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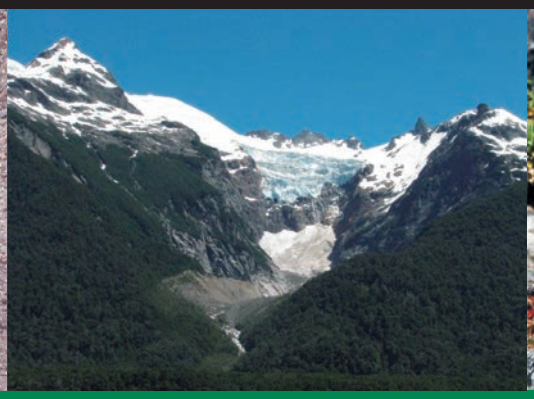

Andean Origin and Diversification of the Genus *Perezia*, an Ancient Lineage of Asteraceae

María José Apodaca,
Jorge V. Crisci, and
Liliana Katinas

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ABSTRACT

Apodaca, María José, Jorge V. Crisci, and Liliana Katinas. Andean Origin and Diversification of the Genus *Perezia*, an Ancient Lineage of Asteraceae. *Smithsonian Contributions to Botany*, number 102, viii + 28 pages, 7 figures, 4 tables, 3 appendixes, 2015.—*Perezia* is an Andean-centered genus and belongs to the early diverging lineages in the phylogenetic tree of the Asteraceae (Compositae). Previous studies in *Perezia* proposed several evolutionary lines and alternative areas of origin. A phylogenetic morphological analysis was performed to test these hypotheses and ancestral areas and dispersal-vicariance analyses were applied. The results of the phylogenetic analysis support *Perezia* as a monophyletic taxon, including the recently excluded *Perezia nutans* and *P. prenanthoides*, and support most of the previously proposed evolutionary lines. The biogeographic results suggest the southern Andes as the probable ancestral area for *Perezia*, with multiple dispersals. Supported by geologic, paleoclimatology, and fossil evidence, it is inferred that the ancestor of *Perezia* may have inhabited the areas above the humid, temperate forests in the southern Andes during the Tertiary. KEY WORDS: Climatic changes, morphology, Mutisioideae, phylogenetic reconstruction, South America.

RESUMEN

Apodaca, María José, Jorge V. Crisci y Liliana Katinas. Origen andino y diversificación del género *Perezia*, un linaje temprano de Asteraceae. *Smithsonian Contributions to Botany*, número 102, viii + 28 páginas, 7 figuras, 4 tablas, 3 apéndices, 2015.—*Perezia* tiene su mayor concentración en los Andes y pertenece a los linajes tempranos del árbol filogenético de Asteraceae (Compositae). En estudios previos en *Perezia* se propusieron varias líneas evolutivas para el género y áreas de origen alternativas. Se desarrolla aquí un análisis filogenético sobre la base de caracteres morfológicos para poner a prueba dichas hipótesis y se aplican los métodos biogeográficos de areas ancestrales y de dispersión-vicariancia. Los resultados del análisis filogenético muestran que *Perezia* es un taxón monofilético si incluye a las recientemente excluidas *Perezia nutans* y *P. prenanthoides*, y sustentan a la mayoría de las líneas evolutivas previamente propuestas. Los resultados biogeográficos sugieren a los Andes del sur como probable área ancestral de *Perezia*, con múltiples dispersiones. Sobre la base de la evidencia geológica, paleoclimatológica, y fósil, se propone que el ancestro de *Perezia* podría haber habitado las áreas por encima de los bosques templados del sur de los Andes durante el Terciario. PALABRAS CLAVE: Cambios climáticos, morfología, Mutisioideae, reconstrucción filogenética, América del Sur.

Cover images, from left to right: *Perezia multiflora* subsp. *multiflora* (habit; photo by L. Katinas); Andes of southwestern Argentina (photo by M. Apodaca); *Perezia recurvata* (habit; photo by M. Bonifacino).

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Andean Origin and Diversification of the Genus *Perezia*, an Ancient Lineage of Asteraceae

María José Apodaca, Jorge V. Crisci, and Liliana Katinas*

INTRODUCTION

Southern South America today has a high diversity of environments, biomes, and biotas probably as the result of the complex interactions through time of plants and animals with several geological forces, including the rising of the Andean Cordillera, sea-level changes, and glaciations (Ortiz-Jaureguizar and Cladera, 2006). The Andean Cordillera, a great series of mountain belts, sweeps up the west coast of South America from the southern tip of Chile and Argentina to Venezuela. The Andes are the world's longest mountain range and boast the highest peaks in the world after the Himalayas; for instance Aconcagua in the Mendoza province of Argentina is 6,962 m high (22,841 ft). The Andean Cordillera is a crucial barrier to atmospheric circulation in the southern hemisphere and has the highest plateau on Earth, the Altiplano-Puna at 3,000–4,000 m, formed at a noncollisional plate margin (Gregory-Wodzicki, 2000).

It has been postulated that the Andes acted as a dispersal route for organisms and as a driver for rapid diversification via allopatric speciation and ecological displacement (Antonelli et al., 2009). This diversification was promoted by the emergence of heterogeneous ecological conditions in island-like habitats after successive Andean uplifts and Quaternary climate fluctuations facilitated geographical isolation (Ritz et al., 2007).

As postulated by several authors, the Andes constitute the backbone of one of the two biogeographical regions of South America. South America was proposed as a subcontinent of hybrid origin that should be divided into two biogeographical areas: southern temperate and northern tropical areas (Humphries, 1981). The southern temperate region, the focus region of this study, is the area south of 30° south latitude in South America but also includes the Andean highlands north of this latitude. This area was named the Patagonian subregion by Kuschel (1969) and southern South America by Crisci et al. (1991) (Figure 1). An approximation of this area may be obtained by looking at the distribution of many individual taxa, such as *Azara* Ruiz et Pav. (Flacourtiaceae), *Escallonia* L.f. (Escalloniaceae), Mummucidae and Daesiidae (Solifugae), Tristiridae (Orthoptera), *Pompilocalus* Roig-Alsina (Hymenoptera), and genera of Coleoptera (Kuschel, 1969; Crisci et al., 1991). Many distributions of genera and species groups of the plant family Asteraceae are also congruent with this distributional pattern, for example, *Lucilia* Cass., *Noticastrum* DC., and members of the tribe Nassauvieae (Crisci, 1974), such as *Leucheria* Lag., *Nassauvia* Comm. ex Juss., *Perezia* Lag., and *Trixis* P. Browne.

Perezia Lag. (Asteraceae, Nassauvieae), with 30 species of perennial herbs (Katinas, 2012), is distributed from Colombia to southern Chile and Argentina, including Islas Malvinas (Falkland Islands) (Figure 1). Its major concentration occurs in the

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FIGURE 1. Map of South America showing the two subregions, Brazilian and Patagonian, established by Kuschel (1969) on the basis of Coleoptera distributions. The distribution of the species of *Perezia* is shown in gray.

southern Andes and in Patagonia, with a few species in the area of southeastern Brazil, Paraguay, Uruguay, and northeastern Argentina. In addition, *Perezia* belongs to the basal grade in the phylogenetic tree of the family (Funk et al., 2009), making this an interesting genus to postulate hypotheses about the early Andean diversification among lineages in southern South America.

The first revisionary work of *Perezia* was performed by Vuilleumier (1970), who established 30 species and proposed seven evolutionary lines of species groups based on morphological, anatomical, palynological, cytological, and chemical data (Figure 2). These evolutionary lines are (1) the *Perezia coerulescens* group, (2) the *P. magellanica* group, (3) the *P. multiflora* group, (4) the *P. prenanthoides* group, (5) the *P. pungens* group, (6) the *P. recurvata* group, and (7) *P. pilifera* Less., which was not included in any of the groups (Table 1). Hypotheses on the origin and radiation of each one of these lineages were proposed by Vuilleumier (1970), and it was suggested that *Perezia* arose during the early middle Tertiary in open, warm forests that covered extratropical South America.

Based on 28 of the 30 species established by Vuilleumier (1970), a phylogenetic analysis to test these groups was developed by Simpson et al. (2009) using molecular sequence data of the nuclear rDNA internal transcribed spacer (ITS) sequences and the chloroplast intergenic spacers *rpl32-ndhF* and *trnL (UAG)-rpl32*. The authors noted the discrepancy between the phylogenies generated with the different markers, and the results of the combined analysis contained several polytomies within *Perezia*. Their combined phylogeny showed that the Brazilian-centered *P. multiflora* group was the sister group of the remainder of the *Perezia* species. The *P. multiflora* and the *P. recurvata* groups were the only species groups of Vuilleumier (1970) that were supported as monophyletic in the molecular analyses, with the *P. recurvata* group including additional species (*P. linearis* Less., *P. pilifera*, and *P. viscosa* Poepp. ex Less.) in one of the trees. Simpson et al.'s (2009) analysis, in contrast with previous hypotheses, suggested an eastern subtropical South American origin for the genus with a radiation into southwestern South America.

A more recent taxonomic revision of *Perezia* (Katinas, 2012) led to drastic specific and generic redefinitions (Table 1). For example, the recognition of *P. atacamensis* (Phil.) Reiche, *P. burkartii* Cabrera, and *P. capito* (Phil.) Reiche was proposed; the inclusion of the new species *P. catharinensis* Cabrera, *P. dentata* (Cabrera) Katinas, *P. eryngioides* (Cabrera) Crisci, and *P. volcanensis* Cabrera, described or transferred from other genera after the first revision of the genus in 1970, was reported; and many species were synonymized with *P. pungens* (Humb. et Bonpl.) Less. and with *P. pinnatifida* (Humb. et Bonpl.) Wedd. *Perezia nutans* Less. and *P. prenanthoides* Less., excluded from the genus in previous studies (Panero, 2007, based on unpublished data; Simpson et al., 2009), were tentatively placed in *Perezia* because no morphological gaps were found to warrant their segregation. These additions resulted in 30 species of *Perezia* being recognized, only 22 of which were included in the phylogenetic study of Simpson et al. (2009). Owing to the recent taxonomic changes that have occurred in *Perezia*, the limited sampling of previous studies, and the competing hypotheses resulting from the different molecular markers, the phylogenetic relationships within the genus needed to be investigated using a new set of data.

In this study all the species of *Perezia* (according to the most recent revision of the genus, Katinas, 2012) were included, and a phylogenetic study was conducted using morphological and palynological characters. The results of this analysis were used to examine previous studies, focusing on the species groups established by Vuilleumier in 1970 because the results in that work are less ambiguous than those of Simpson et al. (2009). On the basis of the resulting phylogenies, we employed here the historical biogeographical approaches dispersal-vicariance analysis (Ronquist, 1997) and ancestral areas (Bremer, 1992) to seek the historical explanations that led to the origin and diversification history of *Perezia* in the Andes.

