

## Cladistic and Biogeographic Analyses of the Genera *Moscharia* and *Polyachyrus* (Asteraceae, Mutisieae)

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**ABSTRACT.** The genera *Moscharia* (two species) and *Polyachyrus* (seven species) form a monophyletic group within tribe Mutisieae, subtribe Nassauviinae, defined by the leaves with auricles at their bases, and the capitula with 1-seriate involucre. A cladistic analysis of the species of the two genera was carried out using 22 characters from life cycle, external morphology, pollen, and trichomes. Polarity of the characters was based on the outgroup comparison method. One cladogram was produced, with 37 steps, a consistency index of 0.73, and a retention index of 0.75. The cladogram defines six monophyletic groups: (((*Polyachyrus annus*, (*P. carduoides*, (*P. cinereus*, (*P. fuscus*, *P. gayi*))), *P. sphaerocephalus*), *P. poeppigii*), (*Moscharia solbrigii*, *M. pinnatifida*)). The probable ancestral geographic area for the group, determined by Bremer's method, is North-Central Chile area (30°–35° south latitude). The study suggests that the Pleistocene could be the period of evolution of the ancestor of *Moscharia* and *Polyachyrus*.

The genera *Moscharia* Ruiz et Pav. and *Polyachyrus* Lag. are found in Chile and Peru, occupying mainly dry habitats. *Moscharia*, with two species, was reviewed by Crisci (1974a) and *Polyachyrus*, with seven species and two varieties, was reviewed by Ricardi and Weldt (1974).

*Moscharia* and *Polyachyrus* belong to subtribe Nassauviinae of Mutisieae, a phylogenetically basal tribe of Asteraceae (Bremer and Jansen 1992). These genera, together with species of *Nassauvia* and *Triptilion*, represent a morphologically distinctive group because the aggregation of their capitula into secondary inflorescences or pseudocephalia (Troll 1928; Leppik 1960; Weberling 1992), which are hypothesized to be an advanced evolutionary feature when compared to a regular capitulum. Stebbins (1967) has suggested that the union of few-flowered capitula into pseudocephalia would be a more efficient mechanism to increase the size of the functional inflorescence than the acquisition of new flowers into a reduced capitulum. There are three steps in the formation of pseudocephalia: (1) the capitula aggregate closely without losing their individual identities; (2) the capitula aggregate into a functional head, the individual capitula being still recognizable and without the formation of a pseudoinvolucre; and (3) obliteration of the identity of the individual capitula and acquisition of a pseudoinvolucre. *Polyachyrus* and *Moscharia* would represent the second and the third stages of this sequence, respectively (Crisci 1974a). *Polyachyrus* (Fig. 1A–B) is characterized by its monomorphic and espiciform pseudocephalia: all the ca-

pitula of the pseudocephalium have the same morphology, i.e., they are 2-flowered with an involucre of five bracts, and the main axis of the pseudocephalium is relatively long with the capitula sessile and spirally disposed on this axis. *Moscharia* (Fig. 1C–F), on the other hand, is characterized by its dimorphic and capituliform pseudocephalia: there is a central 1–2-flowered capitulum with an involucre of 4–7 bracts, that is surrounded by 2-flowered capitula with an involucre of two bracts; the main axis of the pseudocephalium is shortened to form a head-like or capituliform structure. In both genera the pseudocephalium has a common involucre or pseudoinvolucre, which is more developed in *Moscharia*. Each capitulum in *Moscharia* and *Polyachyrus* consists of: a) one inner flower, the flower of the capitulum that is closest to the center of the pseudocephalium; b) one outer flower, the flower of the capitulum that is farthest from the center of the pseudocephalium; c) one pale, the bract situated between the two flowers of the capitulum; and d) one keeled bract, the outermost involucral bract in the capitula that surrounds one or all the flowers of the capitulum. The keeled bract can be convex and humped (*Polyachyrus*) or conduplicate and humped (*Moscharia*). There are three other bracts that surround the inner flower in the capitula of *Polyachyrus*.

With regard to the other genera of Nassauviinae, *Moscharia* and *Polyachyrus* are closely related by homologies in their pseudocephalia (Crisci 1974a; Freire et al. 1993). Other authors (e.g., Hellwig 1985) reject the occurrence of pseudocephalia in *Moscharia*

