

CONSERVATION OF EVOLUTIONARY DIVERSITY IN POTTIACEAE (MUSCI)

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RESUMEN

Veintidós géneros de la familia Pottiaceae que son raros y contienen de una a tres especies son *Aschisma*, *Bryocephospora*, *Calymperastrum*, *Calyptopogon*, *Erythrophyllopsis*, *Erythrophyllastrum*, *Ganguleea*, *Gertrudiella*, *Hilpertia*, *Hymenostyliella*, *Leptodontiella*, *Pachyneuroopsis*, *Phascopsis*, *Quaesticula*, *Sarconeurum*, *Stonea*, *Streptotrichum*, *Teniolophora*, *Tetracoscinodon*, *Trachyodontium*, *Weissiodicranum* y *Willia*. De éstos, seis están restringidos a los Andes, cinco son de distribución australasiática y tres están restringidos a las Antillas. Además de raros, varios de estos taxa comprenden ramas aisladas en la base del cladograma de la familia o en la base de los subclados de las Pottioideae o Merceyoideae, o tienen relativamente muchas autapomorfias, o son miembros de linajes que se distinguen por gran distancia patristica. A nivel genérico, las diferencias evolutivas más importantes en la familia estarían mejor conservadas protegiendo los hábitats de estos 22 taxa.

Palabras clave: Pottiaceae, musgos, análisis cladístico, conservación.

ABSTRACT

Twenty-two genera of the large family Pottiaceae that are quite rare and consist of only one to three species are *Aschisma*, *Bryocephospora*, *Calymperastrum*, *Calyp-topogon*, *Erythrophyllopsis*, *Erythrophyllastrum*, *Ganguleea*, *Gertrudiella*, *Hilpertia*, *Hymenostyliella*, *Leptodontiella*, *Pachyneuroopsis*, *Phascopsis*, *Quaesticula*, *Sarconeurum*, *Stonea*, *Streptotrichum*, *Teniolophora*, *Tetracoscinodon*, *Trachyodontium*, *Weissiodi-cranum* and *Willia*. Of these 22, six are restricted to the Andes Mountains, five are Australasian in distribution, and three are restricted to the West Indies. In addition to rarity, certain of these taxa comprise isolated branches at the base of the family cladogram or at the base of the Pottioideae or Merceyoideae sub-clades, or have relatively many autapomorphies, or are members of lineages distinguished by relatively great patristic distance. At the genus level, major

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evolutionary differences in the family would be best conserved by protecting the habitats of these 22 taxa.

Key words: Pottiaceae, mosses, cladistic analysis, conservation.

The Pottiaceae is the largest family of the mosses in number of genera, 77. There are worldwide seven subfamilies, six tribes, about 1457 species and many infraspecific taxa. As noted in a recent study (Zander, 1993), unless convergence of more than 50 characters on the part of four different moss families (Pottiaceae, Timmiaceae, Ptychomitriaceae, Polytrichaceae) is accepted, the Pottiaceae retains gametophytic features in many of its genera of an ancient group, the Polytrichaceae. Thus, the Pottiaceae, as a large family, is a storehouse of the morphological diversity evolved over a great period of geological time. The habitats of the Pottiaceae are diverse, but are commonly extreme, involving such pressures as desiccation, freezing and disturbance. Morphological and physiological features that may be adaptations are also diverse.

Certain pottiaceous taxa are extremely scattered in distribution, possibly in part because they require environments that are patchy or because they are associated with human activities. For instance, *Didymodon umbrosus* (C. Müll.) Zand. is common in the southwest of the United States and in Mexico, yet has turned up in scattered populated areas in many parts of the world. It is even found in the gorge of the Niagara River in New York State, U.S.A., across from a botanical garden (Eckel, 1986), and is one of a series of unrelated mundivagant species apparently distributed inadvertently by humans. Some of these species that are uncommon but which are becoming widely scattered are increasing in association with easily identified human activities: *Scopelophila cataractae* (Mitt.) Broth. (mining — Shaw, 1987, 1993a,b; Shaw and Beer, 1989), *Chenia leptophylla* (C. Müll.) Zand., *Microbryum starkeanum* (Hedw.) Zand. and *Pseudocrossidium hornschruchianum* (Schultz) Zand. (gardening), and *Leptodontium viticulosoides* (P. Beauv.) Wijk & Marg. (acid rain and associated insect infestations — Zander, 1980).

