MOSS DIVERSITY AND ENDEMISM OF THE TROPICAL ANDES[1]

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ABSTRACT

The mosses of the tropical Andes are examined to determine a conservative estimate of diversity, excluding a significant number of unconfirmed names and dubious reports that have distorted estimates in the past. In this analysis, 1376 species represented by 327 genera and 69 families are recognized. Within this cohort, species endemism for the tropical Andes is estimated at 31%. Regionally, the number of mosses restricted to the northern Andes (321 species) is higher than the number restricted to the central Andes (241 species). Regional endemism exhibits a similar pattern: more endemics in the northern Andes (155 species) than in the central Andes (129 species).

Key words: Diversity, endemism, mosses, tropical Andes.

The tropical Andes are widely acknowledged as one of the world's great centers of biodiversity (Rodríguez-Mahecha et al., 2004). Species richness is one of the criteria that serves to rank the tropical Andes as a major focal point of biodiversity. Other criteria include the level of endemism and past and current environmental degradation (Orme et al., 2005). The very foundation of biodiversity is our knowledge of the organisms. Precise estimates of diversity for most major groups of organisms are, however, elusive for the tropical Andes. It is very likely that diversity and distribution within this region are only well known for birds and mammals; all other estimates—for fungi, plants, and insects, for example—are only vague or approximate. This is due, in part, to required ongoing basic exploration, inventory, discovery of new species, and, most critical to our understanding of diversity, revisionary studies.

Mosses represent just one group of organisms that make the tropical Andes one of the great centers of biodiversity in the world. This region contains about 15%–17% of the estimated 8000 to 9000 mosses in the world. Endemism is relatively high, with 31% of the species considered to be unique to the region (see below). Beyond high diversity and endemism, there is another dimension that ranks these organisms as possibly one of the most important groups in the tropical Andes. Disproportionate to their small size, mosses, rather like the ants so eloquently described by the Harvard entomologist E. O. Wilson, play a major role in the ecosystem they occupy. Mosses, along with hepatics, are the major plant group responsible for the natural conservation of water and soil in the Andes.

The focus of this paper is an assessment of the diversity and endemism for the tropical Andean mosses. This present analysis is, in part, a reevaluation and update of a prior paper addressing moss diversity of the tropical Andes (Churchill et al., 1995). There are several moss publications since 1995 that are specifically related to the tropical Andes. The páramo mosses of Venezuela, Colombia, Ecuador, and Costa Rica were estimated at 543 species (Churchill & Griffin, 1999). The first checklist for the tropical Andean countries enumerated 2089 specific and infraspecific taxa distributed among 362 genera and 76 families (Churchill et al., 2000). A descriptive treatment of the families and genera was provided for the Neotropics (Gradstein et al., 2001) and included an analysis of bryophyte regions and habitats. Various floristic papers for each of the Andean countries are provided on the web page "Overview of Region and Countries" (<http://mobot.mobot.org/W3T/Search/andes/overviewintro.htm>).

OVERVIEW OF THE TROPICAL ANDES

The tropical Andes extend approximately 38 degrees of latitude, from the coastal ranges and

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Cordillera de Mérida of Venezuela to the puna and montane ranges in northwestern Argentina. This arched backbone of South America, the longest mountain chain in the tropics, can be divided between the northern Andes (Venezuela to northernmost Peru) at 11°N to 4–5°S and the central Andes (north-central Peru to northwest Argentina) at 5°S to 27°S. The estimated area of the tropical Andes is 1,542,664 km^2 (Rodríguez-Mahecha et al., 2004). That figure is ca. 39% of the total area of the tropical Andean countries and slightly less than 9% of the total land surface of South America. The Amazon Basin is nearly 4.5 times larger than the tropical Andes. Useful overviews for the tropical Andes are provided on geography by Duellman (1979) and for vegetation by Luteyn and Churchill (2000).

The Myth of Tropical Moss Diversity

It is imperative to have a clear understanding of the misconceptions that impede our knowledge of moss diversity for the tropical Andes. The year 1801 marks two important events with regard to tropical American mosses. Hedwig's opus, *Species Muscorum Frondosorum*, was published in 1801; in time this would be adopted as the official starting point of moss nomenclature, except *Sphagnum* L. This volume includes the first mosses collected in tropical America, those by Olof Swartz from the West Indies. The second event of that year occurred in the Colombian Andes; Alexander von Humboldt and Aimé Bonpland were the first to collect mosses from the Andes. These mosses were later described by William Hooker in *Musci Exotici* (1818–1820).

Historically, the most active period in which Andean mosses were collected and described occurred from about the mid-19th century to the first three decades of the 20th century. During that time period, several thousand new species were described by Europeans, beginning with Ernst Hampe, Carl Müller, William Mitten, and later Viktor Brotherus and Theodor Herzog. North Americans also began to describe species for the Andes in the first half of the 20th century, most notably Robert Williams and Edwin Bartram. The quality of these authors varied considerably. Hampe and Mitten, for the era, produced reasonably sound descriptive treatments, but at the other end of the spectrum was Müller. No single individual described more species than Müller, who was completely, or almost, indiscriminate in describing several thousand species; many of these are viewed as redundantly described species. Of the many collections sent to Müller from South America, almost all were described as new species. Unfortunately for bryology, Müller was blessed with a long life (1818–1899), and, most detrimental to bryology, his collections housed in the Berlin herbarium were destroyed in World War II.

The recognition of species by these 19th- and early 20th-century authors was based mostly on a very narrow species concept, often defined by minute or trivial differences in morphology, e.g., plant stature, leaf shape, seta length, etc. (Pursell, 1994). Many of the described mosses were based on a very limited number of specimens and incomplete knowledge of the species described at that time by different authors. Due to the paucity of specimens, there was almost no idea of how these plants varied or how they could be differentiated from other recently described species from the same region. Other factors also contributed to the increasing confusion: communication was limited or long delayed with regard to correspondence and publications, duplicates were only later distributed if they existed, and in addition, there were various conflicts between the European nations (Kruijer, 2002).

The dilemma of excessive naming of species for the tropical regions has been discussed by Touw (1974) and Magill (1982). Those familiar with the state of tropical bryophytes stress the dire need for revisionary studies. A few examples from revisionary studies of mosses serve to exemplify the problem of excessive naming for the tropical Andes: Frahm (1991) recognized 49 species of *Campylopus* Brid. for the tropical Andes, relegating 58 previously published species to synonymy; Fransén (1995) recognized 12 species of *Bartramia* Hedw., placing 22 into synonymy; and Muñoz (1999) recognized 15 species of *Grimmia* Hedw. for the tropical Andes, with 26 previously published species relegated to synonymy. Among just these revisionary studies, 106 species were thus subtracted from the heretofore accepted mosses, or, viewed another way, the Andes lost 106 endemic species.

The compilation of checklists for mosses, either for individual countries or regions in the tropics, was an important initial phase during the late 20th century in the development of floristic knowledge. In large part, such checklists were compilations from previous floristic and revisionary studies. Embedded within these checklists were numerous species for which the taxonomic status was unknown. Checklists for all the tropical Andean countries were compiled in the 20th century: Bolivia (Herzog, 1916; Hermann, 1976), Colombia (Florschütz-de Waard & Florschütz, 1979; Churchill, 1989), Ecuador (Steere, 1948; Churchill, 1994), Peru (Menzel, 1992), and Venezuela (Pittier, 1936; Pursell, 1973). A complete summary for the tropical Andean countries was provided by Churchill et al. (2000). All of these checklists incorporated the many newly described species, as well as the earlier dubious species reports for the tropical Andes, although adjustments to recognized species were made based on revisionary studies that existed.

A few previous studies have attempted to use data from checklists to analyze and provide generalizations and trends with regard to diversity (Churchill, 1991; Delgadillo, 1994; Churchill et al., 1995; Frahm, 2003). Given the data available, this has on occasion led to rather exaggerated species numbers. Delgadillo (1994) examined moss diversity and endemism in the Neotropics for 24 countries. Three of these countries serve as examples of inflated species numbers: Bolivia, 1182 species, with 359 endemic; Brazil, 1655 species, with 815 endemic; and Paraguay, 148 species, with 54 endemic. Although it is impressive to note that 49% of the Brazilian moss flora is endemic, 36% is endemic to Paraguay, and 30% is endemic to Bolivia, it is far from the reality. Brazil has fewer than 1000 species and probably fewer than 100 endemics, Bolivia has about 900 species and 56 endemics (see below), and, although Paraguay may have on the order of 200 species, it is highly probable that there is not a single endemic in this country (Churchill, pers. obs.). These assumptions are based on a greater knowledge gained through floristic and revisionary studies over the past two decades and on directions suggested by these results that will impact our understanding of species diversity.