MATERIAL AND METHODS

Phylogenetic Analysis

For this study, the 30 species of *Perezia* sensu Katinas (2012) were used as terminal taxa. The morphological and palynological data of the species of *Perezia* were taken from previous studies (Crisci, 1974; Katinas, 2012), derived from the analysis of ~1,300 herbarium specimens, or gleaned from field studies.

The apomorphic character state was identified by the outgroup comparison method (Watrous and Wheeler, 1981). Phylogenetic hypotheses proposed for the tribe Nassauvieae (Crisci, 1974; Katinas et al., 2008a; Luebert et al., 2009; Simpson et al., 2009) provided the basis for choosing *Nassauvia* and *Panphalea* Lag. as appropriate outgroups for the phylogenetic analysis of *Perezia*. Data from 37 morphological and palynological characters were included (Appendix A). Multistate characters (e.g., 2, 3, 6) were treated as unordered (=nonadditive). Some character states were coded as "?" because they are inapplicable characters (e.g., characters of the pappus in *Panphalea*, which lacks a pappus, or characters of the cypsela hairs in taxa with glabrous cypselae) or because there are missing data, as for a few characters in *P. volcanensis*. Variable characters in some taxa (e.g., 5, 7, 9) were treated as polymorphic during the analysis. Appendix B contains the data matrix, which was analyzed with the Wagner maximum parsimony algorithm of PAUP* version 4.0a129 (Swofford, 1999) using the "heuristic search" option. The bootstrap method (Felsenstein, 1985) with 100 replicates was employed to evaluate the reliability of the phylogenetic estimates. The program MacClade version 3.0 (Maddison and Maddison, 1992) was used for examination of the character distribution.

A
B
C
D
E
F
G
H

FIGURE 2. (*Opposite page*) Species representing the *Perezia* lineages: (A) *P. pinnatifida*, of the *P. coerulescens* (=*P. pinnatifida*) species group; (B) *P. magellanica* of the *P. magellanica* species group; (C) *P. multiflora*, of the *P. multiflora* species group; (D) *P. squarrosa*, of the *P. multiflora* species group; (E) *P. prenanthoides*, of the *P. prenanthoides* species group; (F) *P. carthamoides*, of the *P. pungens* species group; (G) *P. recurvata*, of the *P. recurvata* species group; and (H) *P. pilifera*. Photo credits: A, D, G: M. Bonifacino; B, H: Station Alpine Joseph Fourier (France) via Flickriver.com; C: L. Katinas; E: F. Vidoz (www.sib.gov.ar); F: M. Costea (Phytoimages).

Biogeographic Analysis

Areas of Endemism: An area of endemism is defined here as an area of nonrandom distributional congruence among different taxa. It is identified by the congruent distributional boundaries of two or more species, where congruence does not demand complete agreement of those limits at all possible scales of mapping but relatively extensive sympatry is a prerequisite (Platnick, 1991). Areas of endemism used in this analysis (Figure 3) are defined by Cabrera and Willink (1980) and Sick (1969). The areas considered in this study are (A) Subantarctic, (B) northern Andean, (C) southern Andean, (D) Patagonia, (E) Puna, (F) Paranense, (G) Chacoan, (H) Pampean, and (I) Espinal. Islas Malvinas are here included in the Subantarctic (Appendix C).

Dispersal-Vicariance Analysis (DIVA): Ancestral distributions were reconstructed using DIVA 1.1 (Ronquist, 1996) according to the dispersal-vicariance optimization method (Ronquist, 1997). Dispersal-vicariance analysis optimizes distributions for each node of the tree, allowing for vicariance events and minimizing the number of assumed dispersals and extinctions. The analysis assumed that the number of ancestral areas was unconstrained, favoring vicariance and allowing the ancestral distributions to contain the maximum number of areas (Crisci et al., 2003), which for this study was nine (as listed in "Areas of Endemism"). According to Ronquist (1996), the optimizations become less reliable as the root node is approached because it includes most or all of the areas occupied by the terminals. To address this shortcoming, the ancestral areas approach (Bremer, 1992), which determines the ancestral area of *Perezia* under a different assumption, was also employed (assuming only dispersal and not dispersal and vicariance).

Ancestral Areas (AA): A taxon areas tree was constructed, and the ancestral areas method of Bremer (1992) was followed. This method is a cladistic procedure for approximating ancestral areas of an individual group from the topological information in its area tree. The areas are optimized on the tree, 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 determine which individual area(s) had the highest G/L ratio(s) and, therefore, was a part of the hypothetical ancestral area (Crisci et al., 2003). For a critique to this method see Ronquist (1994, 1995).

RESULTS

Phylogenetic Analysis

The phylogenetic analysis resulted in three equally parsimonious trees with a length of 144 steps, a consistency index of 0.375, and a retention index of 0.600. The trees are similar and differ only in their placement of *Perezia carthamoides* (D. Don) Hook. et Arn., *P. volcanensis*, and *P. pungens*: (1) *P. volcanensis* is sister group of *P. pungens* and together they form the sister group of *P. carthamoides*; (2) *P. pungens* is the sister group of *P. carthamoides* and both are the sister group of *P. volcanensis*; and (3) the three species form a trichotomy. We chose the first option (Figure 4) to show the character distribution. The lack of branch support in our analysis is coincident with the low support (50%–60%) or lack of support in many branches in the molecular analyses of *Perezia* (Simpson et al., 2009) based on the two different genes individually and in the combined tree. This could reflect high levels of homoplasy in the genus or very rapid evolution.

The species of *Perezia* form a monophyletic group with 65% support, including *P. nutans* and *P. prenanthoides*, which have been excluded from *Perezia* in other analyses (Panero, 2007; Simpson et al., 2009). *Perezia* is supported by the following unique combination of seven synapomorphies: presence of a scape, a one-seriate involucre with a length of 10–20 mm, outer involucral bracts with a ciliate margin, corollas white and colored, pollen grains with polar elevations, fruits that are densely pubescent, and a capillary pappus. Likely some of these character states may appear in other genera of Nassauvieae, but this combination of features is exclusive to *Perezia*.

Several monophyletic groups are recovered within *Perezia*. Unlike most vegetative characters, which are variable among species, the pubescence of the reproductive parts such as the receptacle and fruit (especially the amount and type of pubescence) are very reliable features that are often used to separate species. Figure 5 shows two diagrams comparing the evolutionary hypothesis of Vuilleumier (1970) (Figure 5A) with our phylogenetic results (Figure 5B). Below we list each of Vuilleumier's (1970) six species groups (see also Table 1) and compare them with the tree obtained here.

1. *Perezia coerulescens* species group (called by us *P. pinnatifida* species group): *P. atacamensis*, *P. burkartii*, *P. ciliosa*,

TABLE 1. Species groups proposed by Vuilleumier (1970) for the genus *Perezia* compared with the species groups obtained in the current analysis; morphological circumscription and geographical distribution are included. Dashes represent species that lack autapomorphies in the phylogenetic trees. See the text for further explanations.

Species groups proposed by Vuilleumier			Species groups proposed by present analysis			
Perezia species group	Species included	Morphological circumscription	*Perezia* species group	Species included	Morphological circumscription	Distribution
1. *P. coerulescens*	*P. ciliosa* *P. coerulescens* *P. pinnatifida* *P. pygmaea*	Reduced stature, compact rosettes tightly appressed to the ground; heads hidden among the leaves	1. *P. pinnatifida*	*P. atacamensis* *P. burkartii* *P. ciliosa* *P. dentata* *P. pinnatifida*	Stem unbranched (scape); basal leaves with marginal cilia	Altiplano of NW Argentina and N Chile to Peru
2. *P. magellanica*	*P. bellidifolia* *P. calophylla* *P. delicata* *P. fonkii* *P. lactucoides* *P. lyrata* *P. magellanica* *P. megalantha* *P. pedicularidifolia* *P. viscosa*	Small, rosette plants; solitary capitula; fruits with long, dense hairs	2. Polyphyletic group: constituted by independent monophyletic groups and individual species	*P. bellidifolia*	—	Argentinian S Andes
				P. calophylla	Pappus white and colored	Argentinian S Andes
				P. capito *P. megalantha*	Involucre hemispherical; involucral bracts orbicular; scarce fruit pubescence	S Andean valleys of Chile and Argentina
				P. delicata *P. lactucoides* *P. magellanica*	Involucral bracts without scarious margin	S Andes of Argentina and Chile, bogs, and *Nothofagus* forests
				P. fonkii	Long and filiform fruit pubescence	S Andes of Chile and Argentina, *Nothofagus* forests
				P. lyrata	—	S Andes of Chile
				P. pedicularidifolia *P. poeppigii*	Fruit apex rostrate	S Andes of Chile and Argentina, *Nothofagus* forests, and central valley between central Chilean Andes
				P. spathulata	—	S Andes of Argentina and Chile, *Nothofagus* forests

3. *P. multiflora*	*P. kingii* *P. multiflora* *P. squarrosa*	Silky, copper-colored fruit hairs; hemispherical involucre; reduced number of involucral bracts	3. *P. multiflora*	*P. catharinensis* *P. eryngioides* *P. kingii* *P. multiflora* *P. squarrosa*	Corymbose inflorescence; fruits with nonglandular hairs exclusively	Paraguay, Uruguay, SE Brazil, NE Argentina, one species extending to N Andes
4. *P. prenanthoides*	*P. nutans* *P. prenanthoides*	Large, foliaceous herbs; showy, open clusters of numerous magenta heads; broad, soft, basal leaves; fruits densely covered by amber-colored hairs	4. *P. prenanthoides*	*P. nutans* *P. prenanthoides*	Inflorescence paniculate; receptacle glabrous; fruits scarcely pubescent	S Andes of Argentina and Chile, *Nothofagus* forests
5. *P. pungens*	*P. carduncelloides* *P. carthamoides* *P. ciliaris* *P. mandonii* *P. pungens* *P. purpurata* *P. sublyrata*	Large, caulescent, polycephalus plants	5. *P. pungens*	*P. carthamoides* *P. pungens* *P. volcanensis*	Leaves with marginal cilia; spherical involucre; fruits scarcely pubescent	Andes and Puna from central Argentina and N Chile to Colombia
6. *P. recurvata*	*P. linearis* *P. poeppigii* *P. recurvata*	Special type of fruit hair; large, turbinate capitula; stiff, lanceolate involucral bracts	6. *P. recurvata*	*P. linearis* *P. recurvata*	Linear leaves, revolute or plicate; fruits scarcely pubescent	Central Chile, *Nothofagus* forests, Patagonia
Isolated species	*P. pilifera*		Not included in a group	*P. pilifera*	Linear leaves with marginal spines; inflorescence shorter than the leaves; fruits with long and filiform, nonglandular hairs	Andes from central Argentina to the S, including Patagonia