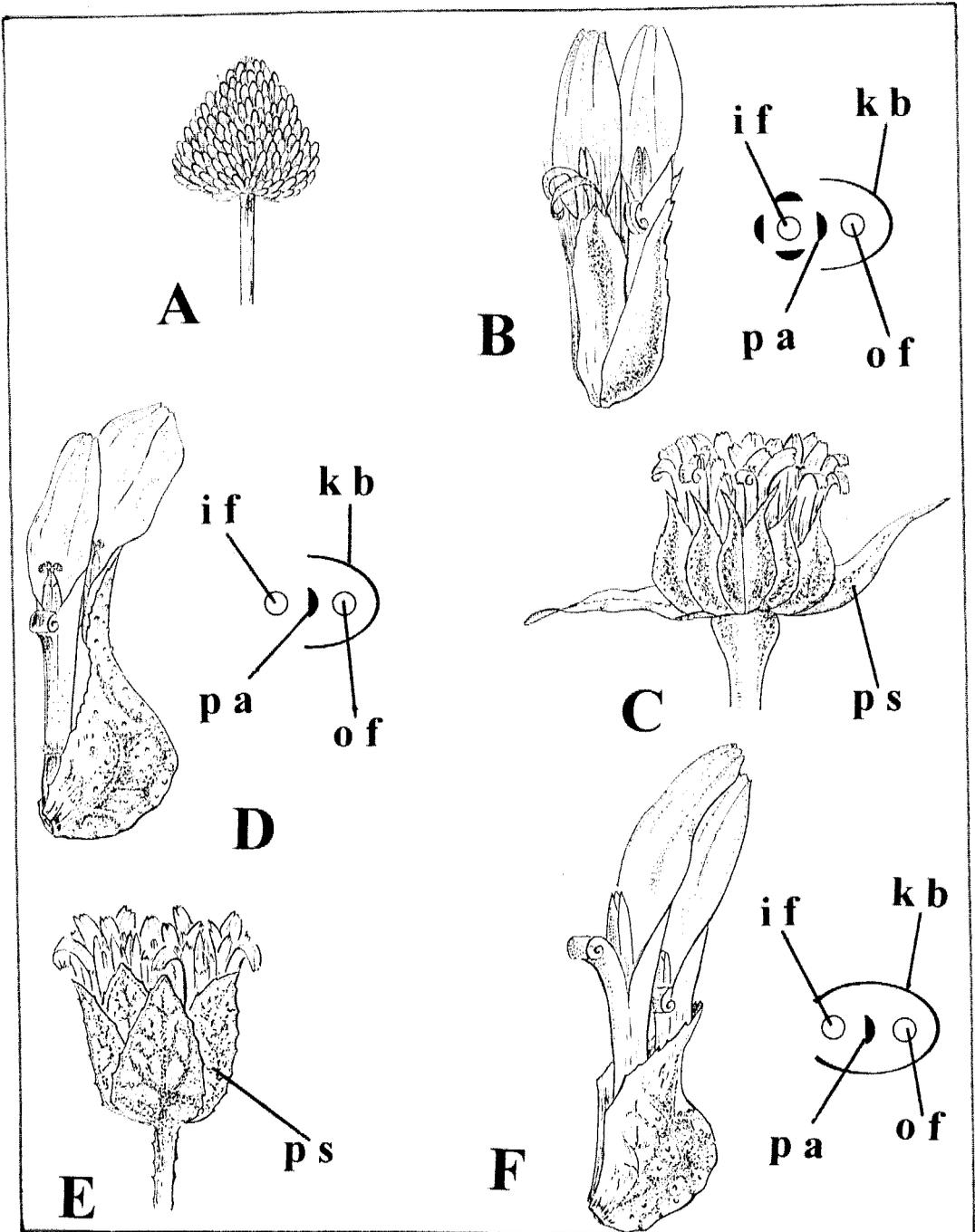


FIG. 1. Pseudocephalia and capitula in *Polyachyrus* and *Moscharia*. A-B, *Polyachyrus foliosus*; A, pseudocephalum espiciform without a developed pseudoinvolucre; B, capitulum. C-D, *Moscharia solbrigii*; C, pseudocephalum capituliform with a developed pseudoinvolucre; D, capitulum. E-F, *M. pinnatifida*; E, pseudocephalum with a developed pseudoinvolucre; F, capitulum. (Modified from Crisci 1974a). if = inner flower; kb = keeled bract; of = outer flower; pa = pale; ps = pseudoinvolucre.

and suggest a close relationship between *Moscharia* and *Leucheria*, another member of Nassauviinae on the basis of head development and chromosome number. In a cladistic analysis of Nassauviinae (Katinas 1994), however, *Leucheria* is not closely related to the *Moscharia-Polyachyrus* group. According to Crisci (1974a) when we compare the pseudocephalium of *Polyachyrus* with the floral head of *Moscharia* the real homology of the latter is easy to ascertain. Each group of two flowers and their surrounding bract in the head of *Moscharia* is equivalent to a primary head in the pseudocephalium of *Polyachyrus*, the difference being that the bracts have been reduced from five to two. The central group of one to two flowers and their surrounding bracts correspond to a much reduced first-order head; these bracts are comparable with the accessory bracts of the capitulum of *Polyachyrus*.

Finally, the geographic distribution of both genera is of interest. *Polyachyrus* is distributed in the Andean and coastal dry areas of Chile and Perú, from 8° to 35° south latitude in South America, and the genus *Moscharia* is endemic to most of the area recognized as Central Chile, from 29° to 35° south latitude. These areas of Chile and Perú are of biogeographic interest because of their high endemism (Rundel et al. 1991; Morrone et al. 1997) and the competing hypotheses that have attempted to explain distributions of taxa in this restricted area (e.g., Kalin Arroyo et al. 1982; Solervicens A. 1987; Rundel et al. 1991; Morrone et al. 1997). The objectives of this paper are: (1) to present results of a cladistic analysis of the species of *Moscharia* and *Polyachyrus*; (2) to analyze the character evolution of leaves, involucre and flowers, and pappus; and (3) to estimate the probable location of an ancestral geographic area for *Moscharia* and *Polyachyrus*.

#### MATERIALS AND METHODS

**Cladistic Analysis.** TAXA. The species of *Moscharia* and *Polyachyrus*, considered here as terminal taxa, form a monophyletic group that is distinguished from other related genera by the leaves with basal auricles, and capitula with 1-seriate involucre (Freire et al. 1993) (Fig. 2). Data for the morphology of the species of *Moscharia* and *Polyachyrus* were taken from previous studies (Crisci 1974a; Ricardi and Weldt 1974) and from the analysis of herbarium specimens. Table 1 lists these species, their acronyms, geographical distribution, and specimens analyzed with vouchers. Nomenclature for

*Moscharia*, *Polyachyrus*, and related genera follows Crisci (1974a, b) and Ricardi and Weldt (1974).

**OUTGROUP SELECTION.** The apomorphic character state was identified by the outgroup comparison method (Watrous and Wheeler 1981). The phylogenetic hypothesis proposed for the subtribe Nassauviinae (Crisci 1980; Freire et al. 1993) provides a basis for choosing an appropriate outgroup for cladistic analysis of *Moscharia* and *Polyachyrus* (Fig. 2). This hypothesis recognizes the group formed by *Cephalopappus* Nees et Mart., *Moscharia*, *Polyachyrus*, *Triptilion* Ruiz et Pav., and *Nassauvia* Lag. (including *Calopappus* Meyen) supported by the reduced capitula. *Moscharia*, *Polyachyrus*, *Triptilion*, and *Nassauvia* form a monophyletic group based on the pappus shorter than the corolla, chaffy pappus, and the pollen grains with a tectum and infratectum of the same thickness. *Triptilion* and *Nassauvia* form a monophyletic group suggested by the deciduous pappus, 2–6 pappus bristles, colpi membranae with sexine processes, spheroidal to spheroidal-oblate pollen, strengthened testa epidermis, and single 2-celled cypsela hairs. The *Triptilion-Nassauvia* group is sister to *Moscharia* and *Polyachyrus*, therefore this group has been used as the outgroup of *Moscharia* and *Polyachyrus*. The outgroup was abbreviated OUT for the analysis.

