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RESEARCH LETTER

Distributional patterns of species of Rhytirrhinini (Coleoptera: Curculionidae) and the historical relationships of the Andean provinces

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Abstract. Based on distributional data of species of twenty-one South American genera of Rhytirrhinini (Coleoptera: Curculionidae), historical relationships of the five provinces herein assigned to the Andean subregion, namely, Paramo, Patagonian, Puna, Central Chilean, and Subantarctic, were investigated through a combined biogeographic approach. A track compatibility analysis led to recognition of two generalized tracks, which share their first portion (Subantarctic and Central Chilean provinces), which is here identified as a node. From the Central Chilean province, one track continues to the north (Puna and Paramo provinces), and the other to the east (Patagonian province). A parsimony analysis of endemicity (PAE) indicates that the cladistic sequence of area fragmentation is: (Paramo (Patagonia (Puna (Central Chilean, Subantarctic)))). It is proposed that these results reflect the progressive depauperation of the Austral biota, and show that the Subantarctic and Central Chilean provinces are its richest (less depauperate) remnants, and that the other provinces have become successively isolated biotic portions.

Key words. Andean subregion, panbiogeography, parsimony analysis of endemicity, Curculionidae, Rhytirrhinini.

INTRODUCTION

Distributional patterns exhibited by representatives of the biota of southern South America led several biogeographers to its recognition as a distinct subregion (Jeannel, 1942; Monrós, 1958; Croizat, 1960; Skottsberg, 1960; Kuschel, 1964, 1969; Fittkau, 1969; Takhtajan, 1986; Cabrera & Willink, 1973; Humphries, 1981; Parenti, 1981; Humphries & Parenti, 1986). Boundaries of this subregion, however, differ according to the author. According to Kuschel (1969) and Humphries & Parenti (1986), southern South America is the area below 30 south latitude that extends also to the Andean highlands north of this latitude. It has been postulated that South America has a hybrid biotic origin, with taxa from its southern subregion most closely related to taxa from other southern areas, e.g. Australia, New Zealand, New Guinea, and New Caledonia, rather than to Neotropical taxa (Kuschel, 1964; Humphries, 1981; Humphries & Parenti, 1986). Furthermore, Crisci *et al.* (1991) suggested that southern South America may have a composite origin in itself.

There are different biogeographic schemes for South America (Ringuelet, 1961; Kuschel, 1969; Cabrera & Willink, 1973; Müller, 1973; Rivas-Martínez & Tovar, 1983). It is here considered a basic division into two subregions, Andean and Neotropical. The former basically comprises the Andean range from northern Venezuela to southern Chile, also extending to the Patagonian steppes in southern Argentina (Fig. 1), whereas the latter comprises the rest of the continent, e.g. the Chacoan and Amazonian dominions of Cabrera & Willink (1973).

Among weevils (Coleoptera: Curculionidae), three groups are characteristic of the Andean subregion: the tribe Rhytirrhinini (Somatodinae), and the *Cylydrorhinus* and *Strangaliodes* generic groups of the Entimini (Entiminae). The tribe Rhytirrhinini, widely distributed in southern cold-temperate regions of South America, Australia, and New Zealand, has twenty-two genera in the Andean subregion. These genera are well known and recent revisions exist for almost all of them (Morrone, 1990, 1992a-c, 1993a-f, 1994a-e, 1995a,b; Morrone & Loiácono, 1992; Marvaldi, 1994). The majority of the species of Rhytirrhinini are endemic to the Andean subregion (only some species extend their ranges to the Chacoan dominion).

