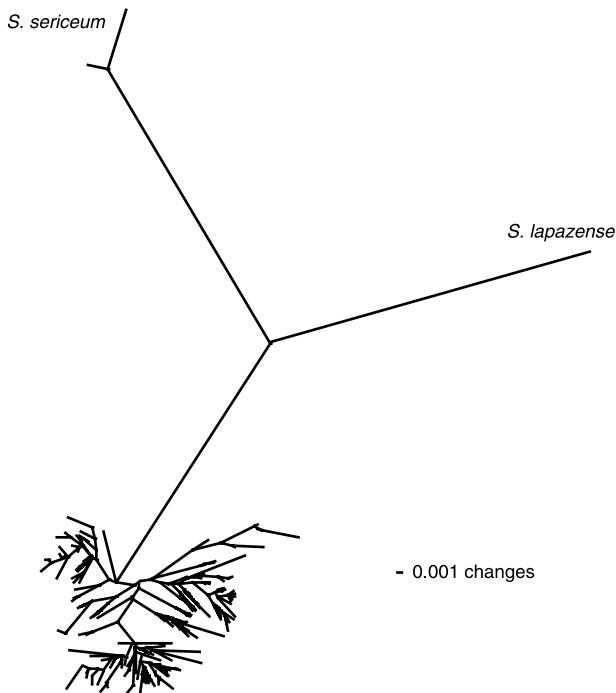


Fig. 2 Phylogram showing one of 6600 most parsimonious trees for 436 accessions of peatmosses based on combined *ITS* and *trnL* sequences. Branch lengths were estimated under maximum likelihood using a GTR + I +  $\Gamma$  model. See text for additional details.

### Molecular biodiversity analyses

PD estimates for the geographical regions, based on combined *ITS* and *trnL* sequences and separately for the two genomic partitions, are shown in Tables 2 and 3. Inclusion or exclusion of *S. sericeum* and *S. lapazense* had a substantial effect on PD estimates. When these two species and all 313 boreal samples were included in the analyses, the boreal zone contained over 50% of peatmoss PD, whether the *ITS* and *trnL* data were combined or considered separately (Table 2). However, when the boreal accessions were subsampled for direct comparison with the nonboreal, tropical and Neotropical geographical partitions (123, 11 and 75 accessions, respectively), boreal PD decreased to less than 40% of the total. Comparing equivalent sample sizes, the boreal zone contains less peatmoss PD than nonboreal, tropical or Neotropical partitions (Table 2).

A rather different picture emerged when *S. lapazense* and *S. sericeum* were excluded from PD estimates (Table 3). Remarkably, these two taxa, represented by only three accessions, accounted for 15–20% of all peatmoss biodiversity. They appear to comprise a slightly larger percentage of the total *trnL* than *ITS* PD. With these two highly divergent tropical taxa excluded from consideration, the boreal zone accounted for over 70% of the total PD when all 313 boreal accessions were included (Table 3). When boreal

accessions were subsampled at levels equivalent to other geographical partitions, however, the boreal zone accounted for about 39–48% of the total PD. Based on equivalent sample sizes (and with *S. lapazense* and *S. sericeum* excluded) there were approximately equivalent levels of PD in the boreal and nonboreal zones for the combined and *ITS* data. There may be slightly higher *trnL* PD in boreal than nonboreal regions ( $47 \pm 4$  vs. 40%). The tropics contain levels of PD comparable to the boreal zone in terms of *ITS* and the combined *ITS* and *trnL* data, but for *trnL* alone the tropics account for only 36% of the total PD (Table 3). Standard deviations for the estimates of boreal PD suggest that the difference in *trnL* diversity between tropical and boreal regions may be significant, but because no equivalent estimates of variation are available for the tropical PD estimates, formal statistical tests cannot be conducted.