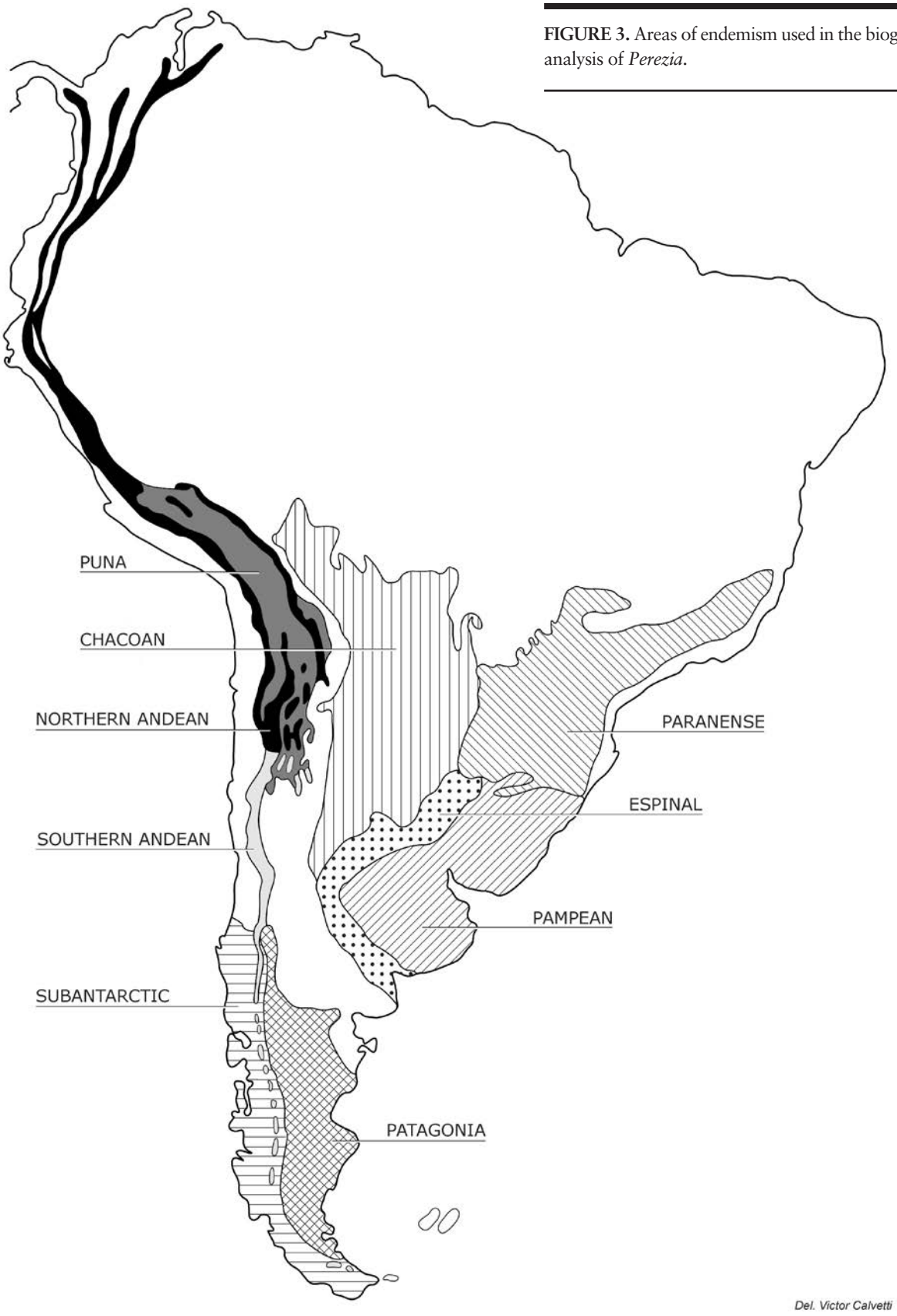

FIGURE 3. Areas of endemism used in the biogeographical analysis of *Perezia*.

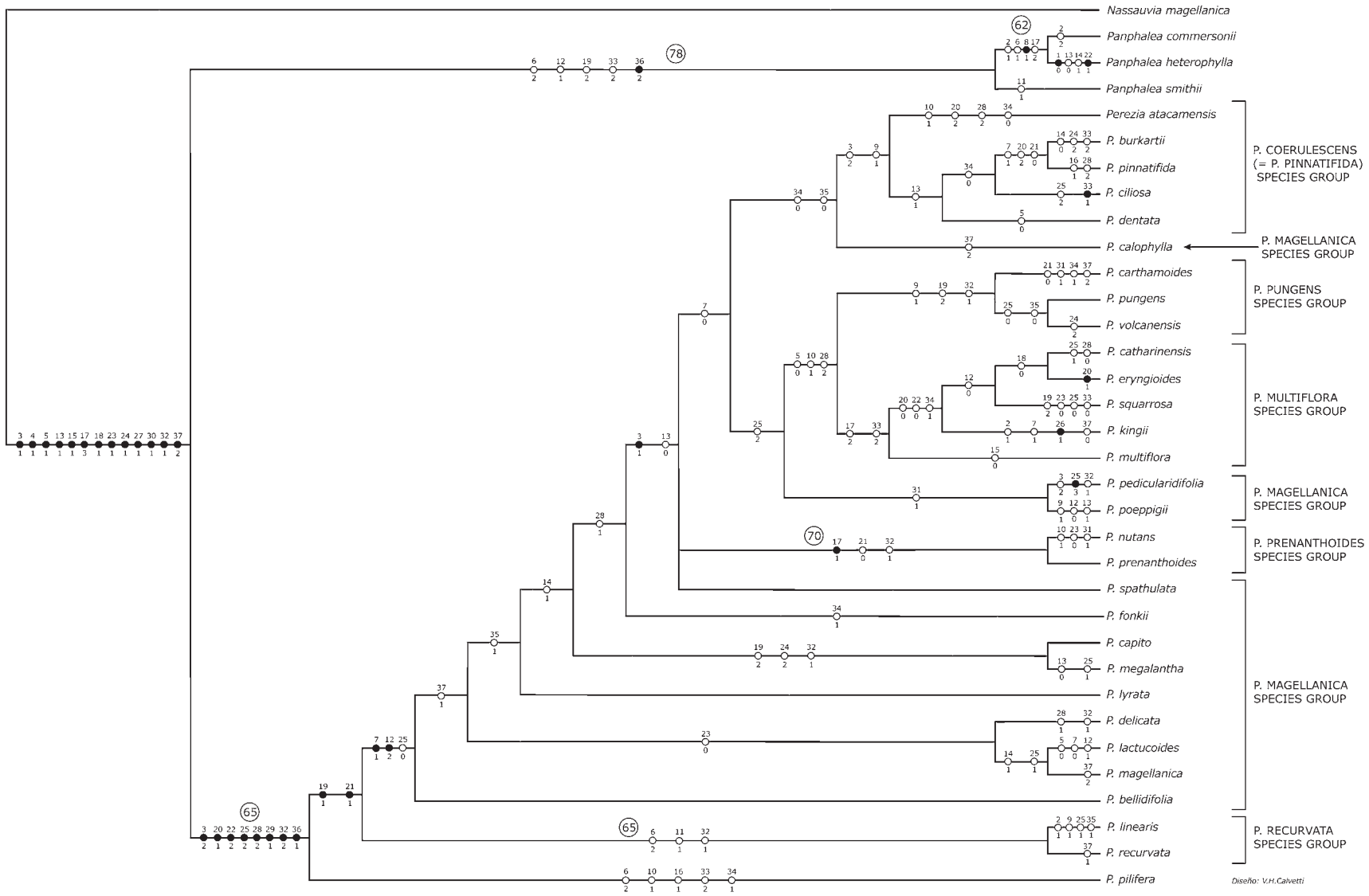

FIGURE 4. One of the three trees obtained from the maximum parsimony analysis of *Perezia*; characters are superimposed onto the tree (see Appendix A). Black circles represent synapomorphies and white circles represent homoplasies (parallelisms and reversals). Numbers within circles above branches are bootstrap values (only values ≥ 50 are indicated).