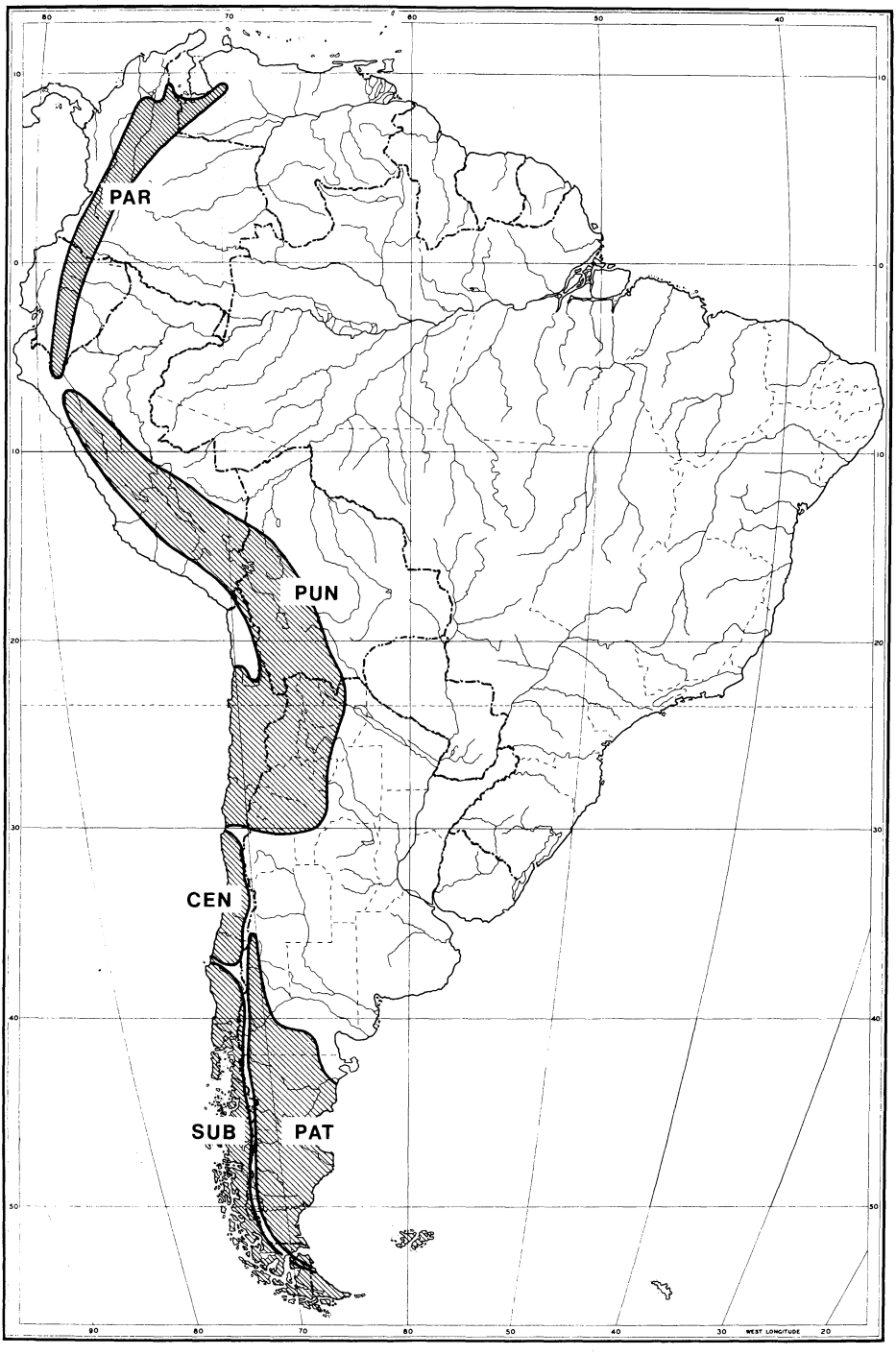

Fig. 1. Map of South America, showing the provinces of the Andean subregion. CEN, Central Chilean; PAR, Paramo; PAT, Patagonian; PUN, Puna; SUB, Subantarctic.

Table 1. Genera of Rhytirrhinini from the Andean subregion, with number of endemic and nonendemic species in each province.