**CHARACTERS.** Data from 22 characters (Table 2) were derived from the life cycle, leaf morphology, pseudoinvolucre morphology, capitula arrangement and morphology, corolla surface and morphology, pollen, cypsela vestiture, and pappus morphology. Multistate characters (2, 6, 13, 20, and 22) were treated as unordered (= non additive). Characters 6, 8, 15, and 16 are inapplicable characters in the outgroup (since they are related to traits absent in it), they were coded as “?” in the data matrix and treated as missing data during the analysis. Character 1 was variable in the outgroup and therefore it was treated as polymorphic during the analysis and coded in the data matrix as “a”. Table 3 contains the data matrix, which was analyzed with the Wagner maximum parsimony algorithm of PAUP\* version 4.0 (Swofford 1999) using the “branch and bound” option (equivalent to ie\* option of Hennig86; Farris 1988). The bootstrap method (Felsenstein 1985) and Bremer support (Bremer 1988; Donoghue et al. 1992) were employed to evaluate the reliability of the phylogenetic estimates. One hundred replicates were performed in the bootstrap method. The program MacClade version 3.0 (Maddison and Maddison 1992) was used for examination of character distribution.

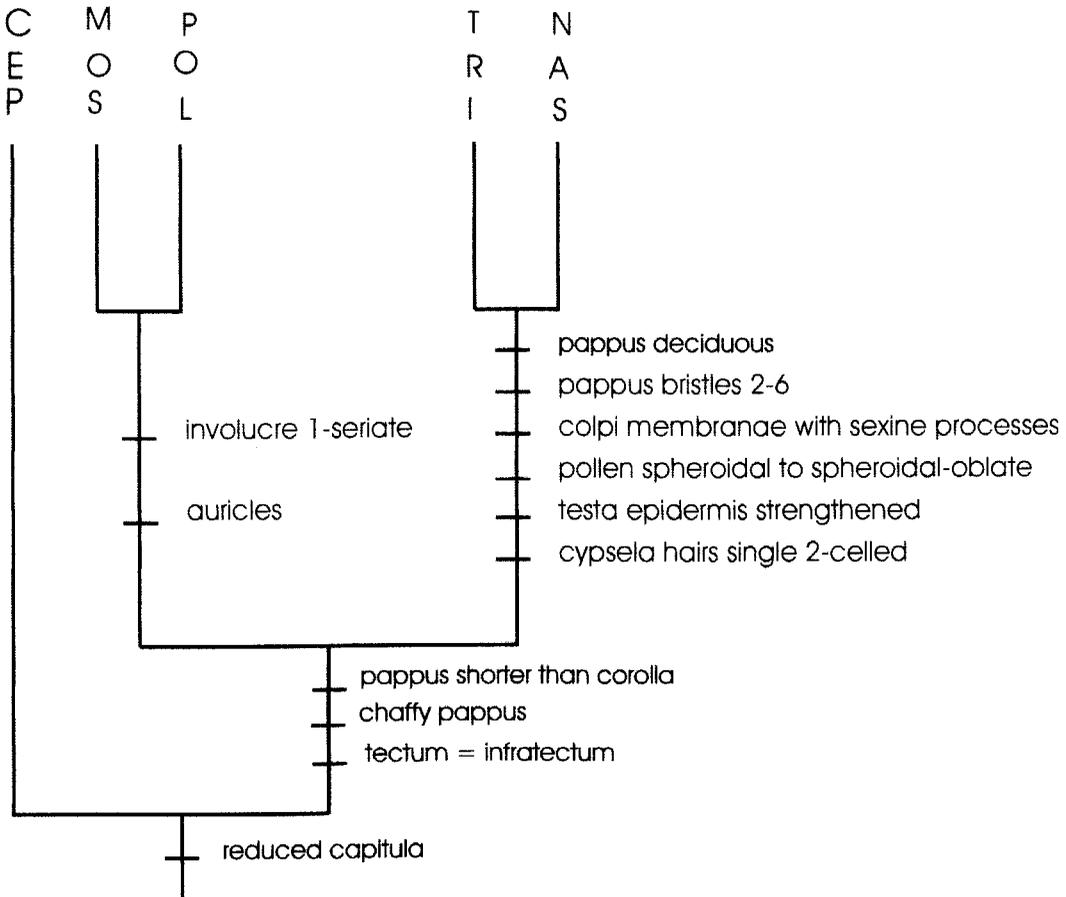


FIG. 2. Outgroup hypothesis for *Moscharia* (MOS) and *Polyachyrus* (POL), simplified from cladograms of Crisci (1980) and Freire et al. (1993). *Nassauvia* = NAS, *Cephalopappus* = CEP, and *Triptilon* = TRI.

**Historical Biogeography** AREAS OF ENDEMICISM. Delimitation of areas of endemism have been discussed by several authors (Humphries and Parenti 1986; Harold and Mooi 1994; Morrone 1994). An area of endemism is usually defined as a geographic region to which one or more taxa are confined. In this study, areas are circumscribed so they comprise several endemic taxa, following the studies of Cabrera and Willink (1980) and Morrone et al. (1997). The areas considered in this study are (Fig. 3):

1. Coastal Desert ranges throughout the Peruvian and Chilean coast from 5° to 30° S latitude. It is a dry area dominated by annual herbs, xerophitic shrubs and cacti. This area is characterized by a high percentage of endemic taxa (Rundel et al. 1991), e.g., *Balsisia peduncularis* (Geraniaceae), *Domeykoa* (Apiaceae), *Eulychnia breviflora* (Cactaceae),

*Leucocoryne narcissoides* (Amarilidaceae), *Neoporteria chilensis* (Cactaceae), *Oxyphyllum*, *Polyachyrus annus*, and *P. cinereus* (Asteraceae).