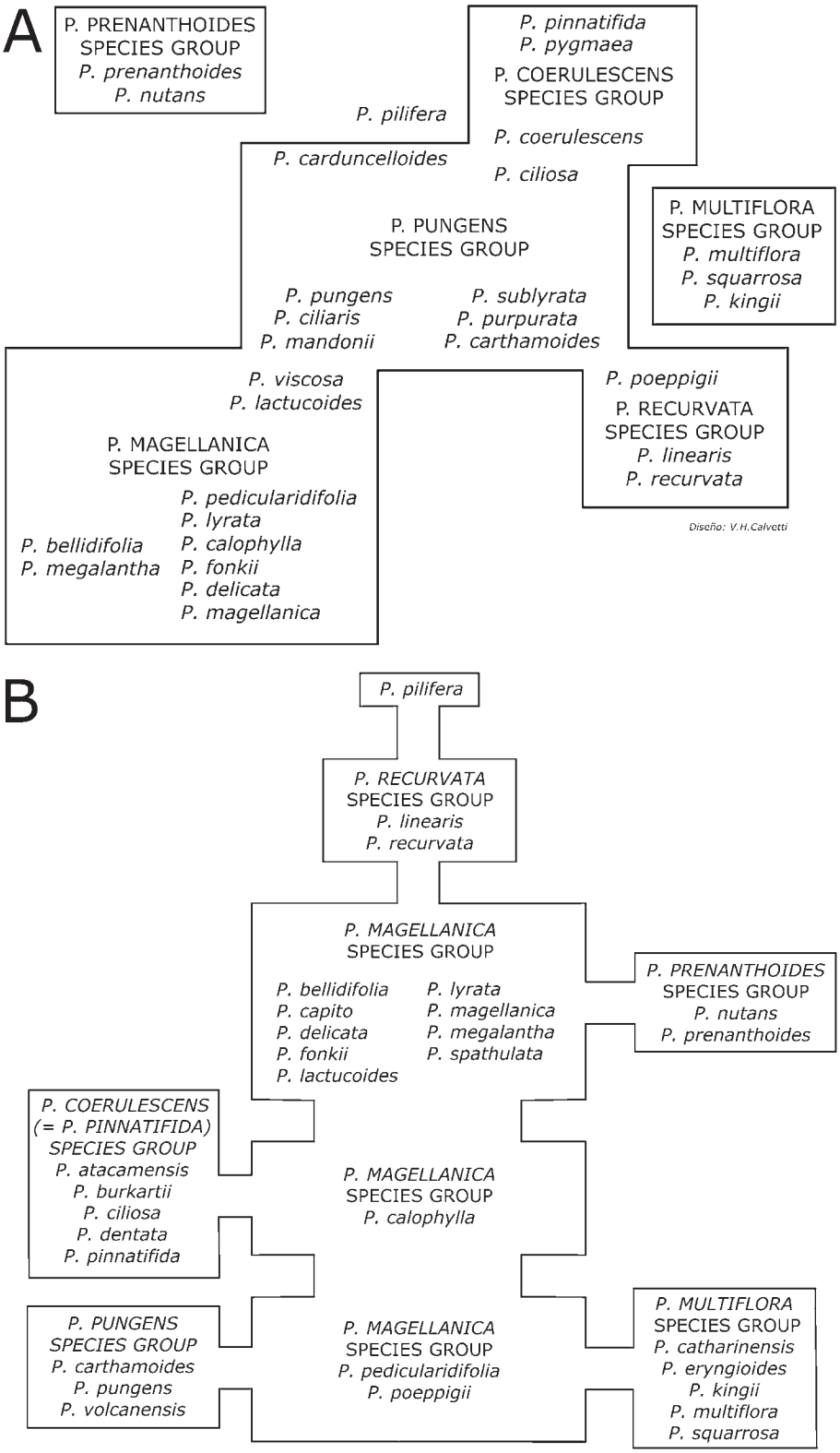

FIGURE 5. Schematic comparison of the relationships among the species and species groups of *Perezia* as presented by Vuilleumier (1970) and based on our phylogenetic tree (shown in Figure 3): (A) hypothesis of Vuilleumier (1970); (B) hypothesis proposed here.

P. dentata, and *P. pinnatifida*. Two of the four species included in this group by Vuilleumier (1970), that is, *P. coerulescens* and *P. pygmaea*, are currently considered synonyms of *P. pinnatifida*. *Perezia burkartii*, established by Vuilleumier (1970) as a synonym of *P. coerulescens* Wedd., is now considered an independent species (Katinas, 2012), and this analysis supports it as the sister taxon of *P. pinnatifida*. *Perezia ciliosa*, placed by Vuilleumier (1970) in an intermediate position between this group and the *P. pungens* species group (Figure 5A), is included here in the *P. coerulescens* group together with *P. dentata* (previously a subspecies of *P. ciliosa*). *Perezia atacamensis* was established by Vuilleumier (1970) as a synonym of *P. pungens*. The phylogenetic analysis, however, shows that *P. atacamensis* belongs to the *P. coerulescens* species group. This group is supported here by the unbranched stems and the basal leaves with marginal cilia.

2. *Perezia magellanica* species group: *P. bellidifolia* (Phil.) Reiche, *P. calophylla*, *P. capito, P. delicata* Vuilleum., *P. fonkii* (Phil.) Reiche, *P. lactucoides* (Vahl) Less., *P. lyrata* (J. Rémy) Wedd., *P. magellanica* (L. f.) Lag., *P. megalantha* Speg., *P. pedicularidifolia* Less., *P. poeppigii* Less., and *P. spathulata* (Lag. ex D. Don) Hook. et Arn. This is the only group that is suggested as non-monophyletic in our analysis. Originally the group consisted of more or less the same species, but now it also includes *P. capito* (previously a synonym of *P. lyrata*) and a name change for *P. viscosa* Poepp. ex Less. (=*P. spathulata*). These species are arranged as follows in our tree: *P. calophylla* is sister taxon of the *P. pinnatifida* species group; the sister species *P. pedicularidifolia* and *P. poeppigii* Less. form the sister group of the *P. pungens* group and the *P. multiflora* group; and the remaining species form a grade in the tree following *P. pilifera* (D. Don) Hook. et Arn. and the *P. recurvata* species group.

3. *Perezia multiflora* species group: *P. catharinensis, P. eryngioides*, *P. kingii* Baker, *P. multiflora* (Humb. et Bonpl.) Less., and *P. squarrosa*. This monophyletic group originally included only *P. kingii* Baker, *P. multiflora*, and *P. squarrosa*. *Perezia catharinensis* and *P. eryngioides* were described after Vuilleumier`s (1970) revisionary study. This group is centered in Brazil and includes *Eryngium*-like (i.e., erect perennial herbs with long, narrow, spiny leaves and paniculate or corymbose inflorescences) species characterized by their corymbose inflorescences and the fruits covered exclusively by nonglandular hairs.

4. *Perezia prenanthoides* species group: *P. nutans* and *P. prenanthoides*. Our analysis supports this as a monophyletic group nested within *Perezia*. Vuilleumier (1970) placed this group in an independent, unrelated position in her evolutionary scheme of the genus (Figure 5A). The group is supported here by capitula arranged in panicles, a glabrous receptacle, and fruits with scarce pubescence.

5. *Perezia pungens* species group: *P. carthamoides*, *P. pungens*, and *P. volcanensis*. Originally this group included *P. carthamoides*, *P. pungens*, and many species (*P. carduncelloides*, *P. ciliaris*, *P. mandonii*, *P. purpurata*, and *P. sublyrata*) that were subsequently considered synonyms of *P. pungens* by Katinas (2012). The only difference in the results presented here is the addition to this monophyletic group of *P. volcanensis*, described after 1970. The group is supported by the presence of leaves with marginal cilia, a spherical involucre, and fruits that are scarcely pubescent.

6. *Perezia recurvata* species group: *P. linearis* and *P. recurvata* (Vahl) Less. Our analysis supports this group on the basis of the basal leaves, which are linear, revolute, or plicate, and cypselae that are densely pubescent. *Perezia poeppigii*, which was placed in an intermediate position by Vuilleumier (1970) between this group and the *P. pungens* species group (Figure 5A), appears in our analysis to be related to the *P. magellanica* species group.

Isolated species, *Perezia pilifera*: This species was not included in any group by Vuilleumier (1970) (Figure 5A). Our results place it as the sister group of the rest of the species of *Perezia*. It is thought to be morphologically close to the *P. recurvata* species group because all three species have characteristic linear leaves.

Biogeographic Analysis

Dispersal-Vicariance Analysis: The results of the DIVA analysis (Figure 6) show the Southern Andes (C) as the probable ancestral area for the extant species of the genus *Perezia* (node 19). The tree of *Perezia* shows 15 dispersal events and 5 vicariance events; these events are depicted in Table 2. There are multiple dispersals from the area of origin, the Southern Andes, to the Subantarctic (A) (e.g., nodes 11, 14, 15), which is the adjacent area at a lower altitude. The most frequent vicariance event shown in Table 2 occurs between the Southern Andes (C) and the Northern Andes (B) (nodes 4 and 6).

Ancestral Areas: In coincidence with DIVA, the application of Bremer's method (1992) indicates that the Southern Andes (C) could be a part of the ancestral geographic range of *Perezia*, giving its relatively high G/L value of 4.00 and AA of 1, which shows a marked departure compared with the G/L and AA values of the other areas (Table 3).

DISCUSSION

Monophyly of *Perezia* and Evolutionary Lines

The results of our phylogenetic analysis provide evidence supporting *Perezia* as a monophyletic genus. Different from other analyses (Panero, 2007, based on unpublished data; Simpson et al., 2009) that excluded *P. nutans* and *P. prenanthoides*, our analysis shows both species nested within the genus. It should be noted that in the chloroplast DNA and nuclear ITS trees obtained by Simpson et al. (2009) both species are well separated from *Perezia* and are the sister group of other genera (*Calopappus* Meyen, *Nassauvia*, and *Triptilion* Ruiz et Pav.) with 91% support. However, in Simpson et al.'s (2009) Bayesian majority-rule tree based on the combined chloroplast DNA and nuclear ITS

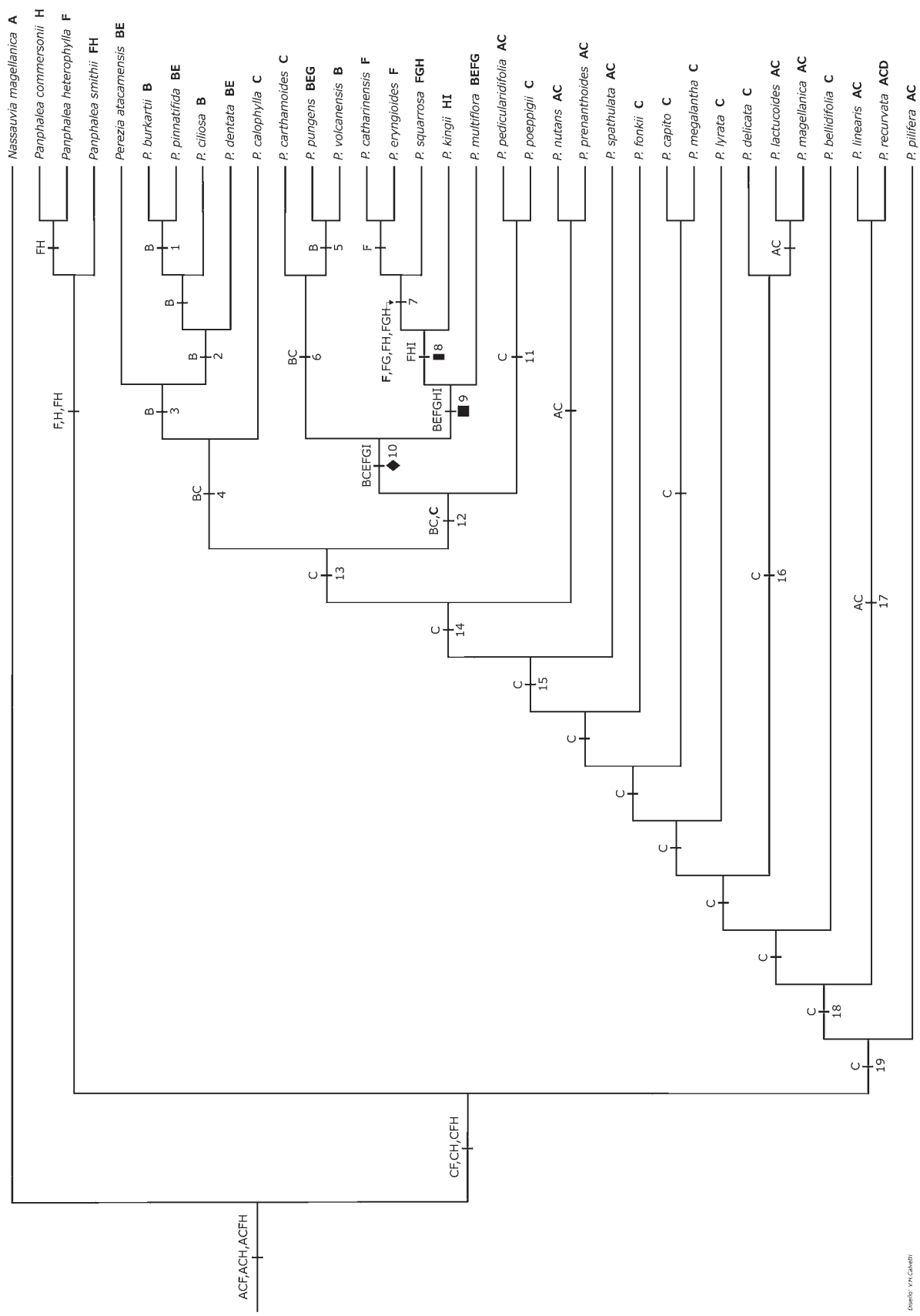

FIGURE 6. Phylogeny of *Perezia*, as shown in Figure 3, with areas optimized by dispersal-vicariance analysis (DIVA). Alternative equally optimal reconstructions are shown at the nodes. The areas used in this analysis are (A) Subantarctic; (B) Northern Andean; (C) Southern Andean; (D) Patagonia; (E) Puna; (F) Paranense; (G) Chacoan; (H) Pampean; and (I) Espinal. Numbers below nodes are events explained in Table 2. Black symbols represent nodes with many alternative optimal reconstructions.