Genera	SUB E	SUB N	PAR E	PAR N	PUN E	PUN N	CEN E	CEN N	PAT E	PAT N	References
Rhigopsidius	—	—	—	—	—	2	—	—	—	—	Morrone & Loiácono (1992)
Philippius	1	—	—	—	—	—	—	—	—	—	Morrone (1990)
Trachodema	—	1	—	—	—	—	—	1	—	—	Morrone (1992a)
Listroderes	—	8	—	—	3	4	11	8	3	1	Morrone (1993a,b,e,f, 1995b)
Germainiellus	11	1	—	—	—	—	—	1	—	—	Morrone (1993c, 1994b)
Acrorius	—	—	5	—	2	—	—	—	—	—	Morrone (1994a)
Hyperoides	—	1	—	—	—	—	2	1	1	—	Morrone (1993d)
Nacodius	—	—	2	—	2	—	—	—	—	—	Morrone (1994b)
Macrostyphlus	—	—	9	—	1	—	—	—	—	—	Morrone (1994d)
Adioristidius	2	—	—	—	31	—	1	—	—	—	Morrone (1994d)
Amathynetoides	—	—	—	—	10	—	—	—	—	—	Morrone (1994d)
Puranius	6	3	—	—	2	—	8	3	—	—	Morrone (1994d)
Acrostomus	—	—	—	—	—	—	—	—	7	—	Morrone (1994b,c)
Lamiarhinus	—	1	—	—	—	—	1	1	—	—	Morrone (1992a)
Antarctobius	9	—	—	—	—	—	—	—	—	—	Morrone (1992b)
Falklandiellus	1	—	—	—	—	—	—	—	—	—	Morrone (1995a)
Telurus	1	—	—	—	—	—	—	—	—	—	O'Brien (1971)
Lanteriella	1	—	—	—	—	—	—	—	—	—	Morrone (1992c)
Falklandius	5	—	—	—	—	—	—	—	—	—	Morrone (1992c)
Neopachytychius	—	1	—	—	—	—	—	1	—	—	Marvaldi (1994)
Haversiella	1	—	—	—	—	—	—	—	—	—	Morrone (1994e)

CEN, Central Chilean; PAR, Paramo; PAT, Patagonian; PUN, Puna; SUB, Subantarctic. E, number of endemic species; N, number of nonendemic species.

This paper refers to the historical relationships of the provinces of the Andean subregion. A combined biogeographic approach based on distributional data of species of Rhytirrhinini, is carried out in order to elucidate these relationships. This combined approach has two levels of analysis.

(1) A panbiogeographic analysis (Craw, 1988; Morrone & Crisci, 1990; Morrone, 1993c; Morrone & Lopretto, 1994) is initially undertaken to determine generalized tracks connecting the Andean provinces.

(2) A parsimony analysis of endemicity (PAE) (Rosen, 1988; Cracraft, 1991; Myers, 1991) is then undertaken to analyse the hierarchical information about area-relationships contained in the taxonomic distributions.

METHODS

Data

The analysis was based on distributional patterns of species of South American Rhytirrhinini. Data were taken from recent revisionary treatments (Table 1). *Listronotus* Jekel (Morrone, Marvaldi & O'Brien, 1995) was the only excluded genus, due to insufficient knowledge of its species.

Areas of endemism

Distributions of taxa were coded with respect to the five provinces herein assigned to the Andean subregion (Fig. 1).

(1) Paramo. Northern Andes of Venezuela, Colombia, and Ecuador, over 3000 m altitude (also known as the North Andean centre; Müller, 1973).

(2) Patagonian. Semidesert east from the southern Andes to the Atlantic coast in Argentina, also extending in some places to Chile.

(3) Puna. High mountain semidesert from central and southern Peru, western Bolivia, northeastern Argentina, and northern Chile, much of it over 3000 m altitude.

(4) Central Chilean. Central Chile between 32° and 37° south latitude (also known as the Andean Pacific centre; Müller, 1973).

Table 2. Data matrix (taxa × areas) for the clique and parsimony analyses.