The geographic distributions of some distinctive taxa, however, cannot easily be accounted for by human association because they are nowhere abundant. For example, a newly discovered species of *Didymodon* (Zander, Stark and Marrs-Smith, in ed.) from western North America is found at one station in each of British Columbia, Nevada, Texas and Chihuahua, apparently associated with gypsum deposits. *Syntrichia ammoniana* (Crum and Anders.) Ochyra is known only from an isolated gorge in eastern North America and from a few sites in South Africa (Magill, 1981). Another rare taxon, *Ganguleea*, from India, has been collected once in southern Brazil (Zander, 1989). There are other taxa with similar desultory distribution patterns. Loss of such taxa or their habitats before examination of the possible reasons for their surprising vicariance would be unfortunate. Patchy environments and largely only guessed at migrational and vicariant histories some-

how combine to yield a situation in which uncommon and rare species become widely distributed.

Centers of apparent morphological diversity of the Pottiaceae include the Andes and Himalayas; the southern extremities of Africa, South America and Australasia; Pacific tropical lowlands; and the Caribbean region (Zander, 1993). Minor centers include northwestern Europe and northwestern North America, the Caucasus, Japan and the Philippines. A distinctive steppe element unites northwestern North America and central Asia. Many of the genera that contribute to the morphological diversity of these areas are also quite rare.

The greatest threats to rare genera of the Pottiaceae, at least anecdotally, are deforestation in the Andes (see paper by Churchill, this issue), housing developments and overgrazing in Mediterranean climates, and generally the damming of ravines below waterfalls, misapprehension of stressed environments as "waste" land suitable only for dumps and other disturbance, and over-collecting in well-known microhabitats. The only taxa that can be definitely ascertained as threatened are those known only from particular microhabitats, such as waterfalls and gorges, that may be eliminated through damming or over-collecting.

There are so few available species-level world monographs (*Aloina*, *Aloinella*, *Crossidium*, *Globulinella*, *Hymenostyliella*, *Pottia*, *Streptocalypta*, *Streptopogon*, *Trichostomopsis*, *Triquetrella*, *Tuerckheimia* — reviewed by Zander, 1993) that the relative number of endemic or very rare species of Pottiaceae worldwide cannot be estimated. It is possible to evaluate areas with a recent flora, however, even if some of the identified rare species may be synonyms of taxa elsewhere in the world. Of the 128 species of Pottiaceae recognized in the recent Moss Flora of Mexico (Sharp *et al.*, 1994), for instance, there are 18 endemic species. Surely the known habitats of these 18 might be considered for protected status. By protected status, I mean only that their habitats should be protected. Since there is no trade in endangered moss species, listing rare species in a legal manner so as to make international transfers of herbarium specimens difficult serves no useful purpose and is, in fact, counter-productive.

In the family Pottiaceae, 22 critical genera (a third of the family) are quite rare (Fig. 1). These genera consist of one to three species, which are sometimes vicariant but always of restricted habitat or range. These rare genera are: *Aschisma*, *Bryocenthospora*, *Calymperastrum*, *Calyptopogon*, *Erythrophylopsis*, *Erythrophyllastrum*, *Ganguleea*, *Gertrudiella*, *Hilpertia*, *Hymenostyliella*, *Leptodontiella*, *Pachyneuroopsis*, *Phascopsis*, *Quaesticula*, *Sarconeurum*, *Stonea*, *Streptotrichum*, *Teniolophora*, *Tetracoscinodon*, *Trachyodontium*, *Weissiodicranum*, and *Willia*. The environments of these taxa include tropical mountainous areas, deserts and plains, tropical shores and islands, Mediterranean climates, and austral islands or Antarctica. Of the 22 genera, six are restricted to the Andes Mountains, five are Australasian in distribution, and three are restricted to the West Indies. Many of these genera comprise isolated branches at the base of the family cladogram (Fig. 1) or at the base of the large, terminal Pottioideae or Merceyoideae subclades. Such short basal branches con-