TABLE 2. Results obtained from the dispersal-vicariance analysis (DIVA) depicting the events of dispersal or vicariance at each node of the tree of Figure 6.

Node	Dispersal events	Vicariance events
1	Northern Andean to Puna	
2	Northern Andean to Puna	
3	Northern Andean to Puna	
4		Southern Andean / Northern Andean
5	Northern Andean to Puna and Chacoan	
6		Southern Andean / Northern Andean
7	Paranense to Chacoan and Pampean	
8		Paranense / Pampean, Espinal
9	Northern Andean, Puna, and Chacoan to Paranense	Paranense, Pampean, Espinal / Northern Andean, Puna, Chacoan
10		Southern Andean, Northern Andean / Puna, Paranense, Chacoan, Espinal
11	Southern Andean to Subantarctic	
12	Southern Andean to Northern Andean, Puna, Paranense, Chacoan, and Espinal	
13	Southern Andean to Northern Andean	
14	Southern Andean to Subantarctic	
15	Southern Andean to Subantarctic	
16	Southern Andean to Subantarctic	
17	Southern Andean and Subantarctic to Patagonia	
18	Southern Andean to Subantarctic	
19	Southern Andean to Subantarctic	

TABLE 3. Gains and losses for the areas of species in the tree of *Perezia*. The most probable ancestral area (AA) for the group corresponds to the higher Gain/Loss (G/L) quotients, in this case the Southern Andean area (C).

Area of endemism	Gain	Loss	G/L	AA
Subantarctic (A)	6	9	0.66	0.165
Northern Andean (B)	3	14	0.21	0.052
Southern Andean (C)	12	3	4.00	1
Patagonia (D)	1	3	0.33	0.082
Puna (E)	5	16	0.3125	0.078
Paranense (F)	1	14	0.0714	0.017
Chacoan (G)	3	14	0.214	0.053
Pampean (H)	2	14	0.143	0.033
Espinal (I)	1	14	0.0714	0.018

data, this position of *P. nutans* and *P. prenanthoides* lacks support based on the maximum parsimony bootstrap value. In addition, Simpson et al. (2009) mentioned that the segregation of this group is justified, but their data (not shown) for several samples of both species suggest that only one species rather than two may be involved in the segregation. Furthermore, the morphological characters established by Panero (2007) for the segregation of *Calorezia* Panero from *Perezia* to support the molecular results do not really support such a distinction (for detailed descriptions and illustrations of *Perezia*, see Katinas, 2012). The following characters were established by Panero (2007):

1. Apices of twin trichomes of cypsela are fused, tapered (versus divergent); nondivergent trichomes are found, for example, in *P. eryngioides* and *P. megalantha*.
2. Glandular trichomes have two distinctive rows of cells of equivalent width and length and form a straight line between adjacent cells (versus staggered, forming a sinuous line); this is a very variable feature that may vary in the same individual and is found in many species of *Perezia* (e.g., *P. delicata* and *P. linearis*).
3. Capitula is sometimes nodding (versus never nodding); this feature may also be found in taxa outside this group, for example in *P. lactucoides*.
4. Florets are pink-mauve or purple (versus blue, white, or yellow, rarely pink or purple); corolla color is highly variable in the genus, and different individuals of the same species may have different corolla colors, with pink corollas commonly found in many species of *Perezia*.
5. Phyllaries are narrowly lanceolate (versus ovate) and usually without hyaline edges (versus with hyaline edges); phyllaries shape is also highly variable in the genus ranging from

linear to orbicular, and the same is true of the hyaline margins, which may vary in the same capitulum (i.e., phyllaries with and without hyaline edges).

Given all these uncertainties, we believe that a monophyletic *Perezia,* including *P. nutans* and *P. prenanthoides* and based on morphological data with 65% support, is valid. This monophyly is in line with the pollen ultrastructure, which shows no difference between these species and the remainder of the species of *Perezia*. Likewise, the morphological comparison among the species of *Perezia* and between *Perezia* and closely related genera also shows no characters that support the segregation of these two species from the genus (Katinas et al., 2008b; Katinas, 2012). Based on the morphological evidence the phylogeny matches the fossil record of the family (Barreda et al., 2010) and the biogeographical scenario proposed for early members of the family in southern South America (Katinas et al., 2013). It seems that the morphological phylogeny presented here is a better fit for what we know about Earth history.

In contrast with the molecular work (Simpson et al., 2009), our results provide evidence for the monophyly of most of the *Perezia* evolutionary lines proposed by Vuilleumier (1970). The only exception is the *P. magellanica* species group, which consists of two grades and one independent species, suggesting that it should not be considered a phylogenetic unit. Both grades include some monophyletic groups, such as those constituted by *P. delicata–P. lactucoides–P. magellanica*, *P. capito–P. megalantha*, and *P. pedicularidifolia–P. poeppigii*. The *P. magellanica* species group does not seem to have any morphological characters that allow a delimitation of this unit; instead, members share the lack of certain features that distinguish the other groups. The main characteristic of this group is its geographical distribution in the southern Andes. Simpson (1973) described this group as an exemplar case of speciation caused by the isolation provided by Pleistocene glaciations in contrast to the *P. prenanthoides* group, which followed phyletic evolution in old and stable habitats. Regarding the other species groups, only two have bootstrap values above 50%: the *P. prenanthoides* species group at 70%, and the *P. recurvata* species group at 65%. Other groups did not receive significant support, although they can be clearly recognized based on morphology. This is the case with the species of the Brazilian-centered *P. multiflora* species group with their eryngioid aspect, the northern Andean-centered *P. pungens* species group with their fruits scarcely pubescent, and the *P. pinnatifida* species groups with their short peduncles and amber-colored fruit pubescence. Molecular analyses (Simpson et al., 2009) support only the *P. multiflora* species group and the *P. recurvata* species group. The characters that support the species groups in our analysis (Figure 4) are, in general, different from those established by Vuilleumier (1970), who defined them on the basis of morphology, cytology, palynology, and chemistry but without a phylogenetic context (Table 1). This agreement between Vuilleumier's (1970) and our results enhance the support of the species groups within *Perezia*. For example, Vuilleumier (1970) distinguished the *P. multiflora* group by the hemispherical involucre with a reduced number of involucral bracts and the silky, copper-colored fruit hairs. In our tree this group is supported by the corymbose inflorescence and the absence of glandular hairs in the fruits. The only coincidence in the characters between Vuilleumier's (1970) work and the results presented here is the type of inflorescence. In the *P. prenanthoides* species group as defined by Vuilleumier (1970), the inflorescence is a showy, open cluster of numerous heads. Here it is characterized as having a paniculate inflorescence. However, the remaining supporting characters in Vuilleumier's treatment (1970; i.e., large, foliaceous herbs; broad, soft, basal leaves; fruits densely covered by amber-colored hairs) are different from those used in our analysis (i.e., glabrous receptacle, scarce pubescence in fruits). These differences are brought about by our distinction between synapomorphies and plesiomorphies in the phylogenetic analysis.

Another remarkable coincidence between our results and those of Vuilleumier (1970) is the position of *P. pilifera*, which appears not related to any species group. Vuilleumier (1970) considered that the distinctive morphology of this species (e.g., different type of pubescence found on the cypsela) made it difficult to determine its relationships. In the phylogeny (Figure 4), *P. pilifera* is the sister of the rest of the species of *Perezia*. Although *P. pilifera* is morphologically close to the *P. recurvata* species group, both having linear leaves that are exclusive to these taxa, the former species has several autapomorphies: leaves with marginal spines, short inflorescences, and long, nonglandular hairs in fruits.

Although viewed as distinctive, Vuilleumier (1970) did not suggest that *P. pilifera* was an early diverging lineage in the genus, as occurs in our analysis, but instead suggested that the northern Andean-centered *P. pungens* group provided the stocks that gave rise to other evolutionary lines. The ancestor was thus hypothesized as a relatively large, leafy, perennial herb with a rhizomatous rootstock, a loose panicle of heads, and a likely chromosome number of $2n = 8$. With regard to the possible early diverging members of the genus, the topology of the trees in the molecular analysis of *Perezia* by Simpson et al. (2009) differs significantly with Vuilleumier's (1970) hypothesis and with our results. The chloroplast DNA, the nuclear ITS, and the combined trees show the Brazilian-centered *P. multiflora* species group as sister of the remaining species of the genus or in a basal polytomy. Simpson et al. (2009) supported the position of *P. multiflora* at the base of the tree by the low chromosome number of this and the other species of the *P. multiflora* group ($2n = 8, 16$; mistakenly registered as $n = 16$), which is similar to the chromosome number of the outgroup *Panphalea* with $n = 8$. The phylogeny presented here shows that the *P. multiflora* group is more highly nested in the tree and that *P. pilifera* is sister group to the remaining species. In addition, the chromosome counts of *P. pilifera* are the same as those of the *P. multiflora* group: $2n =$

16 (Crisci, 1974; Moore, 1981; Nordenstam, 1982). This could be interpreted as the repeated acquisition of polyploidy ($2n$ = 24 in most species groups). The subsequent loss of polyploidy in the *P. multiflora* group, with $2n$ = 16 (in *P. multiflora*; Diers, 1961; Vuilleumier, 1970; and registers of n = 8, Huynh, 1965; Dillon, 1982; Spooner et al., 1995; Carr et al., 1999) and n = 4 (in *P. squarrosa* subsp. *cubataensis*; Coleman, 1968), may have occurred by disploidy decreases (the change in the chromosomal base number through a rearrangement of chromatin and loss of centromeres without necessarily changing the amount of chromatin in the karyotype), which is common in Asteraceae (Semple and Watanabe, 2009).