2. Cardonal covers the west facing slopes of the Andes of Peru and Chile, approximately between 1500 m and 3000 m from 5° to 30° S latitude. It is a narrow belt of open desert scrub dotted with cacti that become the dominant life form in the north. Some endemic taxa are *Ambrosia fruticosa*, *Diplostephium tacorense*, *Mutisia acuminata* var. *bicolor*, *M. hastata*, *M. arequipensis*, *M. mathewsii*, and *Polyachyrus sphaerocephalus* (Asteraceae).

3. North Central Chile ranges from 30° to 35° south latitude in Chile. This is a dry area characterized by the high percentage of endemic taxa, such as *Chaetanthera glandulosa* (Asteraceae), *Echemoides chilensis* (Araneae, Gnaphosidae), *Hyperoides murinus*, *Listroderes hoffmani* (Coleoptera, Curculion-

TABLE 1. Taxa studied, acronyms, geographical distribution, and specimens examined with vouchers (herbarium acronyms from Holmgren et al. 1990).

Taxa	Acronym	Geographical distribution	Specimens examined
<i>Moscharia</i>			
<i>M. pinnatifida</i> Ruiz et Pav.	PIN	Central and South Chile, from Coquimbo to Maule; 0–2000m	Bertero 2404 (MO), Worth & Morrison 16281 (MO), Muñoz et al. 2595 (MO), Cabrera 12559 (LP), Zöllner 2198 (LP), Marticorena & Weltdt 550 (LP)
<i>M. solbrigii</i> Crisci	SOL	Central Chile, endemic to Fray Jorge Forest in Coquimbo; 300–500m	Marticorena et al. 508 (CONC), 521 (CONC, LP)
<i>Polyachyrus</i>			
<i>P. annus</i> I. M. Johnst.	ANN	S Perú, from Arequipa to Moquegua; N Chile, from Tarapacá to Antofagasta; coast, 0–700m	Belmonte 97711 (CONC), Ferreyra 2518 (LP), Ferreyra 12598 (MO), Quezada & Ruiz 24, 244, 294 (CONC), Teillier 574 (CONC), Werdermann 758 (MO), Zöllner 1767 (LP)
<i>P. carduoides</i> Phil.	CAR	N and Central Chile, from Antofagasta to Aconcagua; Andean, 800–3000m	Gulig s.n. (LP), Zöllner 10349 (MO), Martin 264, 586 (LP), Barros 428 (LP), Krapovickas & Hunziker 5768 (LP)
<i>P. cinereus</i> Ricardi et Weltdt	CIN	N Chile, from Antofagasta to Atacama; coast, 0–800m	Roig Juñent 19 (LP), Teillier 474 (MO)
<i>P. fuscus</i> (Meyen) Walp.	FUS	S Perú, in the Sangallan Islands in Ica; N and Central Chile, from Antofagasta to Coquimbo; coast, 0–750 m	Barros 2083 (LP), Aronson 7737 (MO), West 3876 (MO), Zöllner 1766 (LP), Barros 2081 (LP), Werdermann 380 (LP), Cabrera 11345 (LP)
<i>P. gayi</i> J. Rémy	GAY	N and Central Chile, in Atacama and Coquimbo; coast, sea level	Barros 2079 (LP), Zöllner 6871 (LP), Kausel 3935 (LP)
<i>P. poeppigii</i> (Kunze ex Less.) Less.	POE	N and Central Chile, from Antofagasta to Curicó; coast and desert, 0–500m	LP 787251, Lammers et al. 7558 (MO), Zöllner 9260, 10563 (MO), Roig Juñent 10 (LP), Kohler 602 (LP), Jiles 2052, 2641 (LP), Cabrera 12663, 12667 (LP), Mahu 5475, 7654, 10334 (LP)
<i>P. sphaerocephalus</i> D. Don	SPH	Perú, from Lima to Tacna; N Chile, from Tarapacá to Antofagasta; mainly Andean, 100–4000m	Cabrera 10891 (LP), Ferreyra 3533 (MO), Goodspeed 33096 (MO), Velarde O. 1710 (LP), Isern 374 (LP), Cabrera & Fabris 13441 (LP), Barros 2082, 2086 (LP), Cerrate 1906 (LP)

idae), *Marticorenia foliosa*, *Moscharia solbrigii*, *Mutisia spectabilis*, *Polyachyrus gayi* (Asteraceae), *Puranius sylvanius* (Coleoptera, Curculionidae), and *Triptilion gibbosum* (Asteraceae). It contains a mixed formation of sclerophyllous trees and shrubs. This area includes relict temperate forests like Talinay (30° 50' S, 71° 40' W) and Fray Jorge (30° 30' S, 71° 35' W), with predominance of *Nothofagus* spp. (*Nothofagaceae*), *Aextoxicon punctatum* (*Aextoxicaceae*), and *Drimys winteri* (*Winteraceae*).

4. South Central Chile ranges from 35° to 37° 05' south latitude in Chile. It is considered a biogeographic area (Morrone et al. 1997) dominated by sclerophyllous trees and shrubs, with some subantarctic elements such as *Blechnum magellanicum* (*Blechnaceae*), *Lycopodium magellanicum* (*Lycopodiaceae*), and *Saxegothaea conspiciua* (*Podocarpaceae*). Some endemic taxa are *Leucheria apiifolia*, *L. integrifolia* (*Asteraceae*), *Listroderes erinaceus* (*Coleoptera*, *Curculionidae*), *Mendizabalia penai* (*Coleoptera*, *Bu-*

TABLE 2. Characters and character states used in the cladistic analysis of *Moscharia* and *Polyachyrus*.