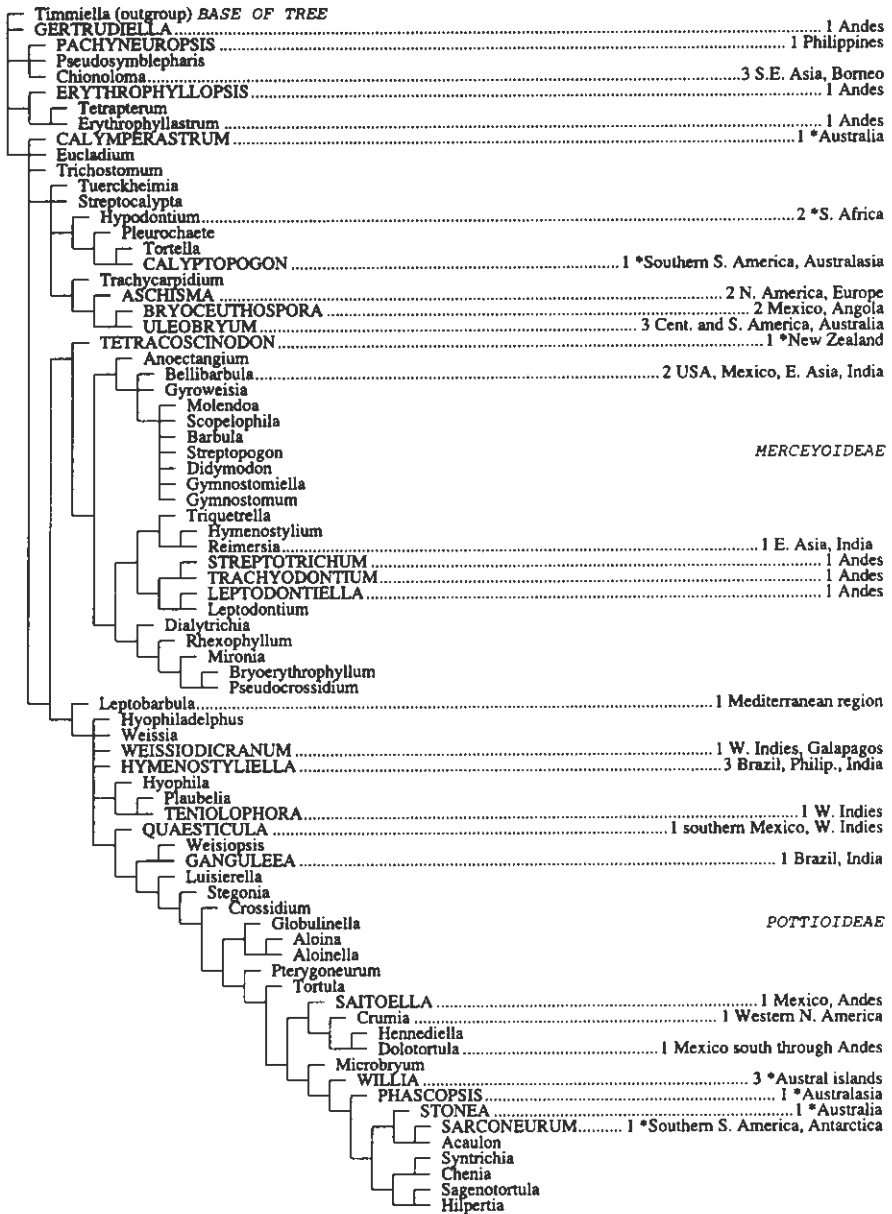


Fig. 1. Strict consensus tree of 77 Pottiaceae genera from Zander (1995). *Timmiella* is functional outgroup, 22 reduction-related characters are weighted at 1:15, tree length is 5367, number of equally parsimonious trees is greater than 1241. Ranges and numbers of species are given for genera of narrow distribution and three or fewer species. Names of 22 genera that are apparently very rare are capitalized.