Historical Biogeography of *Perezia*

Previous hypotheses about the probable place of origin of the ancestor of *Perezia* fall into two categories: (1) warm open forests of extratropical South America, such as the montane habitats of the central Andes (Vuilleumier, 1970), with elements that further colonized the southern areas (Simpson, 1973), or (2) eastern subtropical South America based on the basal position of the Brazilian-centered *Perezia multiflora* species group (Simpson et al., 2009). Our results are in disagreement with both hypotheses. The ancestral areas and dispersal-vicariance approaches applied here are in agreement and strongly support the southern Andes as the probable ancestral area for *Perezia*; this is also the area that holds the majority of species in the genus. This southern location is also congruent with the fossil record of the early diverging lineages of the family that includes *Perezia*. Several fossils of early branching lineages of Asteraceae have been found from the Paleogene in southwestern Argentina, the earliest from the middle Eocene (~50 MYA) (Barreda et al., 2010, 2012). The first and only records to date of fossil pollen of Nassauvieae are from the early Miocene (23–20 MYA) found in Argentina along eastern coast of Patagonia. By the late Miocene (11–9 MYA), fossil findings show an abundance of Nassauvieae taxa representing great morphological diversity (Katinas et al., 2007). This represents strong evidence supporting the southern origin hypothesis of the genus.

Because the Andean orogeny influenced the continental biotas, it is important to note that it was not a continuous process. Orogeny in the Andean Cordillera was intermittent and episodic through Cenozoic times (Ramos, 1989), with uplift events in the southern Andes (Incaic and Quechua phases) from the Paleocene to the late Miocene (65–5 MYA), intercalated with a relatively quiescent period from the late Eocene to the late Oligocene (37–28 MYA) (Taylor, 1991). The late Oligocene–early Miocene interval was a transition time in the vegetation structure, from one dominated by tropical forests to one in which shrubby and herbaceous elements dominated. At this time members of the Asteraceae became increasingly important (Barreda and Palazzesi, 2007). This is the time of the first fossil records of Nassauvieae. During the middle and late Miocene three successive Atlantic marine transgressions, known as the Paranean Sea, were recorded in southern South America. Accordingly, during this time an open seaway, spreading over virtually all of eastern Argentina, western Uruguay, southern Paraguay, and southeastern Bolivia, separated terrestrial environments (Figure 7). This barrier surely affected the organism's distribution, and it could be represented in our DIVA results as some of the vicariant events separating, for example, the southern and northern Andes from the Puna, Paranense, Chacoan, and Espinal areas. During the late Miocene–early Pliocene (11–3 MYA) this widespread surface flooding was succeeded by flat regions or plains reaching central and northern Argentina, Uruguay, and along the eastern slopes of the rising Andes north of Peru. The beginning of these new habitats is correlated with the Quechua phase of the Andean diastrophism when Patagonia and the Andean Cordillera were successively uplifted (14–10 MYA), progressively forming a major barrier to moisture-laden South Pacific winds. The resulting rain-shadow effect on the eastern Patagonian landscapes led to the first stages of the differentiation of the present biogeographic regions of southern South America, that is, the Subantarctic and Patagonia (Ortiz-Jaureguizar and Cladera, 2006). This differentiation is probably the time period when the ancestors of the extant species of *Perezia* adapted to the southern temperate forests and steppe environments, as shown by the high diversity in the Patagonian fossil pollen records of Nassauvieae during the late Miocene.

By the Pliocene (5.3–1.8 MYA), a new Andean diastrophic phase resulted in the elevation of the central cordillera of Argentina and Chile and the eastern orographic systems (e.g., Puna). During this epoch, the final uplift of the Puna had a dramatic effect on the biota, creating the very arid and extreme climatic conditions that are prevalent today. Our results are congruent with this sequence of events and support the hypothesis that the area of origin for *Perezia* is southern and not in younger northern habitats.

Through the Pleistocene, glaciations were the main climatic factor that affected the Andes and, indeed, most of South America. The cyclical advance and retreat of glaciers produced a marked and concurrent expansion and retraction of arid (savanna and steppes) and humid (tropical and subtropical) biomes. During cold–dry glacial periods there was contraction of the areas occupied by subtropical and tropical biomes and expansion and interconnection of open habitats. Conversely, during warm–wet interglacial periods, open areas frequently retreated to high elevations and rainforest ecosystems expanded. These contraction–expansion periods may be the cause of the numerous dispersal events from the highlands of the southern Andes to the adjacent lower Subantarctic area, as showed by DIVA, possibly because the species did not completely adapt to the freezing temperatures. It is interesting to note that the biogeographical approach DIVA minimizes dispersal; despite this fact the results show many dispersal events in the biogeographic history of *Perezia*.

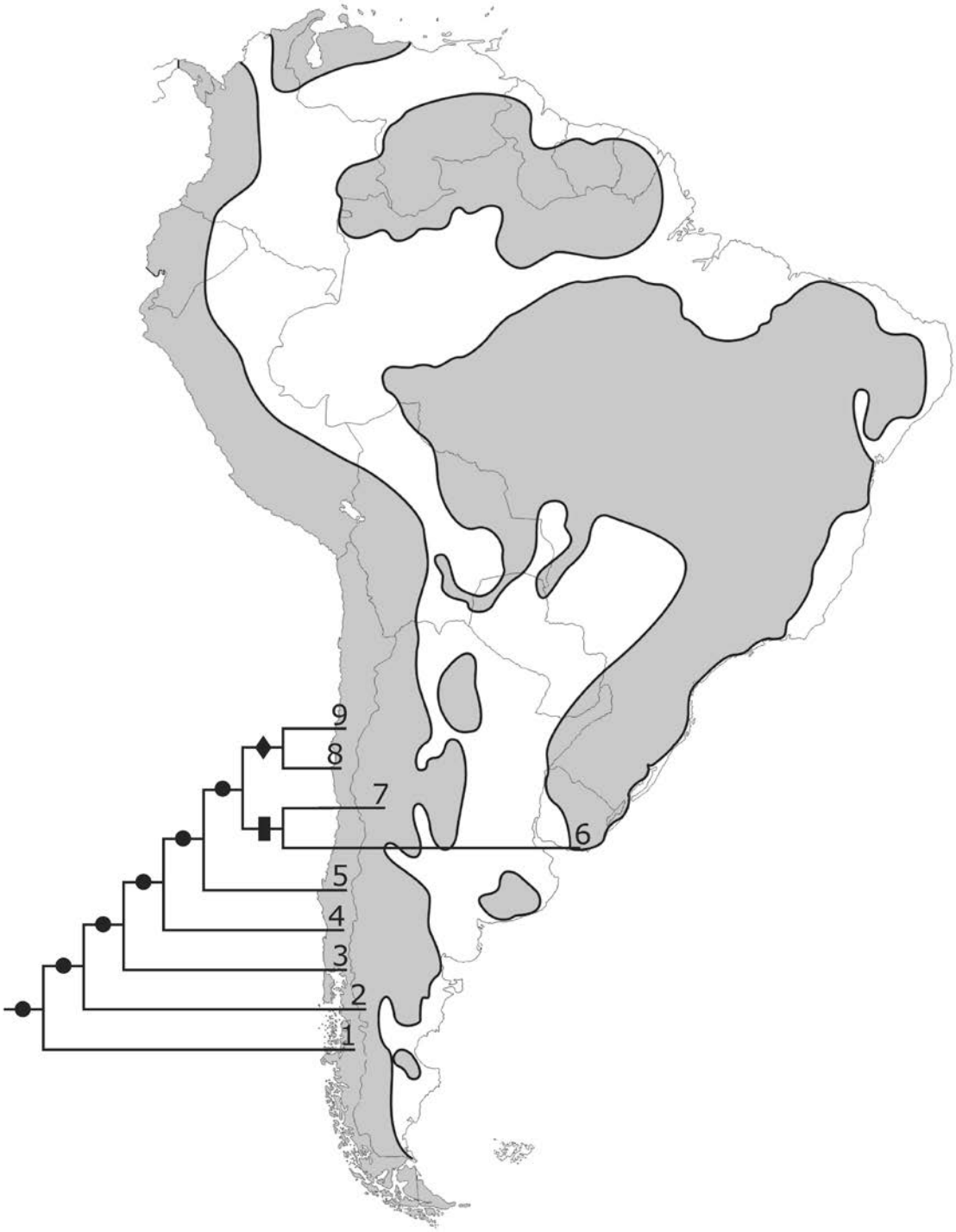

FIGURE 7. Simplified tree of *Perezia* showing the species groups of *Perezia* with their ancestral distributions according to DIVA superimposed onto a map of South America that shows the areas affected by the middle Miocene–late Miocene marine transgression (modified from Ortiz-Jaureguizar and Cladera, 2006). Species groups are (1) *P. pilifera*; (2) *P. recurvata* species group; (3) *P. magellanica* species group; (4) *P. prenanthoides* species group; (5) *P. magellanica* species group; (6) *P. multiflora* species group; (7) *P. pungens* species group; (8) *P. magellanica* species group; and (9) *P. coerulescens* (=*P. pinnatifida*) species group. Symbols represent the areas used in this analysis: Southern Andean (circle); Northern and Southern Andean, Puna, Paranense, Chacoan, and Espinal (rectangle); and Northern and Southern Andean (diamond).

Integration of Morphology, Ecology, Geology, and the Fossil Evidence

The current distribution of *Perezia* and many other plants and animals in the southern Andes is limited by the low temperatures and the winter snow (Cabrera, 1971). Thus, survival in freezing temperatures is key to the southern species. Sierra-Almeida and Cavieres (2010) studied several southern Andes plant species, including *P. carthamoides*, to analyze their freezing resistance. They found that these plants have a high ability to resist freezing temperatures during the growing season. A high proportion of the species, including *P. carthamoides*, lose part or all of their above-ground tissues before the onset of the less favorable winter conditions. This, suggests that they invest resources to protect the growth located below ground, accumulate reserves in below-ground tissues (a rhizome in the case of *Perezia*), or both instead of cold hardening the above-ground organs. In the past (late Oligocene–early Miocene) the southwestern area, hypothesized here as the ancestral area of *Perezia*, was characterized by the dominance of austral elements, indicating a humid, temperate forest (e.g., Nothofagaceae, Araucariaceae, Berberidaceae, and Winteraceae), probably with freezing temperatures in the higher elevations. Adaptation and speciation, and dispersal of early lineages of *Perezia* to adjacent areas, probably occurred under these harsh conditions.