Characters	Character states
1. Life cycle	0 = Annual, 1 = Perennial
2. Leaf pubescence	0 = Glabrous or subglabrous, 1 = Lanose below, 2 = Lanose above and below
3. Leaf margin	0 = Planate, 1 = Revolute to folded on the medial nervature
4. Foliar lobes shape	0 = Deltoid, 1 = Oblong
5. Foliar lobes apex	0 = Mucronate-spinose, 1 = Smooth
6. Leaf base	0 = Decurrent, 1 = Semiamplexicaul, 2 = Amplexicaul
7. Pseudoinvolucre	0 = Absent or reduced, 1 = Developed
8. Pseudoinvolucre bracts shape	0 = Widely oblong-lanceolate, 1 = Linear
9. Type of pseudocephalium	0 = Racemose, 1 = Capituliform
10. Number of capitula per pseudocephalium	0 = More than 50, 1 = Eight to ten
11. Type of capitula per pseudocephalium	0 = Monomorphic, 1 = Dimorphic
12. Involucral bracts number	0 = Five, 1 = One to two
13. Involucral bracts shape	0 = All flat, 1 = One humped, 2 = One conduplicate
14. Involucral bracts pubescence	0 = Glabrous or scarcely pubescent, 1 = Conspicuously pubescent
15. Keeled bract margine	0 = Scarious, 1 = Not scarious
16. Keeled bract degree of coerture	0 = Surrounding only the outer flower, 1 = Surrounding the outer and the inner flower
17. Outer lip corolla morphology	0 = Orbicular-ovate, 1 = Oblong-lanceolate
18. Corolla surface	0 = Not papillose, 1 = Papillose
19. Pollen grains	0 = Tectum with ramifications, 1 = Tectum lacking ramifications
20. Cypsela hairs type	0 = Only twin hairs, 1 = Twin hairs and glandular hairs, 2 = Only glandular hairs
21. Pappus bristles	0 = Plumose (cilia 0.2–0.7 mm long.), 1 = Denticulate (cilia 0.01–0.05 mm long.)
22. Pappus in outer flowers	0 = Long (4.5–8 mm long.), 1 = Short (0.5–1 mm long.) 2 = Absent

prestidae), *Mutisia tridens*, and *M. macrophylla* (Asteraceae).

ANCESTRAL AREAS. A taxon-area cladogram was constructed and the ancestral areas method of Bremer (1992) was followed. This method is a cladistic procedure for approximating ancestral areas of individual groups from the topological infor-

mation in their area cladogram. The method determines relative probabilities of areas as part of the ancestral area given the information on their presence on deep and numerous branches in the cladogram. Each area is treated as a single character, which may be optimized onto the taxon cladogram using either forward or reverse Camin-Sokal par-

TABLE 3. Data matrix used in the cladistic analysis of *Moscharia* and *Polyachyrus*. Refer to Table 1 for acronyms and Table 2 for characters. a = polymorphic character, ? = missing data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
OUT	a	0	0	0	0	?	0	?	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0
ANN	0	1	1	0	0	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0
CAR	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0
CIN	1	2	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
FUS	1	1	1	1	1	1	0	1	0	0	0	0	1	0	0	1	1	0	0	2	0	0	0
GAY	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0
PIN	0	0	0	0	0	2	1	0	1	1	1	1	2	0	1	1	0	0	1	0	1	2	0
POE	1	0	1	0	0	2	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0
SOL	0	0	0	0	0	2	1	0	1	1	1	1	2	1	1	0	0	0	1	0	1	1	1
SPH	1	1	1	0	0	2	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0

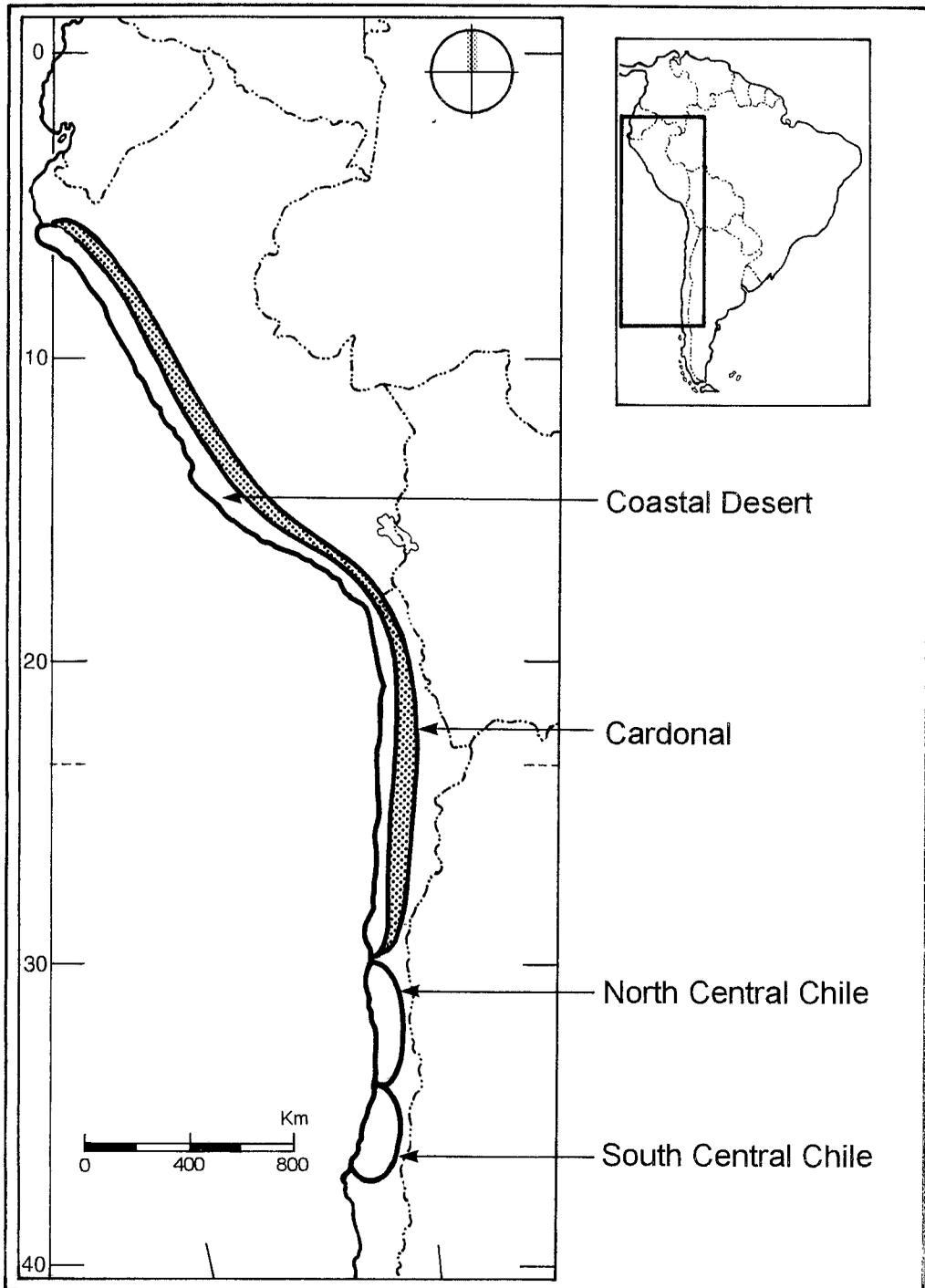


FIG. 3. Areas for the biogeographic analysis of *Moscharia* and *Polyachyrus*.