The Neotropics accounted for 30–35% of total PD for combined *ITS* and *trnL* data and for *ITS* alone. When boreal accessions were subsampled at an equivalent sample size, the boreal zone contained slightly higher PD. The differences were larger than in comparisons of boreal and tropical PD, and the standard deviation for the combined *ITS* and *trnL* data suggests a significant difference. In terms of *trnL*, however, the Neotropics contain only 23% of the total PD, vs.  $38 \pm 3\%$  for the boreal zone based on an equivalent sample size. This lower level of Neotropical *trnL* diversity compared to that contained in boreal accessions is probably biologically significant.

Old vs. New World samples contain roughly equivalent levels of PD in analyses of the combined data and the *ITS* data alone. Inclusion or exclusion of *S. sericeum* and *S. lapazense* had a less dramatic effect on this comparison as the former occurs in the Old World and the latter occurs in the New World; excluding one more or less cancels out the effect of excluding the other. When New World accessions were subsampled at a level comparable to the Old World sample size, there is less *trnL* PD in the New than Old Worlds. This is true whether *S. lapazense* and *S. sericeum* are excluded or included (Tables 2 and 3).

When *S. sericeum* and *S. lapazense* were included in the combined *ITS* and *trnL* data, there were more polymorphic nucleotide sites (*P*) in tropical than boreal samples despite the difference in sample size (Table 4). Neotropical samples, however, contained fewer polymorphic nucleotide sites than did boreal samples. Moreover, when *S. sericeum* and *S. lapazense* were excluded from the data set, boreal sequences contained substantially higher numbers of polymorphic nucleotide sites than did nonboreal, tropical or Neotropical partitions (Table 4). Eliminating *S. lapazense* reduced the number of polymorphic sites among Neotropical accessions by nearly 100 sites, or approximately 35%.

As predicted from general expectations of molecular variation in nuclear ribosomal vs. chloroplast sequences, estimates of molecular diversity were higher for *ITS* than

for *trnL* data. For *ITS* data alone, when *S. lapazense* and *S. sericeum* were included, the nonboreal and tropical partitions contained slightly higher levels of polymorphic sites than did the boreal partition (Table 4). The Neotropics, however, contained almost 50 fewer polymorphic sites. When *S. lapazense* and *S. sericeum* were excluded, the difference was accentuated (Table 4). The same patterns were evident in the *trnL* data when analysed alone (Table 4). When *S. lapazense* and *S. sericeum* were excluded, there were fewer polymorphic nucleotide sites among accessions from outside the boreal zone, and Neotropical accessions contained less than half as many polymorphic sites as boreal accessions (Table 4).

New World accessions contained more polymorphic *ITS* sites than Old World accessions whether *S. lapazense* and *S. sericeum* were included or excluded (Table 4). There were, in contrast, more polymorphic *trnL* sites in Old than New World accessions regardless of *S. lapazense* and *S. sericeum*.

## Discussion

Global patterns of peatmoss biodiversity inferred from DNA sequence data contradict inferences gained from estimates of species richness derived from checklists for different geographical regions. Species numbers suggest that the New World, both North and South America, contain higher peatmoss diversity than do Old World regions, and that northern South America is a hotspot of diversity. In contrast, nuclear and chloroplast sequence diversity indicate that the Neotropics contain only about 20–35% of total peatmoss genetic diversity on a global scale. The tropics contain about the same amount of *Sphagnum* genetic diversity as do boreal regions, and perhaps less diversity of chloroplast DNA variation. Also in contrast to inferences gleaned from species richness data, peatmoss genetic biodiversity is about evenly distributed between New and Old World regions, or the Old World may contain somewhat more diversity.

There are several possible reasons for incongruence between biodiversity estimates derived from species richness vs. molecular data. *Sphagnum* is arguably one of the most difficult and taxonomically contentious genera of bryophytes; various authors differ substantially in the degree of 'lumping' and 'splitting' in their taxonomic assessments of peatmosses. In North America, for example, Andrews (1913) recognized 39 species, Crum (1984) 51 species, and Anderson (1990) recognized 72 species in his continental checklist. McQueen and Andrus (unpubl.) recognize about 90 species in their manuscript treatment of *Sphagnum* for the Flora of North America project.