It was suggested for *Perezia* (Simpson, 1973) and other taxa that many species were generated by splitting during the Pliocene and Pleistocene glaciations. The repetitious occurrence of the glacial cycles allowed opportunities for range expansion and subsequent isolation and speciation. This speciation model, linked to the Quaternary glaciations, has changed over the years in regards to the idea that the Tertiary and Quaternary events had different effects in the biotas. During the Tertiary there were long periods of uniform environmental conditions, sporadically interrupted by geologically short but highly disruptive periods of change. These changes drastically modified the taxonomic and ecological composition of the biotas by means of cladogenesis, extinction, and migration (Ortiz-Jaureguizar and Cladera, 2006). The relationship between Andean orogeny and speciation has been supported by many workers through the analysis of different taxa (e.g., Gentry 1982; Hughes and Eastwood, 2006; Pirie et al. 2006). In contrast, the climatic changes during the Quaternary had larger amplitude and frequency and were responsible for chorological changes, expanding or contracting the distribution areas of taxa, communities, and biomes. Accordingly, we postulate that the main speciation events in *Perezia* took place in the Tertiary, probably during the late Oligocene–late Miocene time span (23–9 MYA), because fossil pollen of Nassauvieae was recovered from the Miocene. The Quaternary was probably a period of distributional changes in species of *Perezia*, mainly dispersal from the Southern Andes to the lower areas of the Subantarctic forest and from the Northern Andes down to the Puna, as suggested by DIVA. Marine introgressions in South America are hypothesized here as one of the main events responsible for the few vicariant events affecting the distribution of species of *Perezia*.

Our results may have implications for better understanding the evolution and historical biogeography of other ancient lineages of Asteraceae, which are undoubtedly linked to the Andes, and to other lineages because, as mentioned in the introduction, the distribution of *Perezia* is part of a generalized distributional pattern shared by many other taxa.

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Appendix A: Characters and Character States

Below is the numbered list of characters and their numbered character states used in the phylogenetic analysis of *Perezia* (Asteraceae).

1. Life cycle: perennial (0); annual (1).
2. Underground organs: rhizome (0); exclusively roots (1); xylopodium (2).
3. Stem branching: at the base (0); at the apex (1); not branched or scape (2).
4. Leaves disposition: spread along the stem (0); in a basal rosette (1).
5. Upper leaves: numerous (0); few (1–3) to absent (1).
6. Blade shape of basal leaves: less than three times longer than wide (e.g., elliptic, lanceolate, obovate) (0); as long as wide (orbicular) (1); at least four times longer than wide (linear) (2).
7. Blade apex of basal leaves: acute (0); obtuse (1).
8. Basal leaves venation: pinnate (0); palmate (1).
9. Basal leaves marginal cilia: absent (0); present (1).
10. Leaves with marginal spines: absent (0); present (1).
11. Basal leaves transection: planate (0); revolute or plicate (1).
12. Basal leaves base: sessile (0); petiolate (1); petiole winged (pseudopetiole) (2).
13. Upper leaves shape: wide (0); linear (1).
14. Upper leaves base: sessile (0); clasping (1).
15. Type of inflorescence: clustered (0); lax (1).
16. Height of inflorescence: surpassing the basal leaves (0); shorter than the basal leaves (1).
17. Capitula disposition: glomerulose (0); paniculate (1); corymbose (2); solitary or 2–3 capitula (3).
18. Number of capitula: 30–50 (0); 1–20 (1).
19. Involucre shape: cylindrical (0); campanulate (1); spherical (2).
20. Involucre length: 5–9 mm (0); 10–20 mm (1); 21–45 mm (2).
21. Receptacle surface: glabrous (0); pubescent (1).
22. Number of series of involucral bracts: 2 (0); 1 (1); 3–5 (2).
23. Scarious margin of involucral bracts: absent (0); present (1).
24. Shape of outer involucral bracts: linear (0); lanceolate to oblong (1); cordate to orbicular (2).

25. Margin of outer involucral bracts: entire (0); ciliate (1); spiny (2); pectinate (3).
26. Length of outer involucral bracts: shorter than the inner bracts (0); as long as or longer than the inner bracts (1).
27. Number of florets per capitulum: 5 (0); more than 5 (1).
28. Corolla color: white (0); colored (1); white and colored (2).
29. Pollen grains polar elevations: absent (0); present (1).
30. Pollen grains tectum: lacking ramifications (0); with ramifications (1).
31. Fruit apex: truncate (0); constricted or rostrate (1).
32. Fruit pubescence: absent (0); scarce (1); densely pubescent (2).
33. Type of fruit hairs: glandular hairs and nonglandular (0); only glandular hairs (1); only nonglandular hairs (2).
34. Nonglandular hairs shape: cylindrical or elliptical (0); very long and filiform (1).
35. Nonglandular hairs color: white to golden (0); reddish (1).
36. Type of pappus bristles: paleaceous (0); capillary (1); absent (2).
37. Color of pappus bristles: white (0); colored (1); white and colored (2).

Appendix B: Data Matrix

TABLE B1. The data matrix used in the phylogenetic analysis of *Perezia*. Character numbers and character states are defined in Appendix A. A question mark (?) indicates inapplicable or missing data. Variable characters in some taxa were treated as polymorphic for the analysis.

	Character state by character number																
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Nassauvia magellanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panphalea commersonii	0	2	1	1	1	1	1	1	0	0	0	1	1	0	1	0	2
Panphalea heterophylla	1	1	1	1	1	1	01	1	0	0	0	1	0	1	1	0	2
Panphalea smithii	0	0	1	1	1	2	0	0	0	0	1	1	1	0	1	0	3
Perezia atacamensis	0	0	2	1	01	0	0	0	1	1	0	2	0	1	01	0	13
Perezia bellidifolia	0	0	2	1	1	0	1	0	0	0	0	2	1	0	1	0	3
Perezia burkartii	0	0	2	1	1	0	01	0	1	0	0	2	1	0	1	0	3
Perezia calophylla	0	0	1	1	1	0	0	0	0	0	0	2	0	1	1	0	3
Perezia capito	0	0	2	1	1	0	1	0	0	0	0	2	1	1	1	0	3
Perezia carthamoides	0	0	1	1	01	0	0	0	1	1	0	2	0	1	1	0	3
Perezia catharinensis	0	0	1	1	0	0	01	0	0	1	0	0	0	1	1	0	12
Perezia ciliosa	0	0	2	1	1	0	0	0	1	0	0	2	1	1	1	0	3
Perezia delicata	0	0	2	1	1	0	1	0	0	0	0	02	1	0	1	0	3
Perezia dentata	0	0	2	1	0	0	0	0	1	0	0	02	1	1	1	0	3
Perezia eryngioides	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	2
Perezia fonkii	0	0	2	1	1	0	1	0	0	0	0	2	1	1	1	0	3
Perezia kingii	0	1	1	1	0	0	1	0	0	1	0	2	0	1	01	0	2
Perezia lactucoides	0	0	2	1	0	0	0	0	0	0	0	1	1	1	1	0	3
Perezia linearis	0	1	2	1	1	2	0	0	1	0	1	0	1	0	1	0	3
Perezia lyrata	0	0	2	1	1	0	1	0	0	0	0	2	1	0	1	0	3
Perezia magellanica	0	0	2	1	1	0	1	0	0	0	0	2	1	1	?	0	3
Perezia megalantha	0	0	2	1	1	0	1	0	0	0	0	0	0	1	1	0	3
Perezia multiflora	0	0	1	1	0	0	01	0	0	1	0	2	0	1	0	0	12
Perezia nutans	0	0	1	1	1	0	1	0	0	1	0	2	0	1	1	0	1
Perezia pedicularidifolia	0	0	2	1	1	0	0	0	0	0	0	2	0	1	1	0	3
Perezia pilifera	0	0	2	1	1	2	0	0	0	1	0	0	1	0	1	1	3
Perezia pinnatifida	0	0	2	1	1	0	1	0	1	0	0	2	1	1	1	1	3
Perezia poeppigii	0	0	1	1	1	0	01	0	1	0	0	0	1	1	1	0	3
Perezia prenanthoides	0	0	1	1	1	0	01	0	0	0	0	2	0	1	1	0	1
Perezia pungens	0	0	1	1	01	0	01	0	01	01	0	12	01	1	01	0	23
Perezia recurvata	0	0	2	1	01	2	0	0	0	01	1	0	1	0	1	0	3
Perezia spathulata	0	0	1	1	1	0	1	0	0	0	0	2	0	1	1	0	23
Perezia squarrosa	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	2
Perezia volcanensis	0	0	1	1	0	0	01	0	1	1	0	2	0	1	1	0	3

TABLE B1. (*Extended*)

Character state by character number (*Continued*)

18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0
1	2	0	0	0	1	1	0	0	1	0	0	1	0	1	2	0	0	2	?
1	2	0	0	1	1	1	0	?	1	0	0	1	0	1	2	0	0	2	?
1	2	0	0	0	1	1	0	0	1	0	0	1	0	1	2	0	0	2	?
1	1	2	1	2	1	1	0	0	1	2	1	1	0	2	0	0	0	1	1
1	1	1	1	2	1	1	0	0	1	2	1	1	0	2	0	0	0	1	2
1	1	2	0	2	1	2	0	0	1	1	1	1	0	1	2	0	0	1	1
1	1	1	1	2	1	1	0	0	1	1	1	1	0	2	0	1	0	1	2
1	12	12	1	2	1	2	0	0	1	2	1	1	0	1	0	0	1	1	1
1	2	12	0	2	1	1	2	0	1	2	1	1	1	1	0	1	1	1	2
0	1	0	1	02	1	1	1	0	1	0	1	1	0	2	2	1	1	1	1
1	1	1	1	2	1	1	2	0	1	1	1	1	0	1	1	?	?	1	1
1	12	1	1	2	0	1	0	0	1	1	1	1	0	1	0	0	0	1	1
1	1	1	1	2	1	1	0	0	1	1	1	1	0	2	0	1	0	1	1
0	1	1	1	02	1	1	2	0	1	0	1	1	0	2	2	1	1	1	1
1	1	12	1	2	1	1	0	0	1	1	1	1	0	2	0	1	1	1	1
01	1	0	1	0	1	1	2	1	1	2	1	1	0	2	2	1	1	1	0
1	1	1	1	2	0	1	1	0	1	2	1	1	0	2	0	0	0	1	1
1	1	12	1	2	1	1	1	0	1	2	1	1	0	1	0	0	1	1	2
1	12	1	1	2	1	1	0	0	1	2	1	1	0	2	0	0	1	1	1
1	1	01	1	2	0	1	1	0	1	2	1	1	0	2	0	0	0	1	2
1	2	12	01	2	1	2	1	01	1	2	1	1	0	1	0	0	1	1	1
01	1	1	1	2	1	1	2	0	1	2	1	1	0	2	2	0	1	1	1
1	01	1	0	2	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1
1	1	1	1	2	1	1	3	01	1	1	1	1	1	1	0	0	1	1	1
1	0	1	0	02	1	1	2	0	1	2	1	1	0	2	2	1	0	1	2
1	01	12	0	2	1	1	0	0	1	2	1	1	01	1	0	0	0	1	1
1	01	12	1	2	1	1	2	0	1	1	1	1	1	2	0	0	1	1	1
1	1	01	0	2	1	1	0	0	1	1	1	1	0	1	0	0	1	1	1
1	12	12	1	2	1	1	02	0	1	2	1	1	0	1	0	0	0	1	1
1	1	1	1	2	1	1	2	0	1	2	1	1	0	1	0	0	0	1	1
1	1	12	1	2	1	1	02	0	1	1	1	1	0	2	0	0	1	1	1
1	2	0	1	02	0	1	0	0	1	2	1	1	0	2	0	1	1	1	1
1	2	1	?	2	1	2	0	0	1	?	1	1	0	1	?	?	?	1	1

Appendix C: Areas of Endemism

Described below are the areas of endemism used in the biogeographic analysis of the genus *Perezia (*Asteraceae) defined by Cabrera and Willink (1980), with the Andes delimited according to Sick (1969). The areas are listed in order from the temperate to the subtropical ones.