simony. Bremer's preference for Camin-Sokal parsimony instead of Wagner parsimony was criticized (Ronquist 1994), but according to Bremer (1995) this method uses Camin-Sokal only as a methodological tool. Therefore, it is not a strategy for optimizing areas at the root and along the branches of the cladogram, and does not involve necessarily any process assumptions. According to this method, the areas inhabited by each taxon are treated as binary characters with two states, present or absent. The areas are optimized on the cladogram, and the number of gains or presences (G) and losses or absences (L) for each individual area are computed. Finally, the G/L ratio for each geographic area was estimated to find what individual area/s had the highest G/L ratios and therefore were a part of the hypothetical ancestral area (AA).

## RESULTS

**Cladistic Analysis.** Cladistic analysis of the nine taxa resulted in one most parsimonious cladogram with a length of 37 steps, a consistency index of 0.73, and a retention index of 0.75 (Fig. 4). Six monophyletic groups were resolved: 1) ANN, SPH, CAR, CIN, FUS, GAY, and POE (perennial herbs, revolute to folded leaf margin, outer lip of corolla oblong-lanceolate, corolla surface papillose); 2) ANN, SPH, CAR, CIN, FUS, and GAY (leaves lanose below); 3) CAR, CIN, FUS, and GAY (semiamplexicaul leaf base, plumose pappus); 4) CIN, FUS, and GAY (oblong foliar lobes, smooth foliar lobes, keeled bract surrounding the outer and the inner flower); 5) FUS and GAY (linear bracts of pseudoinvolucre); and 6) PIN and SOL (developed pseudoinvolucre, capituliform pseudocephalia, 8–10 capitula per pseudocephalium, dimorphic capitula, capitula with 1–2 involucral bracts, one involucral bract conduplicate, keeled bract margin not scarious, tectum of pollen grains lacking ramifications). Clades 4 and 6 are well supported by bootstrap and Bremer support.

**Historical Biogeography.** The application of Bremer's method (1992) indicates that the North Central Chile area could be a part of the ancestral geographic range of *Moscharia* and *Polyachyrus*, given its relatively high G/L value of 1.3 (Table 4; Fig. 5). The subsequent values are that of the Coastal desert and the South Central Chile with 1. Table 4 suggest a dispersal event from the ancestral range both to the north and to the south. The Cardonal area resulted in the lowest G/L value (0.5) sug-

gesting that the most recent dispersal event occurred from lower to higher elevations.

## DISCUSSION

The analysis supports that *Polyachyrus* and *Moscharia* are two distinctive, monophyletic genera (Fig. 4). The genus *Polyachyrus* is defined by four synapomorphies: perennial herbs (character 1, that changes to plesiomorphy in *P. annus*), revolute to folded leaf margin (character 3, that changes to plesiomorphy in *P. carduoides*), corollas with oblong-lanceolate outer lip (character 17), and corollas with papillose surface (character 18, that changes to plesiomorphy in *P. fuscus*). The genus *Moscharia*, on the other hand, is strongly supported by eight synapomorphies: developed pseudoinvolucre (character 7), capituliform pseudocephalia (character 9), 8–10 capitula per pseudocephalium (character 10), dimorphic capitula (character 11), 1–2 involucral bracts per capitula (character 12), one conduplicate involucral bract [character 13 (2)], keeled bract margin not scarious (character 15), and tectum of pollen grains lacking ramifications (character 19).

**Character Evolution.** The cladogram shows that *Moscharia* has all the plesiomorphic states of characters for the leaves, i.e., glabrous or subglabrous leaves (character 2), planate leaf margin (character 3), deltoid foliar lobes (character 4), mucronate-spinose foliar lobes (character 5), and decurrent leaf base (character 6). This genus, on the other hand, shows all the evolutionary novelties in the morphology of the capitula and pseudocephalia. Most variation in leaf characters is exhibited by the species of *Polyachyrus*, that could be interpreted as an adaptation to the deserts and semideserts and high altitudes. From the condition of glabrous or subglabrous leaves (*P. poeppigii*) there is an increase of the pubescence to leaves lanose below (*P. sphaerocephalus*, *P. annus*, *P. fuscus*, and *P. gayi*), with a reversion to glabrous in *P. carduoides* followed by evolution to lanose above and below (*P. cinereus*). All species of *Polyachyrus* have leaves with revolute to folded margin on the medial nervature, that changes to plesiomorphy in *P. carduoides*. There is a reduction in the size of the foliar lobes from deltoid (*P. poeppigii*, *P. annus*, *P. sphaerocephalus*, and *P. carduoides*) to oblong (*P. cinereus*, *P. fuscus*, and *P. gayi*). Another reduction of the lamina occurs in the foliar base from the plesiomorphic condition of amplexicaul leaves to semiamplexicaul (*P. carduoides*, *P. cinereus*, and *P. fuscus*, that changes to plesiomorphy in *P. gayi*). The



TABLE 4. Gains (G) and Losses (L) for the areas of species in the cladogram of *Moscharia* and *Polyachyrus*. The most probable ancestral area (AA) for the group corresponds to the highest G/L quotients.