	SUB	PAR	PUN	CEN	PAT
Trachodema tuberculosa	1	0	0	1	0
Listroderes bruchi	0	0	1	0	1
Listroderes robustior	1	0	1	1	0
L. affinis/L. bruchi/L. robustior	1	0	1	1	1
L. annulipes	1	0	1	1	0
L. bimaculatus	1	0	0	1	0
L. annulipes/L. bimaculatus	1	0	1	1	0
L. delaiguei	1	0	0	1	0
L. apicalis	1	0	0	1	0
L. apicalis/ L. scylla/L. brevisetis/L. howdenae	1	0	1	1	0
L. costirostris	1	0	0	1	0
L. nodifer	1	0	0	1	0
L. tuberculifer	1	0	0	1	0
Listroderes	1	0	1	1	1
Germainiellus planipennis	1	0	0	1	0
Acrorius cuprinus/A. pillahuata/A. plicatifrons	0	1	1	0	0
Hyperoides subcinctus	1	0	0	1	0
Hyperoides	1	0	0	1	1
Nacodius	0	1	1	0	0
Macrostyphlus	0	1	1	0	0
Adioristidius jorgei/A. hirsutus	1	0	0	1	0
A. jorgei/A. hirsutus/A. similaris/A. variegatus	1	0	1	1	0
Puranius vulgaris/P. dubius/P. torosus/P. verrucosus	1	0	0	1	0
P. fasciculiger/ P. elguetai/P. pusillus	1	0	0	1	0
P. hispidus	1	0	0	1	0
P. obrienorum/P. sylvanius/P. tuberosus/P. inaequalis	0	0	1	1	0
P. australis	1	0	0	1	0
P. australis/P. obrienorum/P. sylvanius/P. tuberosus/P. inaequalis	1	0	1	1	0
P. nigrinus	1	0	0	1	0
P. nigrinus/argentinensis	1	0	1	1	0
Lamiarhinus aelficus	1	0	0	1	0
Neopachytychius squamosus	1	0	0	1	0

CEN, Central Chilean; PAR, Paramo; PAT, Patagonian; PUN, Puna; SUB, Subantarctic. Absence = 0; presence = 1. (Rows and columns traversed for presentation).

(5) Subantarctic. Southern Andes, from 37° south latitude to Cabo de Hornos, including the archipelago of southern Chile and Argentina, the Falklands, and Juan Fernandez Islands (also known as Andean Subantarctic region; Rivas-Martínez & Tovar, 1983).

Data analysis

Taxa were coded for their absence (0) or presence (1) in each area of endemism in a data matrix (Table 2). Based on systematic information available, different taxonomic levels were coded hierarchically: species, sister species, species groups, and genera.

For the panbiogeographic analysis, a track compatibility method was applied (Craw, 1988; Morrone & Lopretto, 1994). Program CLIQUE of PHYLIP 3.5 (Felsenstein, 1993) was used to find the largest cliques of compatible tracks. These cliques were combined into generalized tracks and their orientation was determined based on cladistic information regarding species of *Hyperoides* (Morrone, 1993d), *Lamiarhinus* plus *Acrorius* (Morrone, 1994a), and *Antarctobius* plus *Nacodius* (Morrone, 1994b).

PAE (Rosen, 1988; Cracraft, 1991; Myers, 1991) was carried out with Hennig86 (Farris, 1988), applying the implicit enumeration option. The cladogram obtained was rooted with a hypothetical area coded all zeros.