There is a need then to develop a new generation of checklists for bryophytes in the tropical countries based on new stringent criteria. One of the first catalogs concerning bryophytes, in this case the hepatics for Bolivia by Gradstein et al. (2003), took a more pragmatic approach in excluding doubtful names and reports. While very few of those excluded names are now accepted, a greater portion has since been shown to be synonyms. This is a far better approach to take in future efforts of compiling bryophyte checklists particular to areas such as the Neotropics. The analysis of moss diversity and endemism of the tropical Andes will entail error, but it is better to err on the side of a conservative, realistic estimate than to err on the side of an embroidered fantasy of diversity.

Data for this analysis are derived from four sources: (1) the taxonomic treatment of the tropical Andean mosses (<http://mobot.mobot.org/W3T/Search/andes/andesintro.htm>, Churchill & collaborators, 2008); (2) more than 50,000 databased bryophyte collections for the Andean countries in the Missouri Botanical Garden Tropicos system; (3) a compiled world checklist for mosses by Crosby et al. (2000); and (4) recent floristic and taxonomic revisions not found on the aforementioned web page. Accepted taxa include only legitimate names at the level of species and above. Excluded from this analysis are all species whose taxonomic status is unknown or reports considered dubious. All nomina nuda are excluded. Infraspecific categories (subspecies, varieties) are not included in the analysis. The initial species list of the tropical Andean countries (Bolivia, Colombia, Ecuador, Peru, and Venezuela) and the northwestern departments of Argentina (Juyuy, Salta, Tucumán) totaled 1974 and included 1457 accepted species and 517 excluded, most as status unknown or outside the Andean range.

A second set of data was generated from this initial effort that includes only the Andean region (Fig. 1), with the minimum elevation for the tropical Andes defined at 500 m. Outliers for the tropical Andes included in this analysis are the Cordillera de la Costa in Venezuela and the Sierra de Santa Marta in Colombia; in the south the boundary is defined to include only the departments of Jujuy, Salta, and Tucumán in northwestern Argentina. Geographically, the tepui regions (Guayana Highlands) and Atlantic and Pacific islands (e.g., Galápagos) are excluded. The adjoining coastal and interior lowlands in South America less than 500 m elevation (e.g., Amazon Basin and Chocó) are also excluded.

Data were arranged in an Excel (Microsoft Word, Redmond, Washington, U.S.A.) spreadsheet that included: name of family, genus, species, number of synonyms for each genus, elevation range, endemic status, and species present in either the northern or central Andes or present in both, and finally individual countries. This Excel spreadsheet is available on the Andean web page "Overview of Region and Countries" under tropical Andes: <http://mobot.mobot.org/W3T/Search/andes/overviewtropicalandes.htm>.

Taxonomic Diversity

Moss diversity for the tropical Andes is estimated at 1376 species, 327 genera, and 69 families (Appendix 1). The number of species is substantially lower than the 2058 species estimated previously (Churchill et al., 1995), whose figures included a small fraction of the species present in the lowlands. Even the projected estimate of 1500 to 1700 species (Churchill et al., 1995), considered a more realistic figure, is not substantiated. The number of specific and infraspecific moss synonyms presently recorded for the tropical Andes is 929 (Appendix 1), many of which were recognized in the past three decades.

The 10 most speciose families (Table 1) account for 861 species, containing a significant portion (66%) of

Figure 1. Map of the tropical Andes with the numbers of species for each of the countries.

the total moss diversity for the tropical Andes. This is nearly identical to that estimated by Churchill et al. (1995). Differences include in part the recognition of the Macromitriaceae (segregated from Orthotrichaceae, cf. Churchill & Linares C., 1995) and the significant increase in newly described species of *Sphagnum*. Other factors include the reduction of previously recognized names due to new synonymy for the Grimmiaceae, or names excluded in this study as status unknown, for example *Mittenothamnium* Henn., which contains an inordinate number of names, many likely referable to *M. reptans* (Hedw.) Cardot.

Table 1. The 10 most diverse moss families and genera for the tropical Andes.

Family	No. of species	Genus	No. of species
Pottiaceae	172	*Sphagnum* (Sphagnaceae)	61
Bryaceae	130	*Campylopus* (Dicranaceae)	49
Dicranaceae	129	*Fissidens* (Fissidentaceae)	46
Pilotrichaceae	109	*Bryum* (Bryaceae)	44
Bartramiaceae	64	*Zygodon* (Orthotrichaceae)	33
Sphagnaceae	61	*Macromitrium* (Macromitaceae)	30
Sematophyllaceae	52	*Didymodon* (Pottiaceae)	26
Orthotrichaceae	51	*Syntrichia* (Pottiaceae)	26
Macromitriaceae	47	*Lepidopilum* (Pilotrichaceae)	25
Fissidentaceae	46	*Schizymenium** (Bryaceae)	24

* Coequal with *Sematophyllum* (Sematophyllaceae).

The 10 most diverse moss genera in the tropical Andes containing 20 or more species are listed in Table 1. Just these 10 of the 327 genera account for 26% of the total species recorded. Eight of these 10 genera have been revised or under current study so that these numbers seem to be a reliable estimate. This may be the case with *Zygodon* Hook. & Taylor (see families discussed below) but is less certain for *Sematophyllum* Mitt., which lacks modern revisionary studies. At the other end of the generic spectrum, 159 or 49% of the genera recorded for the tropical Andes are represented by a single species; 55 of the 159 represent monospecific genera.

Endemism

A taxon is considered endemic if it is only known from within the geographical range of the tropical Andes; that range may be restricted to a single locality or span the entire length of the tropical Andes. The number of endemic species estimated for the tropical Andes is 428 species distributed among 137 genera and 38 families (Appendix 1). The number of endemic species is 31% of the total recorded for the tropical Andes. Twenty genera are endemic to the tropical Andes (Table 2). All are monospecific with the exception of *Sciuroleskea* Hampe ex Broth., with two

Table 2. Endemic genera of the tropical Andes. Provided for each genus are the family, associated Andean vegetation, elevational range, and distributional range by country.

Genus	Family	Vegetation	Elevation (m)	Country
Aligrimmia	Grimmiaceae	puna	2250–2700	Peru
Allioniellopsis	Sematophyllaceae	low montane forest	750–1400	Ecuador, Peru
Callicostellopsis	Pilotrichaceae	páramo/puna	3480–3620	Venezuela, Bolivia
Flabellidium	Brachytheciaceae	low montane forest	ca. 1400	Bolivia
Gradsteinia	Amblystegiaceae	páramo	ca. 3650	Colombia
Koponenia	Amblystegiaceae	puna	ca. 4600	Bolivia
Leskeadelphus	Leskeaceae	high montane, páramo/puna	1300–4000	Colombia, Bolivia
Leptodontiella	Pottiaceae	open montane	600–4235	Peru
Lindigia	Brachytheciaceae	montane forest	1800–3400	all
Mandoniella	Brachytheciaceae	montane forest	1700–3350	Bolivia
Polymerodon	Dicranaceae	puna	3600–4620	Bolivia
Porotrichopsis	Neckeraceae	mid to high montane forest	2000–3800	Colombia, Bolivia
Pseudohyophila	Dicranaceae	puna	ca. 3820	Peru
Schroeterella	Sematophyllaceae	montane forest	ca. 2200	Bolivia
Sciuroleskea	Stereophyllaceae	montane forest	1300–3160	Ecuador, Peru
Stenocarpidiopsis	Brachytheciaceae	montane forest	1400–2150	Ecuador, Peru
Stenodesmus	Pilotrichaceae	montane forest	700–925	Colombia, Ecuador
Streptotrichum	Pottiaceae	high montane forest	3140–3400	Bolivia
Timotimius	Sematophyllaceae	montane forest	ca. 2350	Ecuador
Trachyodontium	Pottiaceae	montane forest	ca. 2650	Ecuador

Table 3. Families and genera with 10 or more endemic species for the tropical Andes.

Family	No. of species	Genus (family)	No. of species
Pottiaceae	60	*Sphagnum* (Sphagnaceae)	35
Pilotrichaceae	49	*Zygodon* (Orthotrichaceae)	23
Bryaceae	46	*Lepidopilum* (Pilotrichaceae)	15
Dicranaceae	37	*Schizymenium* (Bryaceae)	15
Sphagnaceae	35	*Sematophyllum* (Sematophyllaceae)	14
Orthotrichaceae	33	*Campylopus* (Dicranaceae)	12
Bartramiaceae	23	*Macromitrium* (Macromitaceae)	11
Sematophyllaceae	21	*Daltonia* (Daltoniaceae)	11
Daltoniaceae	18	*Orthotrichum* (Orthotrichaceae)	11
Brachytheciaceae	13	*Cyclodictyon* (Pilotrichaceae)	10
Macromitriaceae	11	*Didymodon* (Pottiaceae)	10
Ditrichaceae	10	*Syntrichia* (Pottiaceae)	10
Polytrichaceae	10		

species. There are a few genera that could be classified as subendemic, i.e., isolated outliers from the main Andean range. For example, the monospecific genus *Gertrudiella* Broth. (Pottiaceae) is primarily found in dry inter-Andean valleys from southern Peru to northwestern Argentina, but has been recorded from a single locality in the Bolivian Chaco forest near the sub-Andean range and also from northernmost Chile.