Area	G	L	G/L	AA
Coastal Desert	4	4	1	0.77
Cardonal	2	4	0.5	0.38
North Central Chile	4	3	1.3	1
South Central Chile	2	2	1	0.77

only exception in this evolution to a reduction of the lamina occurs in character 5 where the spiny lobes of the leaves (*P. poeppigii*, *P. annus*, *P. sphaerocephalus*, and *P. carduoides*) change to leaves with lobes that are smooth (*P. cinereus*, *P. fuscus*, and *P. gayi*).

The keeled involucre bract in the capitula of *Polyachyrus* and *Moscharia* shows some interesting variation. There is an evolution within both genera from a less convex keeled bract to a more convex one. This bract surrounds only the outer flower (character 16) in *P. annus*, *P. carduoides*, *P. poeppigii*, and *P. sphaerocephalus*, but is tightly attached to the two flowers of the capitula in *P. cinereus*, *P. fuscus*, and *P. gayi*. *Moscharia* shows the same variation in its keeled bract. The bract surrounds the outer flower in *M. solbrigii* and is conduplicate around the two flowers, almost closing the capitula in *M. pinnatifida*. It can be hypothesized that the keeled bract surrounding the cypselas in the fertilized flowers plays an important role in fruit dispersal. It is common to see the disjoining of individual capitula in the mature pseudocephalia on specimens of *Moscharia* and *Polyachyrus*. Heads enclosed by the keeled bract are dropped off as a whole without releasing the cypselas before germination, a phenomenon called synaptospermy (Murbeck 1920) that is commonly found in genera of Asteraceae with pseudocephalia (Claßen-Bockhoff 1996). The bracts of the involucre, including the internal bract (interpreted to be homologous to a pale), are also attached to the cypselas and deciduous with them. It has been suggested (Stuessy and Spooner 1988) that the pales in Compositae could serve to protect the fruit from ground predators prior to germination and to keep moisture around the cypselas, especially in arid climates.

Another character observed in this group is the loss or reduction of male sexuality in some specimens of *Polyachyrus annus* and *P. carduoides*. These species show empty or reduced stamens in the

flowers surrounded by the keeled bract. Sterile ovaries, on the other hand, were reported by Ricardi and Weldt (1974) in the inner flowers. This character was not used in the cladistic analysis because it was found sporadically in the specimens analyzed. This change in the sexuality of the flowers, from perfect to functionally pistillate or staminate, has also been found in genera with pseudocephalia belonging to other tribes of Asteraceae, such as *Inuleae* (Freire and Katinas 1995).

Variation of the pappus can also be examined based on the cladogram (Fig. 4). From the condition of a denticulate pappus (character 21) in *Moscharia pinnatifida*, *M. solbrigii*, *Polyachyrus annus*, *P. poeppigii*, and *P. sphaerocephalus*, there is an increase in the length of the cilia to a plumose pappus in *P. carduoides*, *P. cinereus*, *P. fuscus*, and *P. gayi*. Another character of the pappus that shows variation is the reduction of the bristles length or the complete absence of a pappus (character 22). All species of *Polyachyrus* have flowers or fruits with pappus, longer in the outer flowers than in the inner flowers. In *Moscharia solbrigii*, all the flowers have a short pappus, and in *M. pinnatifida* the inner flowers have a short pappus whereas the outer ones lack a pappus. Loss of the pappus in *Moscharia* agrees with the hypothesis proposed by Zohary (1950) in which the reduction of the pappus generally takes place in a centrifugal direction, with a gradual reduction from the central flowers (with a normal long pappus) to the marginal flowers (with no or a reduced pappus). The pappus in *Polyachyrus* and *Moscharia*, when present, is completely deciduous and hardly functions as a dispersal agent of the fruits. As mentioned above, the keeled bract of the capitula probably plays an important role in dispersal. Another mode of dispersal was suggested by Ricardi and Weldt (1974) for *Polyachyrus fuscus*. The presence of this species in the Sangallan islands in Peru, more than 1000 km from the typical growing area of *P. fuscus*, can be explained by the migration of the "guanay" birds (*Phalacrocorax bougainvillei*) to these islands. It was also suggested (Stuessy and Garver 1996) that in Compositae the pappus together with the paleae have a defensive role, so if paleae are present (as in *Moscharia* and *Polyachyrus*) the pappus should be reduced in length.

**Biogeography.** *Moscharia* and *Polyachyrus* occupy well defined geographical areas in southwestern Perú and north and central Chile, in strict concordance with the climatic and orographic conditions of the region (Ricardi and Weldt 1974). From an ecological point of view, species of both