Subantarctic Province (A): The Subantarctic province consists of temperate forests that range up to 2,000 m in altitude and covers an area from 35°S latitude southward to Cape Horn in Chile, extending along the western side of the southern Andes and the Coastal Cordillera, including the Juan Fernandez Islands. In Argentina this province extends along the eastern side of the southern Andes from 38°S latitude to Islas Malvinas (Falkland Islands) and South Georgia Island. The climate is cold temperate, with abundant snow in the winter and frosts during almost the entire year. The predominant vegetation is the temperate mixed deciduous and evergreen forest, represented mainly by the genus *Nothofagus* (Nothofagaceae). The parasitic plant family Misodendraceae is endemic to this area—endemic genera of this family include *Austrocedrus*, *Fitzroya*, and *Pilgerodendron* (Cupressaceae) and *Macrachaenium* (Asteraceae). And several other endemic plant and animal species are present, such as *Dromiciops australis* and *Rhyncholestes raphanurus* (Marsupialia); *Felis guigna* (Carnivora); *Pudu puda* (Artiodactyla); and *Irenomys australis*, *Akodon herschkovitzi* (Rodentia).

Northern Andean (B): This area belongs to the Altoandean highlands with its typical dry and cold high-mountain climate. The main forms of precipitations in the Altoandean highlands are snow and hail, especially in the winter. The predominant vegetation type is the grassy and chamaephyte steppes, with plant adaptations to extreme climatic conditions. The Northern Andean section consists of the Andean highlands at 3,000–4,500 m, reaching the permanent snow and extending from 27°–28°S latitude to the northern end of the Andes. This section with subtropical climate contrasts with the adjoining temperate southern section. The symmetry of the precipitation distribution, with heavy rainfalls on both sides of the northern range, gives way at approximately 4°S latitude to a dry west side, due to the influence of the Pacific anticyclones, and a humid eastern side, within the range of easterly air-streams (Sick, 1969). Endemic taxa include, for example, *Hyppocamelus antisensis* (Artiodactyla); *Auliscomys boliviensis*, *Chinchilla brevicaudata*, and *Phyllotis magister* (Rodentia); *Felis jacobita* (Carnivora); *Lapageria*

rosea (Philesiaceae); *Aciachne flagellifera* and *A. pulvinata* (Poaceae); *Aschersoniodoxa chimborazensis* (Brassicaceae); *Astragalus fabrisii* (Fabaceae); and *Leucheria pteropogon* and *Mutisia grandiflora* (Asteraceae).

Southern Andean (C): This unit also belongs to the Altoandean highlands but ranges from 27°–28°S latitude to the southern end of the Andes, and altitude decreases from 3,000 m to 500 m in the southern Argentinian province of Tierra del Fuego (at 54°S). The border between the Northern and the Southern Andean areas is a complex region that coincides with the boundaries among the Frontal Cordillera, the Cuyo Precordillera, the Principal Cordillera (Ramos et al., 2002), and the southern end of the Puna area. There is a transition from subtropical to temperate climate, with temperatures decreasing toward the south. The eastern and western slopes of the vast mountain range overall also differ in the amount of precipitation received but in a manner opposite to that in the northern Andes. The influence of the westerly winds can be traced, with cyclonic winter rain in association with summer dryness. Endemic taxa include, for example, *Hyppocamelus bisulcus* (Artiodactyla), *Astragalus bellus* (Fabaceae), and *Nassauvia pinnigera*, *N. argentea*, *Leucheria eriocephala*, *L. nutans*, and *Mutisia linearifolia* (Asteraceae).

Patagonia (D): This area comprises the extra-Andean semidesert area of Argentina and Chile from 37°S (Argentina) and 43°S (Chile) to Cape Horn at 56°S latitude. It includes the Pacific and Atlantic lowlands and coasts, the southern archipelagos, and the valleys, tablelands, and high plains extending between the Andes and the Atlantic and Pacific Oceans. This area is included in the circulation zone of the southern westerlies, reaching strong intensity in southern areas. In terms of vegetation it is a semiarid shrubby steppe with a predominance of cushion plant adaptation. There are many endemic genera, *Ameghinoa, Pantacantha, Benthamiella,* and *Lepidophyllum* (Asteraceae), and endemic species, such as *Nassauvia axilaris, N. glomerulosa, and Chuquiraga avellanedae* (Asteraceae); *Retanilla patagonica* (Rhamnaceae); *Festuca pallescens* (Poaceae); and *Akodon iniscatus*, *Notiomys edwardisii*, *Ctenomys colburni*, *C. haigi*, and *C. sericeus* (Rodentia).

Puna (E): This area comprises the highland plateaus located in Peru, western Bolivia, northwestern Argentina, and northern Chile, basically between 15° and 30° S latitude and higher than 3,000 m altitude. It stretches for 1,800 km along the Central Andes and attains a width of 350–400 km. Climate is cold and dry, with summer rains. It is a semiarid shrubby steppe, with some areas of grassy steppe and open forests of *Polylepis tomentella* (Rosaceae). Endemic taxa include, for example, *Nardophyllum armatum* and *Parastrephia lepidophylla* (Asteraceae), *Hoffmansegia minor* (Fabaceae), *Solanum acaule* (Solanaceae), *Chaetophractus nationi* (Edentata), *Vicugna vicugna* (Artiodactyla), and *Auliscomys sublimis* and *Phyllotis osgoodi* (Rodentia).

Paranense (F): The Paranense area is a subtropical forest that ranges across southern Brazil (west of Serra do Mar), eastern Paraguay, and northeastern Argentina. The climate is warm and humid with precipitation during the entire year. There are different communities, such as forests of *Araucaria angustifolia* (Araucariaceae) and *Euterpe edulis* (Arecaceae) and grassy savannas. Endemic taxa include, for example, *Nectandra lanceolata* and *Ocotea lancifolia* (Lauraceae); *Mikania summinima* and *Viguiera misioensis* (Asteraceae); *Dyckia mitis* and *D. niederleinii* (Bromeliaceae), *Monodelphis scalops* (Marsupialia); and *Thomasomys dorsalis*, *T. pictipes*, *Oryzomys buccinatus*, *Akodon nigrita*, *A. serrensis*, *Euryzygomatomys spinosus*, and *Kannabateomys amblyonyx* (Rodentia).

Chacoan (G): The Chacoan area extends over southern and western Bolivia, western Paraguay, and north-central Argentina. Its vegetation is a sclerophyllous, deciduous forest with tickets of savannas, grasslands, and shrubby steppes. There are forests of species of *Schinopsis* (Anacardiaceae), *Prosopis* (Fabaceae), and *Aspidosperma quebracho-blanco* (Apocynaceae). The climate is warm and dry, with more precipitation in the east. Endemic taxa include, for example, *Alternanthera collina* (Amaranthaceae), *Aristolochia schulzii* (Asclepiadaceae), *Grindelia chacoensis* and *Hyaloseris andrade-limae* (Asteraceae), *Opuntia colubrina* (Cactaceae), *Marmosa formosa* (Marsupialia), *Vampyrops dorsalis* (Chiroptera), and *Oryzomys chacoensis*, *Pseudoryzomys wavrini*, *Andalgalomys pearsoni*, *Bibimys chacoensis*, *Ctenomys argentinus*, and *C. bonettoi* (Rodentia).

Pampean (H): The Pampean area is a grassy steppe that extends between ~30° and 38°S latitude in southeastern Brazil, Uruguay, and east-central Argentina. This flat area is interrupted by the Tandilia and Ventania ranges (500 m and 1,000 m high, respectively). Precipitation decreases from northeast to southwest and occurs throughout the year, with mild summer water deficits in the east and more severe winter dry periods in the west. Endemic taxa include, for example, *Baccharis rufescens* and *Hieracium burkartii* (Asteraceae), *Rorippa ventanensis* (Brassicaceae), *Adesmia pampeana* (Fabaceae), *Bromus bonariensis* (Poaceae), *Eryngium cabrerae* (Apiaceae), and *Thomasomys oenax*, *Oryzomys delticola*, *Akodon kempi*, *Holochilus magnus*, *Ctenomys australis*, *C. minutus*, *C. pearsoni*, *C. porteousi*, and *C. talarum* (Rodentia).

Espinal (I): The Espinal area is a belt-shaped system of open xerophytic forests, with parklands, palm groves, bushy steppes, and savannas that surround the Pampean biogeographic province. The climate is warm and humid in the north and temperate semiarid in the west and south sections. The tree overstory has varying densities dominated by *Prosopis* and *Acacia* species (Fabaceae). Tree species richness declines southward, and plant species found in this area are generally found in other surrounding biogeographic provinces. Endemic taxa include, for example, *Grindelia globularifolia* and *Hieracium caespitosa* (Asteraceae); *Adesmia lihuelensis* and *Prosopis caldenia* (Fabaceae); *Cereus argentinense* and *Gymnocalycium mesopotamicum* (Cactaceae); *Oxypetalum fontellae* (Asclepiadaceae); *Croton laureltyanus* (Euphorbiaceae); *Ctenomys azarae* and *C. perrensis* (Rodentia); and *Sturnella defilippii* (Aves).

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