There are 13 families that include 10 or more endemic species (Table 3). Significantly, just these 13 families of the total 69 Andean families account for 87% of species endemism. Within these, 12 genera contain 10 or more endemic species, and these 12 encompass 42% (177) of the 428 total Andean endemics.

Noteworthy Moss Families of the Tropical Andes

Twenty of 69 families of the tropical Andes (Appendix 1) that are considered significant for reasons of diversity, endemism, ecology, and distribution are discussed below.

AMBLYSTEGIACEAE

The majority of the genera and species are found in the high montane to páramo and humid puna. Ecologically, a number of the genera are a major component and play a significant role, second only to Sphagnaceae, in the Andean aquatic systems (i.e., lakes and ponds, streams and rivers, bogs and marshes). Aquatic and semi-aquatic genera include *Cratoneuron* (Sull.) Spruce, *Drepanocladus* (Müll. Hal.) G. Roth, *Pseudocalliergon* (Limpr.) Loeske, *Scorpidium* (Schimp.) Limpr., *Straminergon* Hedenäs, and *Warnstorfia* Loeske. Endemic genera, all monospecific and only known from the type collection, include *Gradsteinia* Ochyra, found on rocks in streams of the Colombian Eastern Cordillera, and *Koponenia* Ochyra, found on rocks in springs or streams of the Real Cordillera of Bolivia (Table 2). The Amblystegiaceae were recently revised by Hedenäs (2003) for the Neotropics.

ANDREAEACEAE

Andreaeaceae is almost exclusively found in páramo and puna on rocks. A few species are semi-aquatic or aquatic, e.g., *Acroschisma wilsonii* (Hook. f. & Wilson) A. Jaeger, *Andreaea nitida* Hook. f. & Wilson, and *A. subulata* Harv. A major portion of the 20 ecostate *Andreaea* Hedw. species previously described from the Andes have not been reevaluated; revisionary studies may add five to 10 species based on observed morphological variation of selected *Andreaea* types and general collections examined by the author, of which some will likely be endemic.

BARTRAMIACEAE

Bartramiaceae is the fifth largest family for the Andes, with 64 species, 23 of which are endemic. Nearly all of the genera of the Bartramiaceae are terrestrial, common in the open montane to páramo and puna. *Leiomela* (Mitt.) Broth. is the exception, mostly found in montane forest as an epiphyte. *Breutelia* (Bruch & Schimp.) Schimp. is a common component of bogs, and *Philonotis* Brid. is common along streams and seeps. Revisionary studies are required for *Philonotis*, where the status is unknown for 21 species and the nonclasping, leaf-based species of *Breutelia*.

BRACHYTHECIACEAE

The Brachytheciaceae is the tenth largest family, with most genera associated with the montane forest.

The family, as now circumscribed, includes five genera previously associated with the Meteoriacaeae: *Aerolindigia* M. Menzel, *Lindigia* Hampe, *Meteoridium* (Müll. Hal.) Manuel, *Squamidium* (Müll. Hal.) Broth., and *Zelometeorium* Manuel (Ignatov & Huttunen, 2002). All five genera generally occur as epiphytes, often common and abundant, in montane forest throughout the Andes. There are four Andean endemic monospecific genera (Table 2), all occurring as epiphytes: *Flabellidium* Herzog, *Mandoniella* Herzog, *Lindigia*, and *Stenocarpidiopsis* M. Fleisch. ex Broth. The only exclusively aquatic genus is *Platyhypnidium* M. Fleisch., typically occurring on rocks in streams. The outstanding unrevised taxa of the Brachytheciaceae involve the generic complex *Rhynchostegium* Bruch & Schimp. and *Eurhynchium* Bruch & Schimp.; both have rather numerous names (status for 19 unknown) but probably few species, and likely even fewer or no endemics.

BRYACEAE

Bryaceae is the second largest Andean family, with 130 species and 46 endemics (Appendix 1). The majority of genera and species are terrestrial and found in the open montane to páramo and puna. Important genera of the high montane and páramo/puna regions are *Anomobryum* Schimp., *Pohlia* Hedw., and most notably, *Schizymenium* Harv. *Acidodontium* Schwägr., with nine of 11 species endemic, is exclusively epiphytic, often occurring as twig epiphytes, as are about half of the species of *Brachymenium* Schwägr. Genera with at least some forest species include *Bryum* Hedw., *Epipterygium* Lindb., *Orthodontium* Schwägr., and *Rhodobryum* (Schimp.) Limpr. The treatments by Ochi (1980, 1981) for *Acidodontium*, *Anomobryum*, *Brachymenium*, *Bryum*, and *Rhodobryum* provided a very important foundation for these diverse genera; however, all would benefit by at least a regional revision. Revisionary studies are required for the taxa associated with *Mielichhoferia* Nees & Hornsch. and *Schizymenium*.

DALTONIACEAE

This family is restricted exclusively to the montane forest of the tropical Andes. The most notable genus of this family is *Daltonia* Hook. & Taylor, with 11 of the 17 species endemic to the tropical Andes, which also appears to be the center of diversity for the genus. Species are small and inconspicuous, characteristically one or a few individuals are found on twigs of shrubs (e.g., *Baccharis* L.) and trees and are often present on nodes of bamboo (*Chusquea* Kunth). Only *Calyptrochaeta* Desv. and *Leskeodon* Broth. remain to be revised.

DICRANACEAE

Rich in genera, the Dicranaceae is the third largest family for the tropical Andes, with 129 species distributed among 28 genera. Many of the species are terrestrial, found on soil, humus, rocks, and logs. However, a significant portion or all of the following genera are epiphytic: *Campylopus*, *Chorisodontium* (Mitt.) Broth., *Eucamptodontopsis* Broth., *Holomitrium* Brid., *Leucoloma* Brid., *Schliephackea* Müll. Hal., and *Symblepharis* Mont. *Campylopus* is the second largest genus in the tropical Andes, with 49 species, amply diversified in most habitats (except aquatic). *Schliephackea*, with two species in the northern Andes, is the only genus of this family with a pendent growth form in the New World. Critical revisionary studies are needed for the generic complex that includes *Dicranella* (Müll. Hal.) Schimp. and *Microdus* Schimp. ex Besch. *Pseudohyophila* Hilp. is the only endemic genus for the family (Table 2); although it is placed in the Dicranaceae, its systematic position is unclear.

DITRICHACEAE

Astomiopsis Müll. Hal., *Bryomanginia* Thér., *Pleuridium* Rabenh., and *Tristichium* Müll. Hal. are very small-statured, cleistocarpic or gymnostomous genera. Six of the nine species of these genera are endemic, all confined, for the most part, to the páramo and puna. *Chrysoblastella* R. S. Williams and *Distichium* Bruch & Schimp., both with a single species, are also restricted to the páramo and puna. *Ditrichum* Hampe may have a few additional species and some possibly endemic, but revisionary studies are needed.

FISSIDENTACEAE

The majority of the *Fissidens* Hedw. species belonging to this monogeneric family are small and inconspicuous. Species occur on nearly all substrates. Many of the species are widespread in the Neotropics, although 62% of the 93 recognized species are endemic to the region (Pursell, 2007). It is rather surprising that of the 46 species present in the Andes, only four are endemic. *Fissidens* is the third largest genus for the tropical Andes (Table 1), with about 50% of the recognized Neotropical species occurring within the Andean range.

GRIMMIACEAE

The majority of genera and species are found on rocks in the high montane to páramo and puna.

Grimmia, as with *Andreaea*, is a typical component of the páramo and puna, with 15 species. Eight of the 40 species of this family are endemic to the Andes. Endemic monospecific genera restricted to the central Andes are *Aligrimmia* R. S. Williams and *Coscinodontella* R. S. Williams. The genus requiring revisionary study is *Schistidium* Bruch & Schimp., which may have as many as 15 species, and some will certainly be endemic to the Andes; the status of 12 species is unknown.

HYPNACEAE

The Hypnaceae contains 17 genera, 33 species, and only five endemic species. In terms of distribution, many of the genera and species are widespread and common throughout the Andes. Ecologically, several genera are very abundant and conspicuous in montane forests, often occurring in extensive mats, e.g., *Ctenidium* (Schimp.) Mitt., *Hypnum* Hedw., and *Mittenothamnium*. The most problematic genus requiring revisionary study is *Mittenothamnium*, for which numerous names have been proposed (28 names considered in this study as status unknown); it is likely that fewer than 10 species will be recognized.