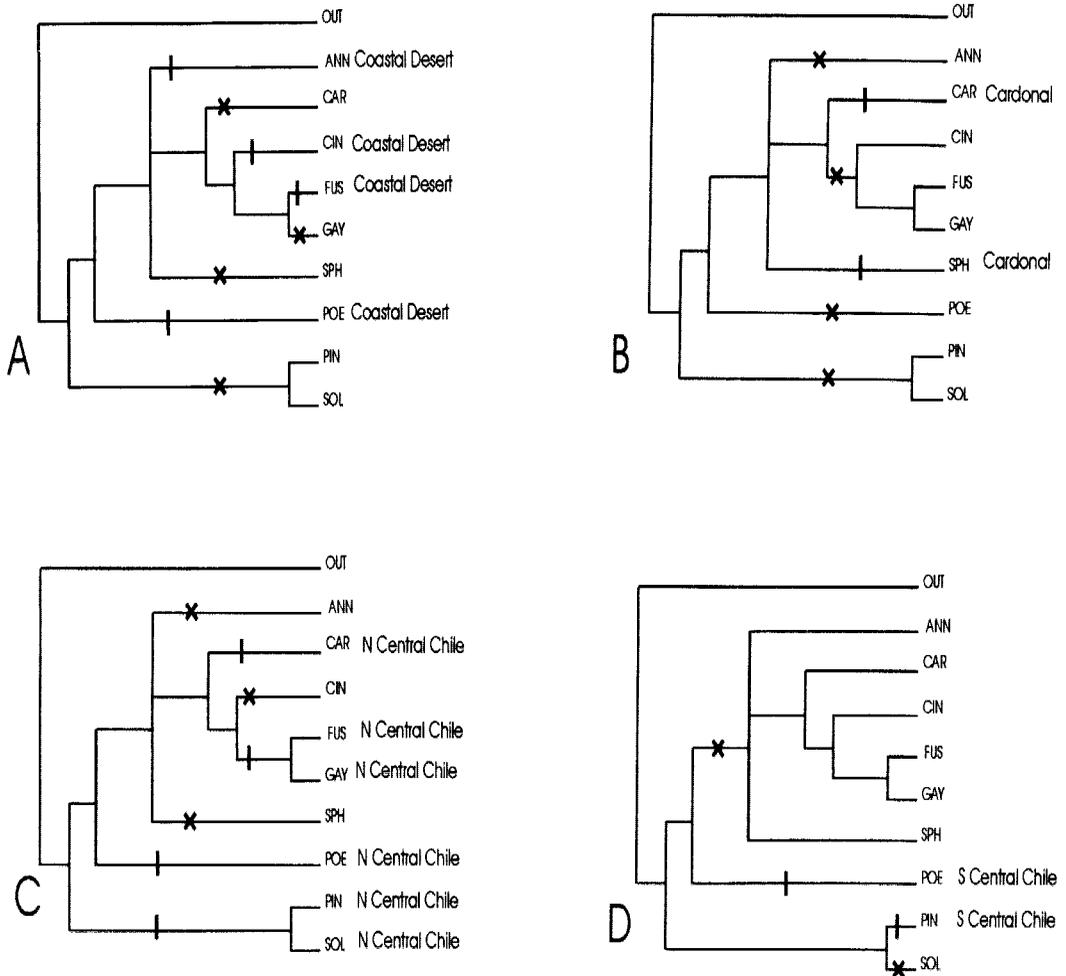


FIG. 5. A–D, taxon area-cladograms for *Moscharia* and *Polyachyrus*, as shown on Fig. 4. Gains (lines) and losses (crosses) under forward and reverse Camin-Sokal parsimony, respectively, are indicated for all four areas, Coastal Desert (A), Cardonal (B), North Central Chile (C), and South Central Chile (D).

genera grow in three main habitats, i.e., part of the central valley and the dry littoral in Chile and Peru (*Polyachyrus annus*, *P. carduoides*, *P. fuscus*, *P. cinereus*, *P. poeppigii*, *P. gayi*, and *Moscharia pinnatifida*), the dry Andean west facing slopes (*Polyachyrus carduoides*, and *P. sphaerocephalus*), and the humid temperate forests of Fray Jorge and Talinay in Chile (*Polyachyrus fuscus*, *P. poeppigii*, *Moscharia pinnatifida*, and *M. solbrigii*). Within all this range, the area commonly known as Central Chile (30°–37° south latitude) is of special interest because of its high percentage of endemic plant and animal taxa at different taxonomic ranks (Morrone et al. 1997). The North-Central Chile area, identified as the an-

cestral area with the highest quotient G/L of 1.3, holds a high diversity of species of *Moscharia* and *Polyachyrus* with six species in the Coquimbo province. This diversity also can be seen north of this area, in the Atacama province (with five species) and in the Antofagasta province (with six species). The Atacama province was postulated to be the center of dispersal of *Polyachyrus* by Ricardi and Weldt (1974).

Different geological events in southern South America may have played an important role in the evolution of the biota of this area, including *Moscharia* and *Polyachyrus*, among them the uplift of the Andes and Quaternary glaciations. The uplift of the

Andean cordillera began in the late Oligocene and underwent major uplift in the Pliocene. The first record of the Andean vegetation corresponds to the upper Pliocene, with an increase in biodiversity during Quaternary (Villagrán et al. 1983). By cutting off the Pacific wind drift, together with the development of the Antarctic ice cup that allowed the establishment of the Humboldt Current, the uplift provoked aridity of wide areas of southern South America (Kalin Arroyo et al. 1983; Rundel et al. 1991; Morrone 1993). In Pleistocenic times the glaciations also played a significant role (Simpson Vuilleumier 1971; Hammen 1974), altering the South American vegetation through a series of wet-dry cycles. The wetter Pleistocene climate period would have favoured the development of the *Nothofagus* forest communities, restricted to Antarctica and southern South America (Kalin Arroyo et al. 1983), that extended northward along the coastal range of Central Chile (Troncoso et al. 1980). Finally, there was an expansion of the sclerophyllous forest due to more arid conditions in the Holocene (Heusser 1983; Pérez and Villagrán 1985), this being the dominant type of vegetation found today in the Central Chilean area.

According to these geological and biotic events and the results of the biogeographic analysis obtained here, it can be hypothesized that the ancestor of *Moscharia* and *Polyachyrus* may have inhabited a part of the area of North Central Chile (30°–35° south latitude). During humid climate periods, the biota inhabiting this region increased its range both to the south (S Central Chile area) and to the north (Coastal Desert area), with the high Andean slopes (Cardonal area) being the last area to be occupied. The subsequent lowering of the sea-level would have provided opportunities for the coastal elements to disperse (Dillon, pers. com.). From the cladogram, it would appear that there have been multiple introductions into the Peruvian desert (lomas formation) and perhaps another in the Andean Cordillera Occidental. Evolution of the xeromorphic states of characters in the leaves, and the keeled bract development to protect the capitula of *Moscharia* and *Polyachyrus*, could represent an adaptation to hyperaridity. Species of both genera still remain in the humid relict forests of Fray Jorge and Talinay. It is probable that the major dispersal of the ancestor of *Moscharia* and *Polyachyrus* occurred in the Pleistocene, when these relict forests communities were favoured by the wet past climate. The Pleistocene has also been proposed as the period of evolution of other members of Asteraceae in

South America, such as *Chuquiraga* in the subfamily Barnadesioideae (Ezcurra et al. 1997), and *Abrotanella* in the tribe Senecioneae (Swenson and Bremer 1997).

It is possible that the events that led to the present distribution of *Moscharia* and *Polyachyrus* were a combination of dispersal and vicariant events promoted by tectonic phenomena. Further investigations on other plant and animal taxa are needed to understand the complex history of the biotas and the areas of southern South America.

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