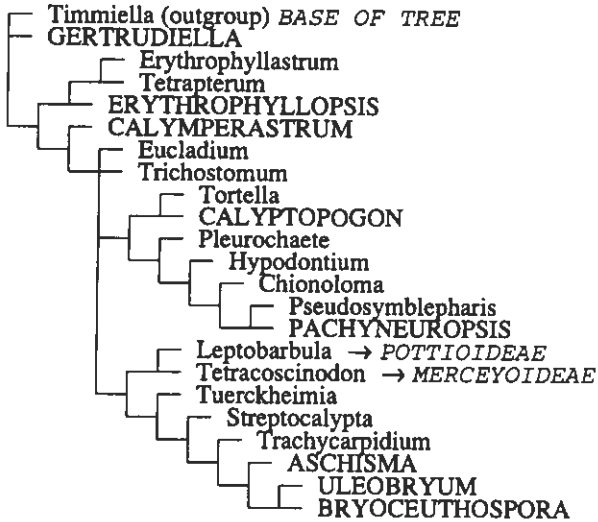


Fig. 2. A strict consensus tree of only basalmost Pottiaceae genera in figure 1, with the Pottioidae and Merceroideae represented solely by *Leptobarbula* and *Tetracoscinodon*, respectively. The base of the tree is better resolved than in figure 1. *Timmiella* is functional outgroup, 22 reduction-related characters are weighted at 1:15, tree length is 1583, number of equally parsimonious trees is five. Names of genera that are apparently very rare are capitalized.

sisting of morphologically quite distinctive taxa may be interpreted as relics of once larger evolutionary lineages.

This paper extends to the Pottiaceae a current interest on the part of many botanists (e.g., Faith, 1992; Vane-Wright *et al.*, 1991) of using cladistic techniques in studies of threatened species. There are three groups of taxa with high potential scientific value, 1) those that appear at the base of the family cladogram or at the bases of the major branches, 2) those with many autapomorphies, and 3) those that have high patristic distance as measured by the sum of the numbers of characters at each node that differentiates them from other terminal taxa.

In the first case (Fig. 1, 2), many basal taxa are relatively restricted in range or habitat. This includes taxa of the extreme southern hemisphere (e.g., *Calymperastrum* and *Tetracoscinodon*) and certain large-statured taxa found only in the Andes (e.g., *Gertrudiella*, *Erythrophyllopsis*, *Trachyodontium* and *Streptotrichum*). Several rare austral taxa (*Phascopsis*, *Sarconeurum*, *Stonea*, *Willia*) are found rather high in the Pottioidae subclade. The apparent extreme morphological reduction of these austral taxa make phylogenetic placement problematic and the many additional characters provided by gene sequencing studies may someday reveal their true relationships. This is also true for other rare and highly reduced taxa like, for instance, *Achisma*, *Bryocephalospora* and *Uleobryum*, which are possibly misassociated in the cladogram.

Autapomorphies (see Fig. 3) are defined here in the sense of Stuessy (1990: 145), being the recently evolved characters that distinguish a terminal taxon from its nearest neighbor in a cladogram, both unique characters and homoplasies. These characters are not phylogenetically informative but probably reflect evolutionary events through anagenesis or cladogenesis followed by extinction. A study of the Caribbean species *Barbula agraria* Hedw. has shown this species to be best viewed as a monotypic genus (Zander, 1995), *Hyophiladelphus* (C. Müll.) Zand. Figure 1 is the consensus tree of the Pottiaceae showing *Hyophiladelphus* removed to the base of the Pottioideae in the company of *Hyophila* and several other tropical and essentially Caribbean area taxa. Further analysis of the Pottioideae subclade assigns the rare genera of the subfamily Pottioideae the following number of autapomorphies: *Ganguleea* 4, *Hilpertia* 6, *Hymenostyliella* 6, *Phascopsis* 0, *Quaesticula* 3, *Sarconeurum* 3, *Stonea* 2, *Teniolophora* 4, *Weissiodicranum* 2, and *Willia* 4. The average number of autapomorphies for the subfamily is 3.3. Clearly, rare genera as a group are not distinguished by large large numbers of autapomorphies. If the number of autapomorphies is a measure of evolutionary distance, then one might note the considerable success of widespread but phylogenetically isolated genera like *Acaulon* with 5 autapomorphies and *Aloina* with 7, and of regionally restricted but locally abundant genera like *Hyophiladelphus* with 6 autapomorphies and *Luisierella* with 7.