MACROMITRIACEAE

Macromitrium Brid. is one of the principal generic elements of the Andean montane forest. The center of species diversity for this genus will likely prove to be the tropical Andes. Most species are epiphytic and commonly present in the canopy of high montane forest. More species will be recognized, based on examined types and general collections from the tropical Andes, and may total up to 50, with as many as half endemic. *Schlotheimia* Brid. requires revisionary studies; 14 species have been reported or described from the central Andes, particularly in Bolivia, but fewer than seven will likely be recognized.

NECKERACEAE

Despite having relatively few species (26) and only four endemics, the Neckeraceae is a significant component of montane forest throughout the Andes. This is particularly true of the mostly epiphytic genera *Neckera* Hedw., *Porotrichodendron* M. Fleisch., and *Porotrichum* (Brid.) Hampe, which can form extensive dendroid tufts on trunks and branches of trees. *Porotrichopsis* Broth. & Herzog, with one species, is the only endemic genus in the Neckeraceae for the Andes (Table 2). *Porotrichopsis flacca* Herzog is rather small and inconspicuous, resembling a depauperate species of *Porotrichum*.

ORTHOTRICHACEAE

Represented by two diverse genera, *Orthotrichum* Hedw. and *Zygodon*, the majority of the species are epiphytic and concentrated in the transitional high montane forest and páramo-puna zone. Both genera contain a significant number of endemic species: *Orthotrichum* with 11 of 18 species and *Zygodon* with 22 of 33 species. *Zygodon*, monographed by Malta (1926), requires a reevaluation of the species, but will likely remain one of the most diverse genera for the tropical Andes as can be presumed from the revision of the southern South American taxa by Calabrese (2006). *Orthotrichum* was revised by Lewinsky (1984, 1987).

PILOTRICHACEAE

The family is the fourth largest for the tropical Andes, with 19 genera and 109 species (Appendix 1). The Pilotrichaceae is the second most diverse family in the number of endemics, with 49 species (Table 3). The center of diversification of the Pilotrichaceae is in the northern Andes and, to a great extent, in Central America. Many of the genera and species are associated with montane cloud forest. The combination of diversity and endemism marks this family as the single most important in the cloud forest ecosystem. A number of genera are typically found over leaf litter, humus, and logs; epiphytic genera include *Actinodontium* Schwägr., *Lepidopilum* (Brid.) Brid., *Pilotrichum* P. Beauv., and *Stenodesmus* (Mitt.) A. Jaeger. *Crossomitrium* Müll. Hal. is one of very few moss genera in which several species are commonly epiphyllous. Genera requiring revisionary studies include *Callicostella* (Müll. Hal.) Mitt., *Cyclodictyon* Mitt., and *Trachyxiphium* W. R. Buck.

POLYTRICHACEAE

The family is exclusively terrestrial. Nearly all of the species in the Andes are found in open mid to high montane, páramo, and puna. The species of this family play a significant role in the colonization of disturbed montane slopes and are among the first plants to stabilize recent landslides and newly cut road banks. Very few species are associated with montane forest; genera include *Atrichum* P. Beauv., *Steereobryon* G. L. Sm., and a few species of *Pogonatum* P. Beauv. Within the Neotropics, the tropical Andes contain the highest diversity of genera (9) and species (23) for this family. The genus *Polytrichadelphus* (Müll. Hal.) Mitt.

has its center of diversity and names in the tropical Andes; it is the only genus of the Polytrichaceae that still requires a careful revisionary study.

POTTIACEAE

The Pottiaceae is the single most diverse family for the tropical Andes in terms of genera, species, and endemics (Appendix 1, Tables 1, 3). The majority of the genera are common in the wet and dry páramo and puna, and in the dry inter-Andean valleys occurring on soil and rocks. In the montane region, a number of genera are common in open forested areas and deforested sites. Genera with some or all species found as montane epiphytes include *Streptopogon* (Taylor) Wilson ex Mitt., *Leptodontium* (Müll. Hal.) Hampe ex Lindb. p.p., and *Syntrichia* Brid. p.p.; three other genera represent monospecific endemics, each known from a particular country: *Leptodontiella* R. H. Zander & E. H. Hegew. (Peru), *Streptotrichum* Herzog (Bolivia), and *Trachyodontium* Steere (Ecuador). The entire family is now being revised by bryologists from Universidad de Murcia (Cano et al., 2008), with treatments completed or near completion for *Didymodon* Hedw., *Hennediella* Paris (Cano, 2008), *Syntrichia*, and *Tortula* Hedw. (Cano & Gallego, 2008).

SEMATOPHYLLACEAE

Represented by 14 genera, the Sematophyllaceae is the seventh largest family for the tropical Andes, with 52 species (Appendix 1). The most diverse genus, *Sematophyllum*, is found throughout the Andean montane region, occurring as epiphytes in forested areas and equally associated with streams and rivers on rocks. Among the genera in critical need of revisionary study are both *Sematophyllum* and *Trichosteleum* Mitt. The former is likely to have additional recognized species and endemics; the status of some 17 species is unknown. Three monospecific genera, all epiphytic, are endemic to the tropical Andes (Table 2): *Allioniellopsis* Ochyra, known only from three localities in Ecuador and Peru; *Schroeterella* Herzog, from a single locality in Bolivia; and *Timotimius* W. R. Buck, also from a single locality in Ecuador.

SORAPILLACEAE

This monogeneric family is of interest for its rather peculiar gametophytic morphology and distribution. *Sorapilla* Spruce & Mitt. is represented by two species, *S. sprucei* Mitt. and *S. papuana* Broth. & Geh., the former from the Neotropics and the latter from Australasia. The genus exhibits a leaf structure similar to that of *Fissidens*. The phylogenetic relationship of this taxon is thought to be with the Neckeraceae (Allen, 1981). *Sorapilla sprucei* is only known from a collection made by Richard Spruce in 1857 from the lower montane forest of Abitagua at about 1850 m.

SPHAGNACEAE

Sphagnum is the single most important genus of the aquatic ecosystems of the Andes. It is a typical component of bogs, lake, and stream margins in the páramo and humid puna, but it is also found associated with seeps and springs in montane areas. Nearly all of the 35 of 61 species considered endemic to the Andes were described by Howard Crum between 1985 and 1997. It seems likely that a reevaluation of these species will result in some being reduced to synonymy, in some cases entailing emended species concepts. Others are very likely to be considered distinct and endemic. Given the very important role of this genus in the Andean ecosystem, a revision is imperative.

Regional and Country Diversity

The tropical Andes may be divided geographically into two areas, the northern and central Andes. For pragmatic purposes, in this analysis the northern Andes are defined as including the cordillera systems of Venezuela, Colombia, and Ecuador, and the central Andes are defined as including the cordillera systems of Peru, Bolivia, and the northwestern portion of Argentina. The generally accepted division between the two regions is the Huancabamba Depression in the extreme north of Peru (Duellman, 1979), but too little collection data exist for this area of Peru. The number of mosses common to both the northern and central Andes is 816 (59%). More than half of these species are common and widespread throughout the Andes, as exemplified by *Plagiomnium rhynchophorum* (Harv.) T. J. Kop. (for this and other species discussed below, view maps in Tropicos); other species appear as disjuncts such as the endemic *Porotrichopsis flacca*, but this may simply be a collecting artifact. The northern Andes contain 321 unique species (23% of total), thus the total for this region is 1137 species. At least a number of the species are more restricted in their distribution, as exemplified by *Polytrichadelphus ciliatus* (Hook. & Wilson) Mitt. The central Andes contain 241 unique species (18%), a total of 1057 species. Again, some of the species are narrowly distributed, such as the endemic *Streptotrichum ramicola* Herzog, which may be more widespread, extending even into Peru, but the substrate this moss

Table 4. Summary of moss diversity for the five individual countries and three provinces (Jujuy, Salta, and Tucumán) in northwestern Argentina.

Country	Total in country	Total in Andean portion	% of total Andes
Venezuela	734	681	53%
Colombia	915	883	67%
Ecuador	807	796	59%
Peru	775	761	56%
Bolivia	901	884	66%
Northwestern Argentina	125	122	9%

occupies, nodes of bamboo, is rarely sampled. A comparison of two families, Pilotrichaceae and Pottiaceae, serves to emphasize the difference between the two regions based on vegetation and ecology. The Pilotrichaceae are most diverse in montane cloud forest, many as epiphytes, while the Pottiaceae are most common in open montane, páramo, and puna regions, nearly all terrestrial. This is reflected in the differences between Colombia and Bolivia. The Pilotrichaceae in Colombia has 78 species, and Bolivia, 47. The Pottiaceae in Bolivia has 118 species, and in Colombia, 69. This likely reflects the more complex and extensive cordillera system of montane forest in Colombia as compared with a much smaller and less complex cordillera in Bolivia. Conversely, the Bolivian puna (humid, semi-humid, desert) and dry inter-Andean valleys are extensive compared with Colombia, which has distinctly isolated páramos and dry inter-Andean valleys.