Most *Sphagnum* species can be classified unambiguously into six infrageneric sections. Within these sections, however, complexes of closely related taxa are generally the source of taxonomic disagreement, and such complexes

exist within each of the four large sections. One such group is the '*S. recurvum* complex' (Flatberg 1992). Whereas Crum (1984) recognized one species, *S. recurvum* P. Beauv. Andrus (1980) and McQueen and Andrus (unpubl.) divided the group into about nine species. Also contributing to the ambiguity of species richness estimates for quantifying geographical patterns of biodiversity in a taxonomically difficult genus such as *Sphagnum* is that individual taxonomists sometimes apply different species concepts in different geographical regions. Crum (1984) recognized 51 North American species of *Sphagnum*, but described over 90 species from South America (in many papers too numerous to cite individually), including numerous segregates of species he did not even recognize in North America. Some of the global patterns in species richness simply reflect geographical variation in taxonomic concepts rather than in genuine species richness.

Another reason that species richness may conflict with genetic estimates of biodiversity is that species are not all equivalent in biodiversity value. Closely related species in the *S. recurvum* complex, for example, do not represent as much genetic variation (diversity) as an equivalent number of species chosen at random from the genus. A striking case of nonequivalence among species of biodiversity value is exemplified by *S. sericeum* and *S. lapazense* in the present study. The *ITS* and *trnL* sequences of these two species are remarkably different from those of all other *Sphagnum* taxa, and comparable differences occur in at least nine other genes from the nuclear, chloroplast and mitochondrial genomes (Shaw, unpubl.). The three accessions of *S. lapazense* and *S. sericeum* make up only 0.7% of the samples included in the current molecular analyses, yet contributed 15–20% of the phylogenetic diversity of peatmosses. These results were so surprising that extractions, PCR amplifications and sequencing were repeated several times.

Morphological diversity provides an alternative for estimating biodiversity and such estimates might conflict with both species richness and DNA-based metrics. Some species are morphologically aberrant but genetically mainstream, whereas others are genetically isolated but morphologically typical. *S. macrophyllum*, *S. pylaesii* Brid. and *S. aongstroemii* Hartm. represent morphologically unusual taxa, previously segregated into their own monotypic sections of *Sphagnum* (*Isocladus*, *Hemitheca* and *Insulosa*, respectively; e.g. Isovita 1966; Crum 1984), but which are not especially distinctive in DNA sequences. Thus, if biodiversity is estimated using morphological characters, these species add an inordinate amount of diversity to any region in which they occur, but they add no more than many other morphologically typical species if genetic data are utilized. If species richness is the metric, they have unit value, like any other *Sphagnum* species.

*S. sericeum* is morphologically distinctive enough that sphagnologists since Lindberg (1862) have segregated it as

a separate subgenus or section of *Sphagnum*. Warnstorf (1911) grouped it with the morphologically aberrant *S. macrophyllum* in the subsection *Sericea* because both taxa lack reinforcing fibrils in the chlorophyll-free hyaline cells of the branch leaves. These fibrils constitute one of the unique features that set *Sphagnum* apart from all other mosses. As noted above, *S. macrophyllum* is nested within one of the larger *Sphagnum* sections (*Subsecunda*) and is not especially distinctive in terms of DNA sequences (Shaw 2000). The lack of fibrils in *S. macrophyllum* is clearly a secondarily derived feature and the morphological distinctiveness of this species (not limited to the lack of fibrils) is not paralleled by molecular differentiation. Eddy (1977) suggested, in contrast, that the lack of fibrils in *S. sericeum* is a primitive feature, and phylogenetic analyses based on 12 genes support that view (Shaw, unpubl.).