Patristic distance (see Fig. 3, 4) may be measured by the sum of the number of character state changes at the intervening nodes between terminal taxa (not counting that of the shared ancestor). The tribe Leptodontieae (Fig. 4) is clearly the most isolated of the family's tribes. Three out of the seven genera of the tribe Leptodontieae are monotypic and very rare. Judging from a previous analysis of the Merceyoideae (Zander, 1993), the Leptodontieae differs from its sister group, the tribe Barbuleae, by a patristic distance of five characters. The subclade including *Leptodontiella*, *Leptodontium*, *Streptotrichum* and *Trachyodontium*, with three of the four being monotypic rare genera, differs from the remainder of the tribe by eight characters. Also, *Streptotrichum* and *Trachyodontium* together differ from the remainder of the tribe by five characters. Thus, advanced taxa of the Leptodontieae are good candidates for protection because although they are apparently advanced taxa, occurring at the end of a subclade high in the family tree, they may well represent an old line. Evidence that there has probably been considerable extinction associated with the Leptodontieae tribe is that: 1) the rare genera are monotypic, 2) they differ from each other by several phylogenetically important characters, 3) they are geographically somewhat distant, and 4) the subclade is symmetric and inserted deeply in the subfamily Merceyoideae lineage. The very rare species of the Leptodontieae are found only in the Andes (*Leptodontiella* endemic to Peru, *Streptotrichum* to Bolivia, and *Trachyodontium* to Ecuador).

Recent work (Zander, 1995) indicates that the circum-Tethyan region (the Tethys Sea was a Mesozoic geosyncline) is associated with two groups in the Pottiaceae: a tropical island and shores element (including *Hyophila*, *Quaesticula*, *Wei-*