The number of species recorded for each country varies from 734 to 915, excluding northwestern Argentina (Table 4). Colombia is the most diverse, with 915 species, but nearly equal is Bolivia, with 901. Ecuador, for its small size, is notably diverse, with 807 species. Both Venezuela and Peru have fewer species. The number of species recorded for Venezuela (734) may be due to the smaller area occupied by the Andes, or more likely, further inventory will discover additional species. There is little doubt that Peru is undercollected, with only 775 species, and will be equal to or greater than the number of species recorded for Bolivia or Colombia. The Andean portion of each country (Table 4) shows that there are only a few species from the lowlands that are not present in the Andes. Venezuela has more non-Andean species than any of the countries; this may be due to the Caribbean coastal regions and the tepui regions.

Table 5. The distribution of 428 endemic species for the tropical Andes, northern and central Andes, and individual countries including northwestern Argentina (endemics shared between the two regions is 144 species).

Area	Country	No. of species	% of total
Northern Andes		51	12%
	Venezuela	13	3%
	Colombia	49	11%
	Ecuador	42	10%
Central Andes		39	9%
	Peru	31	7%
	Bolivia	56	13%
	Northwestern Argentina	3	>1%

Regional and Country Endemism

Endemism for the regions and countries differs slightly from the overall results for the countries, again excluding northwestern Argentina (Table 5). The number of shared endemics between the northern and central Andes is 144 species. There are slightly more endemics recorded for the northern Andes (155) than for the central Andes (129). Among the countries, the difference is with Bolivia, which contains more endemics (56) than Colombia (49), followed by Ecuador (42), Peru (31), and Venezuela (13).

Trends in Moss Diversity for the Tropical Andes

patterns of diversity

The patterns of diversity can be viewed at different levels. The supposition for the observed pattern of moss diversity in the tropical Andes is that alpha diversity may be comparable to other forested areas (e.g., lowland forest) but beta diversity, species turnover, is significantly higher, accounting for species differences within and between elevational gradients and ecoregions present in the tropical Andes (Churchill et al., 1995). The result is that gamma diversity is exceptionally high for the tropical Andes. This scenario has not been tested. This explanation appears to be supported by the observed differences in moss diversity (gamma) seen in data comparing the Amazon Basin to the tropical Andes. The area of the Amazon Basin, slightly less than the size of the contiguous United States, is nearly 4.5 times larger than that of the tropical Andes. The mosses of the Amazon Basin are estimated at 311 species (Churchill, 1998), compared to 1376 species for the tropical Andes; thus, the much smaller area of the Andes is 4.4 times more diverse than the Amazon.

LATITUDINAL GRADIENT

The cordillera systems of Central America and the Andes are the only reason mosses do not serve as a classic contrary example to the latitudinal gradient norm that diversity increases toward the equator (Churchill, 1991; Churchill et al., 1995; Shaw et al., 2005). Latitudinal gradient is a rather loose, broad generalization with various "classic" examples (e.g., birds, trees), but in some cases this appears to be avoiding other patterns of distributional diversity. The contrast in moss diversity between the two largest geographical regions of tropical South America, the Amazon Basin and the tropical Andes, could not be clearer (see discussion above). In the absence of elevated topography (i.e., the cordillera systems of Central and South America), moss diversity in the Neotropics would be the same as in the Amazon Basin, i.e., ca. 300 species (or slightly greater). It is oversimplified but accurate to note that bryophytes generally reach their greatest diversity in environments of overall cool temperatures and continual precipitation in the form of rain or mist fogs (e.g., in the montane forest) or pronounced seasonality of precipitation (e.g., in the páramo or puna)—essentially equivalent to the environment of temperate and boreal forest, and tundra of the Northern Hemisphere.

ELEVATION

One obvious trend of major interest for the tropical Andes is elevational gradient. Mosses, as well as liverworts, reach their highest diversity levels in the montane regions of the tropical Andes. This narrow band of vegetation, including both forested and open montane areas, contains an estimated 60% or more of the mosses of the tropical Andes. An analysis of elevational distribution of Colombian mosses demonstrated a gradual increase in species diversity maximizing at 2500–3000 m, with the next highest level of species diversity at 2000–2500 m, and the third at a higher elevation, 3500–4000 m. The number of unique species found within an elevational range showed a similar pattern in Colombia; for example, the 2500–3000 m range also contained the greatest number of species not present at other elevation ranges. In a study of ferns and bryophytes from various tropical Andean localities, Kessler (2000) noted that elevational boundaries were well correlated with major ecological changes, essentially two such zones. One major zone could be interpreted as the transition between lowland forest and low montane forest (premontane). The second significant change occurred at the highest forest boundary, the transitional high montane forest with páramo-puna. Between these low and high zones, species composition showed little change.

ECOREGION DIVERSITY

The diversity and composition of mosses present in the various ecoregions (essentially equal to vegetation types) have not been well documented. Although it may be intuitively apparent based on casual observation that certain ecoregions are more diverse than others, for example that montane forests are more species-rich than dry inter-Andean valleys, there is a need to quantify such patterns. Bolivia, for which there are preliminary data (Churchill, Sanjines & Aldana, in prep.), is presented as an example. There are seven major ecoregions recognized in Bolivia (Fig. 2). Bolivia can be divided into two general areas: the highlands (Andes), occupying ca. 40% of the land surface, and the much larger lowlands (Oriente), occupying 60%. In the highlands, the Yungas montane forest occupies only 5% of the country's land surface but is disproportionately the most diverse ecoregion, containing 61% of the 901 mosses recorded for Bolivia. The puna is the second most diverse ecoregion with 30%, followed by the Tucumán–Bolivian montane forest with 25%, and the dry inter-Andean valleys with 7%. In the lowlands, diversity corresponds to a precipitation gradient of high in the north to low in the south; the Amazon forest, occupying 34% of the Bolivian land surface, is the most diverse region in the lowlands with 11% of the total number recorded for the country, followed by the Chiquitano forest, with 10%, and Chaco, with an estimated 3%. The diversity of mosses for these ecoregions may be similar to other tropical Andean countries; only the Chiquitano is unique to Bolivia, and Chaco is also present in northwestern Argentina. This also serves to demonstrate that the tropical Andes is more than just montane forest, with significant contributions from the dry inter-Andean valleys, páramo, and puna that add to the rich moss diversity of the region.

Trends in Activities

There are some notable trends, both positive and negative, that have an impact on our developing knowledge of the tropical Andean mosses. The most encouraging development has been the progress of bryology in the Andean countries. Much of this has occurred in the past decade. There are now individuals in all the tropical Andean countries involved at some level of bryological research. These individuals have contributed significantly in developing and expanding research collections that were