*S. lapazense*, although as isolated as *S. sericeum* in terms of DNA sequences, is not particularly distinctive with regard to morphology. Crum (2001) included *S. lapazense* in section *Sphagnum* when he described the species from Bolivia as new. Crum noted that *S. lapazense* lacks several of the typically diagnostic features of section *Sphagnum*, but in general the species is no more atypical than are several other species of South American section *Sphagnum*. Nevertheless, like *S. sericeum*, *S. lapazense* is remarkably isolated from other species of *Sphagnum* in the *ITS* and *trnL* sequences utilized in this study, as well as in nine other nuclear, chloroplast and mitochondrial genes (Shaw, unpubl.). These two taxa provide an especially compelling demonstration of the nonequivalence of species in terms of biodiversity value, and the extreme genetic isolation of these species would not have been predicted from their morphological features (not even *S. sericeum*).

In addition to incongruence between the geographical patterns in peatmoss biodiversity inferred from species richness vs. DNA sequence data, *ITS* and *trnL* provide quantitatively different inferences. Tropical (and Neotropical) samples account for less *trnL* diversity, relative to boreal samples, than they do in *ITS* sequence diversity. To the extent that *ITS* diversity is representative of the nuclear genome and *trnL* is representative of chloroplast DNA, these observations suggest that the packaging of biodiversity among global peatmoss populations is genome-specific. This can be tested by sampling additional loci. Nevertheless, the differences between *ITS* and *trnL* patterns are quantitative rather than qualitative, so the same general conclusions hold for each.

There are many advantages and disadvantages to utilizing molecular markers vs. morphological or ecological traits to quantify biodiversity (Moritz 1994; Merilä & Crnokrak 2001; Reed & Frankham 2001; McKay & Latta 2002; van Tienderen *et al.* 2002). Neutral molecular markers potentially provide insights into historical processes such as migration patterns, population bottlenecks and gene

flow, which should affect the whole genome, while functional traits may be more informative about adaptation and adaptability. In a conservation context, biodiversity ideally provides a measure of 'option value' – the potential for adaptation to changing future conditions. There is an obvious tradeoff between the ability to quickly generate biodiversity data from neutral markers vs. more tedious, but perhaps more relevant, data on quantitative traits. Because of rapid technological advances, it is now easier to survey molecular markers specific for ecologically important traits (van Tienderen *et al.* 2002), an approach that will ultimately combine the advantages of both strategies. However, individual loci underlying adaptive polygenic traits may, in fact, behave as if they were neutral because selection is diluted across the multiple loci (Lande 1976). The relationship between marker loci and quantitative traits is still poorly understood but promises to be complex. Genic interactions (epistasis) increase in relative importance as the number of QTLs underlying adaptive traits increase, adding yet another level of complexity (McKay & Latta 2002).

We utilized several alternative estimates to quantify peatmoss molecular biodiversity. Phylogenetic diversity (Faith 1992) is an historical metric that takes the amount of past evolution separating taxa explicitly into account. By using a model of nucleotide substitution, PD corrects for rate heterogeneity among sites and multiple hits at individual sites. Nonhistorical metrics such as the number of polymorphic sites,  $\theta$  or  $\pi$ , quantify standing diversity without regard to the mutational processes that gave rise to that diversity. It can be argued that from a conservation standpoint, it is the latter that is most important; how diversity came to be is irrelevant with regard to future option value. From an evolutionary perspective, however, historical perspectives provided by PD estimates can be enlightening. It is possible, for example, that high peatmoss species richness but relatively low PD in the Neotropics may reflect recent radiations of *Sphagnum* in South America. These taxa may be ecologically and morphologically diverse, but are characterized by relatively little evolutionary divergence in neutral sequences. In some cases, regions with high PD may be evolutionary hotspots where biodiversity is generated, and therefore of particular value for the conservation of option value (Sechrest *et al.* 2002). Hotspots can also represent 'museums' where diversity has persisted, and may not be centres of current evolutionary activity. They may nevertheless be important for future adaptive evolution.

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