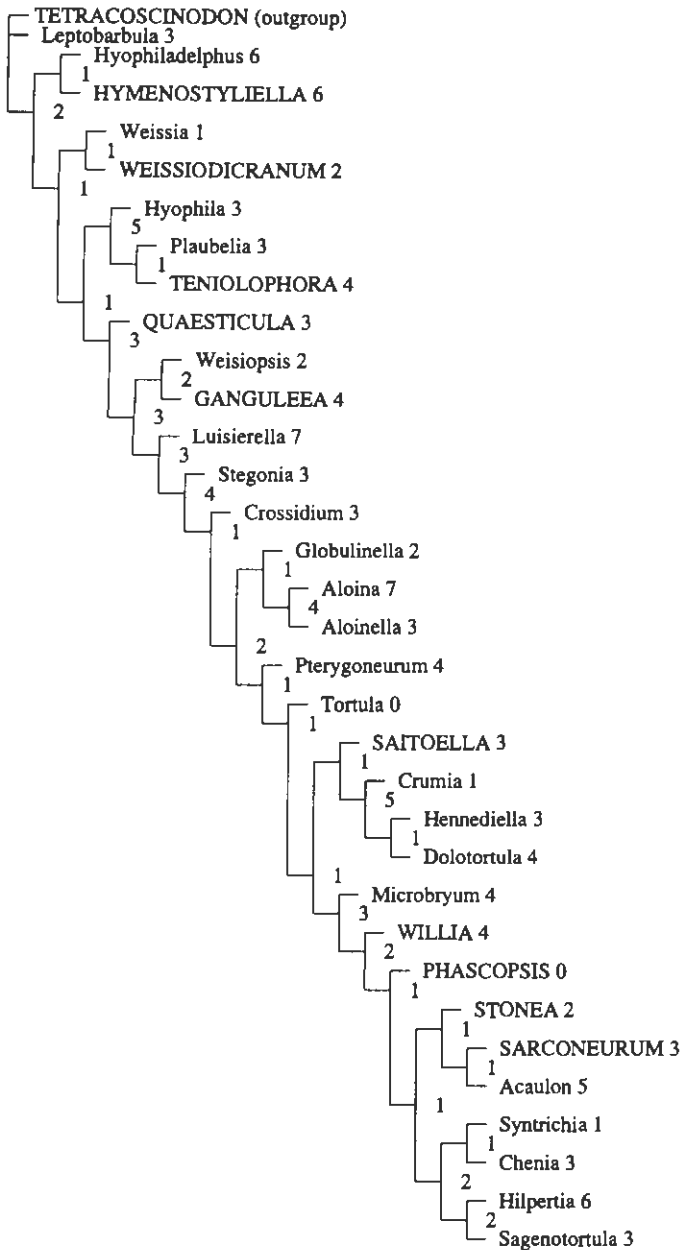


Fig. 3. Single tree of Pottiaceae genera (except the outgroup *Tetracoscinodon*) from Zander (1995). Patristic distance in terms of numbers of character state changes are given for each node, and number of autapomorphies are given after the name of each terminal taxon. Names of genera that are apparently very rare are capitalized.

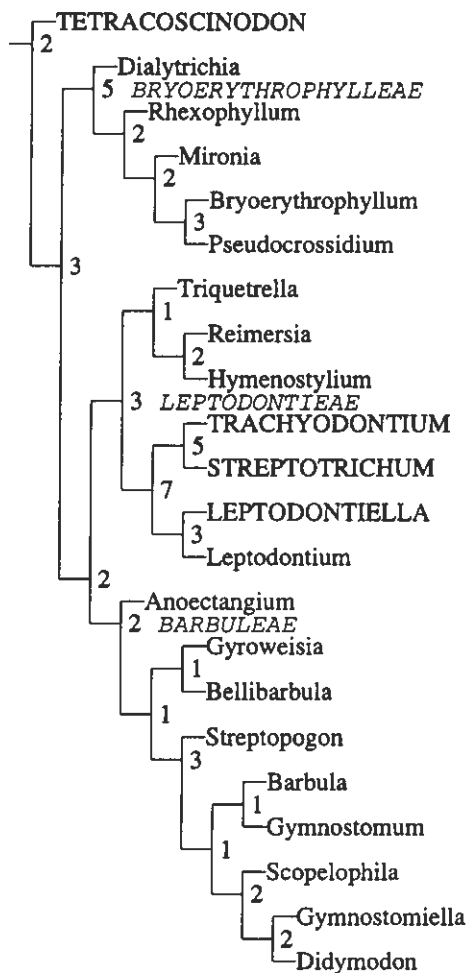


Fig. 4. Merceyoideae portion of the single tree of Pottiaceae genera from Zander (1993). Patristic distance in terms of numbers of character state changes are given for each node. Names of genera that are apparently very rare are capitalized.

siopsis, *Luisierella* and other genera) and a more highly evolved inland desert element (including such genera as *Stegonia* and *Crossidium*). Climate changes (increasingly dry summers after the pluvial periods of glacial times) in the Mediterranean area may have eliminated the majority of the first group there. The remaining representatives of that group, now largely in the Caribbean area, are of considerable importance for conservation, representing basal branches of the Pottiaceae subclade (Fig. 1, 3). In figure 3, terminal taxa from *Leptobarbula* through *Pterygoneurum* are circum-Tethyan taxa. The basalmost genera, from *Leptobarbula*

through *Luisierella*, are largely an island-and-shores element with many rare genera. A group of inland desert genera, from *Stegonia* through *Pterygoneurum*, appear next in the Pottioideae lineage, and these genera are not rare. There is little difference between the two groups or between them and the remainder of the Pottioideae in average patristic distance or average autapomorphies for each of the three groups.

In summary, from information at the genus level, major evolutionary differences in the family would be best conserved by protecting at least the above 22 rare genera, with special attention paid to Andean, Australasian and West Indian environments and to patristic distance. Further study needs to be done at the species level using both morphology and gene sequencing techniques.

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