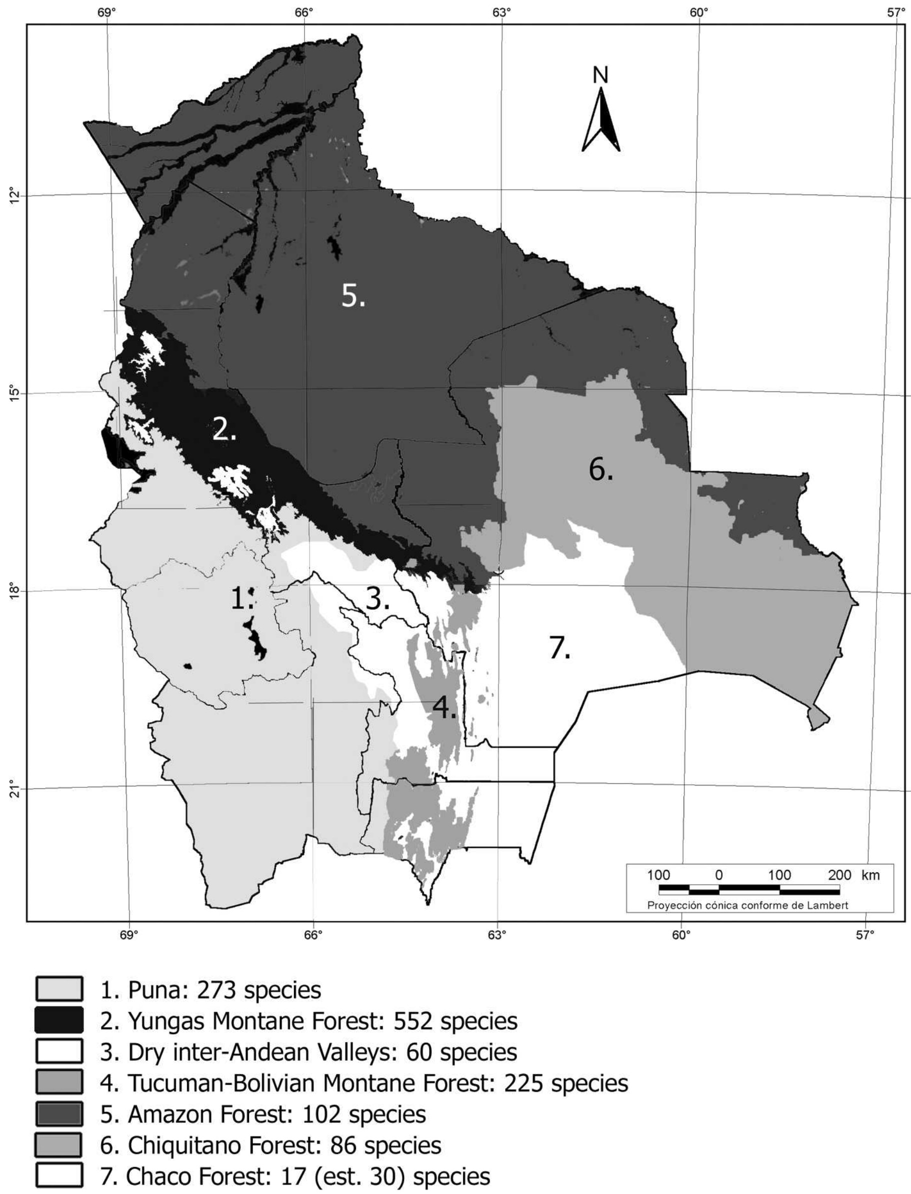

Figure 2. Moss diversity among the seven ecoregions of Bolivia.

heretofore in most cases meager or nonexistent. Colombia provides a good example of these trends as reflected in the number of publications. In three 6-year intervals, the number of bryological publications by Colombians has increased significantly: 1990–1995 (2), 1996–2000 (9), 2001–2005 (22). The other development has been a web page devoted to the mosses of the tropical Andes (Churchill & collaborators, 2008). This web site provides the following main sections: Overview of Region and Countries, Key to Andean Moss Families, Family Treatments and Checklists (English), Spanish Family Treatments and Checklists, Index of Synonyms and Other Names, Bibliography and Literature Cited, Author List, Collector List, and Bryophytes of Bolivia. Both family treatments are linked to the Tropicos database (<http://www.tropicos.org/>, Missouri Botanical Garden).

The negative trend is the significant downturn of revisionary studies. Our understanding of Neotropical mosses has increased significantly in the past 30 years. A notable number of bryologists from North

America, Europe, and Japan focused their research in various regions of the Neotropics, both in terms of fieldwork and revisionary studies. This trend, in the form of publications, could be said to have increased almost exponentially beginning in the late 1960s and early 1970s, peaked in the 1980s, and by the late 1990s began a sharp decline. This trend was a result of economic growth of the 1960s and the concurrent expansion in universities and faculty. As new bryologists gained expertise, the number of publications increased in the 1980s and most of the 1990s until an economic downturn, university cutbacks, and faculty attrition through retirement or death resulted in a noticeable decrease in publications. The commencement of biodiversity studies in the 1980s, which can be coupled with the publication of *Biodiversity* (Wilson & Peter, 1988), was in fact the beginning of a decline in taxonomic expertise. What was accomplished in ca. 20 years, however, was almost certainly a 10-fold increase of new collections in the Neotropics, as well as equally important revisionary studies that advanced our understanding of 35%–45% of the taxa, providing a better understanding of diversity.

Conclusion

Given the state of knowledge of the tropical Andean mosses, estimates of the number of taxa, particularly species, are and will continue to be in a state of flux. There are species to be newly described, even more to be relegated to synonymy, and new species records for the region and the individual countries (particularly for Peru). Over the next few decades, there will be a significant level of uncertainty with regard to moss diversity and composition for the tropical Andes. The estimates presented at any one time for moss diversity are relative. And I cannot refrain from saying (after more than 20 years studying the Andean mosses) that uncertainty and relativity apply wonderfully well to our attempts to delineate species and vegetation.

A priority for the tropical Andes must be to provide a better resolution of species through revisionary studies and floras to promote an understanding of moss diversity. This would allow a greater understanding of distribution and ecology and provide a better means of assessing rarity and conservation. There is urgency to this priority given the major role mosses and hepatics play in the Andean ecosystem. Degradation of the Andean landscape has had a major impact on the ecosystem. The predicted loss of glaciers throughout the Andes in the next few decades (Bradley et al., 2006; Vergara et al., 2007) will severely alter the humid puna and páramo ecosystems. This can only exacerbate the situation faced by the major Andean cities (with ever-increasing population growth) that depend on water from these ecosystems. The continuing loss of glacial water will likely impact the montane forest, which is currently the second most important source of water. Any attempt to further alter these forests can only lead to a greater loss of water and soil, to say nothing of the plant and animal diversity contained in this narrow band of forest that spans the length of the tropical Andes. To ensure the continuing function of the montane forest, the area must be recognized as an endangered ecosystem and protected, not only for the water it provides but also for the rich diversity it contains, including mosses.

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APPENDIX 1. Summary of moss diversity for the tropical Andes, which encompasses 1376 species and 327 genera in 69 families. Families and genera are listed in alphabetical order. The numbers after families are genera/species, endemic species are in parentheses, and endemic genera are denoted by an asterisk. The number of specific and infraspecific Andean synonyms (929) is in brackets.

Amblystegiaceae 19/33 (4) [16]

Amblystegium Schimp. in Bruch, Schimp. & W. Gümbel 4, *Anacamptodon* Brid. 1 [1], *Calliergonella* Loeske 1, *Campyliadelphus* (Kindb.) R. S. Chopra 1, *Campylium* (Sull.) Mitt. 1, *Campylophyllum* (Schimp.) M. Fleisch. 1 [2], *Cratoneuron* (Sull.) Spruce 1 [4], *Drepanocladus* (Müll. Hal.) G. Roth 5 [5], *Gradsteinia* Ochyra* 1 (1), *Hamatocaulis* Hedenäs 1, *Hygrohypnum* Lindb. 1, *Koponenia* Ochyra* 1 (1), *Leptodictyum* (Schimp.) Warnst. 1, *Pseudocalliergon* (Limpr.) Loeske 2 [1], *Sanionia* Loeske 1, *Scorpidium* (Schimp.) Limpr. 2 [2], *Straminergon* Hedenäs 1, *Vittia* Ochyra 2 (1) [1], *Warnstorfia* Loeske 5 (1)

Andreaeaceae 2/9 (3) [2]

Acroschisma Lindl. 1, *Andreaea* Hedw. 8 (3) [2]

Anomodontaceae 2/2 [1]

Anomodon Hook. & Taylor 1 [1], *Herpetineuron* (Müll. Hal.) Cardot 1

Aulacomniaceae 1/1 [2]

Aulacomnium Schwägr. 1 [2]
Bartramiaceae 8/64 (23) [46]
Anacolia Schimp. 1 [1], *Bartramia* Hedw. 12 (5) [21], *Breutelia* (Bruch & Schimp.) Schimp. 20 (4) [13], *Conostomum* Sw. ex F. Weber & D. Mohr 3 (2) [2], *Flowersia* D. G. Griffin & W. R. Buck 2, *Leiomela* (Mitt.) Broth. 6 (4) [3], *Philonotis* Brid. 19 (8) [6], *Plagiopus* Brid. 1
Brachytheciaceae 14/45 (11) [57]
Aerolindigia M. Menzel 1 [4], *Brachythecium* Schimp. 13 (4) [25], *Eurhynchium* Bruch & Schimp. 4 [2], *Flabellidium* Herzog* 1 (1), *Mandoniella* Herzog* 1 (1), *Lindigia* Hampe* 1 (1) [1], *Meteoridium* (Müll. Hal.) Manuel 2 [4], *Palamocladium* Müll. Hal. 1, *Platyhypnidium* M. Fleisch. 2 (1), *Rhynchostegium* Bruch & Schimp. 4 (2), *Rozea* Besch. 2, *Squamidium* (Müll. Hal.) Broth. 7 [17], *Stenocarpidiopsis* M. Fleisch. ex Broth.* 1 (1), *Zelometeorium* Manuel 5 [4]
Bruchiaceae 2/3 (1)
Eobruchia W. R. Buck 1 (1), *Trematodon* Michx. 2
Bryaceae 11/130 (46) [93]
Acidodontium Schwägr. 11 (9) [5], *Anomobryum* Schimp. 9 (6) [3], *Brachymenium* Schwägr. 13 (2) [15], *Bryum* Hedw. 44 (9) [31], *Epipterygium* Lindb. 1 [1], *Leptobryum* (Schimp.) Wilson 2 [3], *Mielichhoferia* Nees & Hornsch. 4 (3) [1], *Orthodontium* Schwägr. 3 (1) [3], *Pohlia* Hedw. 11 [6], *Rhodobryum* (Schimp.) Limpr. 8 (1) [2], *Schizymenium* Harv. 24 (15) [23]
Calymperaceae 3/28 [23]
Calymperes Sw. ex F. Weber 8 [2], *Leucophanes* Brid. 1, *Syrrhopodon* Schwägr. 19 [21]
Catagoniaceae 1/2
Catagonium Müll. Hal. ex Broth. 2
Cryphaeaceae 5/16 (6) [12]
Cryphaea D. Mohr & F. Weber 10 (4) [12], *Dendrocryphaea* Paris & Schimp. ex Broth. 1 (1), *Dendropogonella* E. Britton 1, *Schoenobryum* Dozy & Molk. 2 (1), *Sphaerotheciella* M. Fleisch. 2
Daltoniaceae 4/31 (18) [9]
Adelothecium Mitt. 1, *Calyptrochaeta* Desv. 4 (3), *Daltonia* Hook. & Taylor 17 (11) [9], *Leskeodon* Broth. 9 (4)
Dicranaceae 28/129 (37) [107]
Amphidium Schimp. 1, *Aongstroemia* Bruch & Schimp. 3 [1], *Atractylocarpus* Mitt. 2 (1) [6], *Bryohumbertia* P. de la Varde & Thér. 1 [2], *Camptodontium* Dusén 2 (2), *Campylopodiella* Cardot 1 [1], *Campylopus* Brid. 49 (12) [60], *Chorisodontium* (Mitt.) Broth. 3 (1) [5], *Dicranella* (Müll. Hal.) Schimp. 12 (5) [7], *Dicranodontium* Bruch & Schimp. 2 [1], *Dicranoweisia* Lindb. ex Milde 1, *Dicranum* Hedw. 2 [3], *Eucamptodontopsis* Broth. 1 (1), *Holodontium* (Mitt.) Broth. 1 [1], *Holomitrium* Brid. 10 (1) [7], *Hygrodicranum* Cardot 1 (1), *Leucoloma* Brid. 6 (1) [1], *Microcampylopus* (Müll. Hal.) M. Fleisch. 1 [2], *Microdus* Schimp. ex Besch. 6 (2), *Oreoweisia* (Bruch & Schimp.) De Not. 4 (2) [4], *Orthodicranum* (Bruch & Schimp.) Loeske 3 (1), *Pilopogon* Brid. 6 (3) [4], *Polymerodon* Herzog* 1 (1), *Pseudohyophila* Hilp.* 1 (1), *Rhabdoweisia* Bruch & Schimp. 3 [1], *Schliephackea* Müll. Hal. 2 (1), *Sphaerothecium* Hampe 1 (1), *Symblepharis* Mont. 3 [1]
Diphysciaceae 1/2 (1) [1]
Diphyscium D. Mohr 2 (1) [1]
Ditrichaceae 10/21 (10) [10]
Astomiopsis Müll. Hal. 2 (1), *Bryomanginia* Thér. 1 [1], *Ceratodon* Brid. 2 [3], *Chrysoblastella* R. S. Williams 1 [2], *Distichium* Bruch & Schimp. 1, *Ditrichum* Hampe 6 (3) [4], *Pleuridium* Rabenh. 4 (4), *Rhamphidium* Mitt. 1, *Tristichium* Müll. Hal. 2 (1), *Wilsoniella* Müll. Hal. 1 (1)
Encalyptaceae 1/3 (1) [4]
Encalypta Hedw. 3 (1) [4]
Entodontaceae 3/11 (2) [8]
Entodon Müll. Hal. 8 (2) [4], *Erythrodontium* Hampe 2 [2], *Mesonodon* Hampe 1 [2]
Erpodiaceae 1/4
Erpodium (Brid.) Brid. 4
Eustichiaceae 1/1 [1]
Eustichia (Brid.) Brid. 1 [1]
Fabroniaceae 1/3 [8]
Fabronia Raddi 3 [8]
Fissidentaceae 1/46 (4) [28]
Fissidens Hedw. 46 (4) [28]
Fontinaliaceae 1/1 (1)
Fontinalis Hedw. 1 (1)
Funariaceae 3/12 (3) [31]
Entosthodon Schwägr. 9 (3) [28], *Funaria* Hedw. 2 [3], *Physcomitrium* (Brid.) Brid. 1
Gigaspermaceae 2/2
Lorentziella Müll. Hal. 1, *Neosharpiella* H. Rob. & Delgad. 1
Grimmiaceae 8/40 (8) [42]
Aligrimmia R. S. Williams* 1 (1), *Coscinodon* Spreng. 1 (1) [1], *Coscinodontella* R. S. Williams 1 (1), *Grimmia* Hedw. 15 (1) [27], *Jaffueliobryum* Thér. 2 (1) [1], *Ptychomitrium* Fürnr. 6 [8], *Racomitrium* Brid. 7 (1) [2], *Schistidium* Bruch & Schimp. 7 (2) [3]
Hedwigiaceae 3/12 (1) [9]
Braunia Bruch & Schimp. 10 (1) [7], *Hedwigia* P. Beauv. 1, *Hedwigidium* Bruch & Schimp. 1 [2]
Helicophyllaceae 1/1
Helicophyllum Brid. 1
Hookeriaceae 1/1
Hookeria Sm. 1
Hylocomiaceae 2/3 (1) [1]
Loeskeobryum M. Fleisch. ex Broth. 1, *Pleurozium* Mitt. 2 (1) [1]
Hypnaceae 17/33 (5) [24]
Caribaeohypnum Ando & Higuchi 1, *Chryso-hypnum* Hampe 2 [1], *Ctenidium* (Schimp.) Mitt. 1 [2], *Ectropothecium* Mitt. 2 (1) [1], *Herzogiella* Broth. 1 [1], *Hypnum* Hedw. 2 [2], *Isopterygium* Mitt. 5 (1) [7], *Mittenothamnium* Henn. 8 (3) [5], *Phyllodon* Bruch & Schimp. 1, *Platygyriella* Cardot 1, *Pseudotaxiphyllum* Z. Iwats. 1, *Puiggariopsis* M. Menzel 1, *Pylaisia* Bruch & Schimp. 1 [3], *Rhacopilopsis* Renauld & Cardot 1, *Syringothecium* Mitt. 1 [1], *Taxiphyllum* M. Fleisch. 3, *Vesicularia* (Müll. Hal.) Müll. Hal. 1 [1]
Hypopterygiaceae 1/1 [8]
Hypopterygium Brid. 1 [8]
Lembophyllaceae 2/7 (1) [5]
Orthostichella Müll. Hal. 4 [5], *Pilotrichella* (Müll. Hal.) Besch. 3 (1)
Leptodontaceae 1/3
Forsstroemia Lindb. 3
Lepyrodontaceae 1/1 [2]
Lepyrodon Hampe 1 [2]
Leskeaceae 6/11 (4) [7]
Haplocladium (Müll. Hal.) Müll. Hal. 1, *Leptopterigynandrum* Müll. Hal. 4 [2], *Leskea* Hedw. 3 (2) [1], *Leskeadelphus* Herzog* 1 (1) [3], *Lindbergia* Kindb. 1, *Pseudoleskea* Bruch & Schimp. 1 (1) [1]
Leucobryaceae 2/10 [3]
Leucobryum Hampe 7 [2], *Ochrobryum* Mitt. 3 [1]
Leucodontaceae 2/2 [3]
Leucodon Schwägr. 1 [2], *Pterogoniadelphus* M. Fleisch. 1 [1]
Leucomiaceae 2/4 [3]
Leucomium Mitt. 1 [2], *Rhynchostegiopsis* Müll. Hal. 3 [1]
Macromitriaceae 5/47 (11) [14]

Cardotiella Vitt 1, *Groutiella* Steere 7 [1], *Macrocoma* (Hornsch. ex Müll. Hal.) Grout 4 [2], *Macromitrium* Brid. 30 (11) [9], *Schlotheimia* Brid. 5 [2]
Meesiaceae 1/2
Meesia Hedw. 2
Meteoriaceae 6/8 [9]
Barbellopsis Broth. 1, *Floribundaria* M. Fleisch. 1, *Lepyrodontopsis* Broth. 1, *Meteorium* (Brid.) Dozy & Molk. 3 [7], *Toloxis* W. R. Buck 1 [2], *Trachypus* Reinw. & Hornsch. 1
Mniaceae 2/2 [1]
Mnium Hedw. 1, *Plagiomnium* T. J. Kop. 1 [1]
Myriniaceae 1/1 [2]
Helicodontium (Mitt.) A. Jaeger 1 [2]
Neckeraceae 9/26 (4) [34]
Homalia Brid. 1, *Isodrepanium* (Mitt.) E. Britton 1, *Neckera* Hedw. 6 (2) [12], *Neckeropsis* Reichardt 2, *Pinnatella* M. Fleisch. 1 [1], *Porotrichodendron* M. Fleisch. 3 [6], *Porotrichopsis* Broth. & Herzog* 1 (1), *Porotrichum* (Brid.) Hampe 10 (1) [14], *Thamnobryum* Nieuwl. 1 [1]
Octoblepharaceae 1/6
Octoblepharum Hedw. 6
Orthotrichaceae 2/51 (33) [37]
Orthotrichum Hedw. 18 (11) [16], *Zygodon* Hook. & Taylor 33 (22) [21]
Phyllogoniaceae 1/3 [5]
Phyllogonium Brid. 3 [5]
Pilotrichaceae 19/109 (49) [61]
Actinodontium Schwägr. 1, *Amblytropis* (Mitt.) Broth. 3 (2), *Brymela* Crosby & B. H. Allen 7 (5) *Callicostella* (Müll. Hal.) Mitt. 9 [1], *Callicostellopsis* Broth.* 1 (1), *Crossomitrium* Müll. Hal. 5 [2], *Cyclodictyon* Mitt. 15 (10) [5], *Helicoblepharum* (Spruce ex Mitt.) Broth. 3 (3), *Hemiragis* (Brid.) Besch. 1, *Hypnella* (Müll. Hal.) A. Jaeger 6 (1) [4], *Lepidopilidium* (Müll. Hal.) Broth. 2 [2], *Lepidopilum* (Brid.) Brid. 25 (15) [32], *Philophyllum* Müll. Hal. 1, *Pilotrichidium* Besch. 1, *Pilotrichum* P. Beauv. 8 (2) [3], *Stenodesmus* (Mitt.) A. Jaeger* 1 (1), *Stenodictyon* (Mitt.) A. Jaeger 1 [1], *Thamniopsis* (Mitt.) M. Fleisch. 9 (3) [2], *Trachyxiphium* W. R. Buck 10 (6) [9]
Plagiotheciaceae 1/4 [5]
Plagiothecium Bruch & Schimp. 4 [5]
Polytrichaceae 9/23 (10) [35]
Atrichum P. Beauv. 2 [2], *Notoligotrichum* G. L. Sm. 1, *Oligotrichum* DC. 1, *Pogonatum* P. Beauv. 7 (2) [22], *Polytrichadelphus* (Müll. Hal.) Mitt. 6 (6) [2], *Polytrichastrum* G. L. Sm. 1 [1], *Polytrichum* Hedw. 3 (1) [7], *Psilopilum* Brid. 1 (1), *Steereobryon* G. L. Sm. 1 [1]
Pottiaceae 42/172 (60) [101]
Aloina Kindb. 3 (2) [1], *Aloinella* Cardot 6 (5), *Anoectangium* Schwägr. 1 [1], *Barbula* Hedw. 10 (5) [1], *Bellibarbula* P. C. Chen 1, *Bryoerythrophyllum* P. C. Chen 10 (2) [8], *Calyptopogon* (Mitt.) Broth. 1, *Chenia* R. H. Zander 3 (2), *Crossidium* Jur. 1 (1), *Didymodon* Hedw. 26 (10) [12], *Dolotortula* R. H. Zander 1, *Erythrophyllastrum* R. H. Zander 1, *Erythrophyllopsis* Broth. 1 (1) [3], *Gertrudiella* Broth. 1 (1), *Globulinella* Steere 2 (1), *Gymnostomiella* M. Fleisch. 1, *Gymnostomum* Nees & Hornsch. 1, *Hennediella* Paris 9 (5) [5], *Hymenostylium* Brid. 1, *Hyophila* Brid. 1, *Leptodontiella* R. H. Zander & E. H. Hegew.* 1 (1), *Leptodontium* (Müll. Hal.) Hampe ex Lindb. 17 (4) [29], *Mironia* R. H. Zander 1 [1], *Molendoa* Lindb. 1 [2], *Plaubelia* Brid. 1, *Pleurochaete* Lindb. 1 [1], *Pseudocrossidium* R. S. Williams 9 (3) [2], *Pseudosymblepharis* Broth. 1, *Rhexophyllum* Herzog 1 [1], *Sagenotortula* R. H. Zander 1 [1], *Saitobryum* R. H. Zander 1 [1], *Scopelophila* (Mitt.) Lindb. 2 [2], *Streptocalypta* Müll. Hal. 1, *Streptopogon* (Taylor) Wilson ex Mitt. 4 [7], *Streptotrichum* Herzog* 1 (1), *Syntrichia* Brid. 26 (10) [15], *Timmiella* (De Not.) Limpr. 2, *Tortella* (Lindb.) Limpr. 5 (2), *Tortula* Hedw. 4 (1) [3], *Trachyodontium* Steere* 1 (1), *Trichostomum* Bruch 7 (2) [4], *Weissia* Hedw. 3 [1]
Prionodontaceae 1/5 (1) [16]
Prionodon Müll. Hal. 5 (1) [16]
Pterobryaceae 9/17 (3) [6]
Calyptothecium Mitt. 2 [1], *Henicodium* (Müll. Hal.) Kindb. 1, *Jaegerina* Müll. Hal. 1, *Orthostichidium* Müll. Hal. ex Dusén 1 [1], *Orthostichopsis* Broth. 3 [1], *Pireella* Cardot 5 (1) [1], *Pterobryon* Hornsch. 2 (1) [2], *Pterobryopsis* M. Fleisch. 1 (1), *Renauldia* Müll. Hal. ex Renauld 1
Racopilaceae 1/2 [2]
Racopilum P. Beauv. 2 [2]
Regmatodontaceae 1/1 [1]
Regmatodon Brid. 1 [1]
Rhacocarpaceae 1/4 (1) [3]
Rhacocarpus Lindb. 4 (1) [3]
Rhizogoniaceae 4/5 [2]
Hymenodon Hook. f. & Wilson 1, *Leptotheca* Schwägr. 1 [1], *Pyrrhobryum* Mitt. 2, *Rhizogonium* Brid. 1 [1]
Rhytidiaceae 1/1
Rhytidium (Sull.) Kindb. 1
Rigodiaceae 1/1 [3]
Rigodium Kunze ex Schwägr. 1 [3]
Rutenbergiaceae 1/1
Pseudocryphaea E. Britton ex Broth. 1
Seligeriaceae 2/3 (1)
Blindia Bruch & Schimp. 2 (1), *Brachydontium* Fürnr. 1
Sematophyllaceae 14/52 (21) [11]
Acroporium Mitt. 3 (1) [2], *Allioniellopsis* Ochyra* 1 (1), *Aptychella* (Broth.) Herzog 1 [4], *Aptychopsis* (Broth.) M. Fleisch. 1 (1), *Donnellia* Austin 2, *Heterophyllium* (Schimp.) Kindb. 1, *Meiothecium* Mitt. 2, *Pterogonidium* Müll. Hal. 1, *Schroeterella* Herzog* 1 (1), *Sematophyllum* Mitt. 24 (14) [4], *Taxithelium* Spruce ex Mitt. 1 [1], *Timotimius* W. R. Buck* 1 (1), *Trichosteleum* Mitt. 10 (1), *Wijkia* H. A. Crum 3 (1)
Sorapillaceae 1/1 (1)
Sorapilla Spruce & Mitt. 1 (1)
Sphagnaceae 1/61 (35) [5]
Sphagnum L. 61 (35) [5]
Splachnaceae 5/12 (3) [2]
Brachymitrion Taylor 4 (1) [1], *Splachnum* Hedw. 2, *Tayloria* Hook. 4 (2) [1], *Tetraplodon* Bruch & Schimp. 1, *Voitia* Hornsch. 1
Splachnobryaceae 1/1
Splachnobryum Müll. Hal. 1
Stereophyllaceae 6/10 (2) [2]
Entodontopsis Broth. 4 [1], *Eulacophyllum* W. R. Buck & Ireland 1, *Juratzkaea* Lorentz 1, *Pilosium* (Müll. Hal.) M. Fleisch. 1, *Sciuroleskea* Hampe ex Broth.* 2 (2) [1], *Stereophyllum* Mitt. 1
Symphyodontaceae 1/1 [1]
Symphyodon Mont. 1 [1]
Thuidiaceae 3/15 (1) [2]
Pelekium Mitt. 8 (1) [3], *Rauiella* Reimers 2 [1], *Thuidium* Bruch & Schimp. 5 [1]