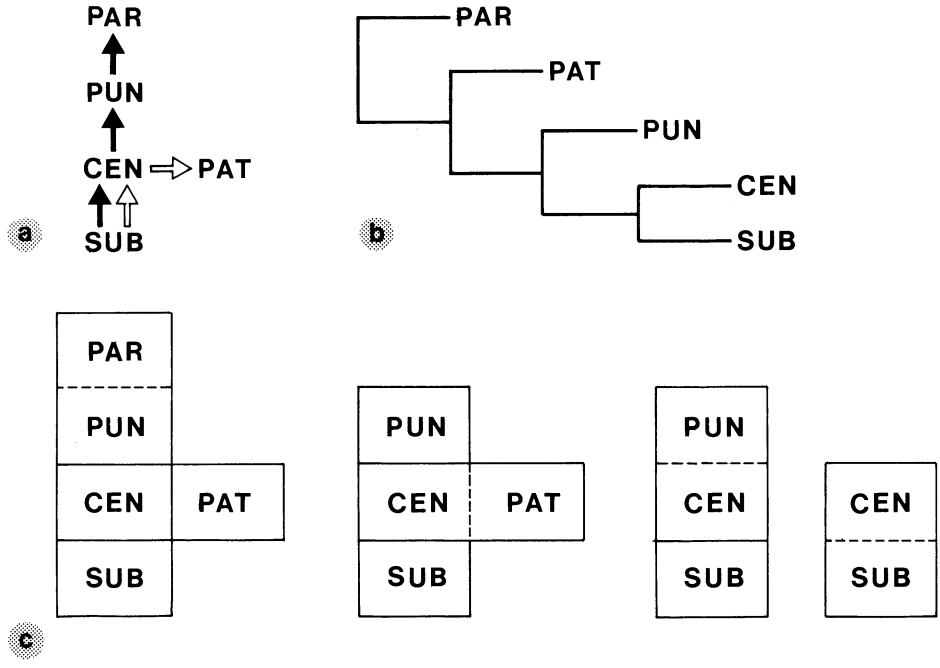

Fig. 2. Historical relationships of the provinces of the Andean subregion. (a) Two generalized tracks; (b) area-cladogram; (c) sequence of area fragmentation. CEN, Central Chilean; PAR, Paramo; PAT, Patagonian; PUN, Puna; SUB, Subantarctic.

RESULTS

Twenty-one genera of South American Rhytirrhinini were analysed. Information about number of endemic and nonendemic species for the five Andean provinces is detailed in Table 1. The majority of the species are endemic to a certain province, and the majority of the genera (61%) contain only endemic species.

Based on thirty-one codings of informative Rhytirrhinini taxa (Table 2), the track compatibility analysis produced seven cliques, which were oriented and combined in two generalized tracks (Fig. 2a). Both generalized tracks share their first portion, which unites the Subantarctic and Central Chilean provinces, and is thus herein identified as a node. From the Central Chilean province one track leads to the north (Puna and Paramo provinces) and the other to the east (Patagonian province).

PAE yielded a single most parsimonious area-cladogram, with thirty-eight steps, consistency index of 0.84, and retention index of 0.85 (Fig. 2b). The following sequence of area fragmentation results: (Paramo, (Patagonian (Puna (Central Chilean, Subantarctic)))).

Results of both analyses can be combined to explain the history of the fragmentation of the different provinces (Fig. 2c).

DISCUSSION

Although the Andean provinces have been recognized in previous biogeographic schemes (Ringuelet, 1961; Cabrera & Willink, 1973; Müller, 1973; Rivas-Martínez & Tovar, 1983), little consideration has been given to understanding their historical relationships, and they have usually been grouped on ecological criteria. We may wonder what does the hypothesized pattern says about the diversification of the Austral biota. Therefore, it is postulated here that:

(1) an ancient Austral biota was originally restricted to the southern portion of the Andean subregion (Subantarctic and Central Chilean provinces);

(2) this biota spread then to occupy all the extension of the subregion;

(3) it was finally affected by the uplift of the Andes (Kuschel, 1969) and the development of open country communities (Pascual & Ortiz Jaureguizar, 1990).

The cladogram shows the progressive depauperation of this Austral biota, with the Paramo, Patagonian, and Puna provinces representing three portions successively separated. The Subantarctic and Central Chilean provinces represent its richest (less depauperate) remnants.

This hypothesis agrees basically with Kuschel's (1969) proposal, and contradicts biogeographic schemes that classify the Subantarctic province in a separate dominion (Ringuelet, 1961; Cabrera & Willink, 1973; Rivas-Martínez & Tovar, 1983). This may be due to the taxa analysed by the different authors: when 'Austral' elements are emphasized, the remaining Andean provinces are joined to the Subantarctic (Kuschel, 1969), whereas emphasis on 'tropical' elements leads authors to join these provinces to the Chacoan and Amazonian dominions (Ringuelet, 1961; Cabrera & Willink, 1973; Rivas-Martínez & Tovar, 1983).

It could be possible that the pattern obtained is strongly influenced by dispersal, which would conceal the vicariant events. There are two possible ways to test if the herein proposed working hypothesis represents the 'true' relationships of the areas analysed:

(1) a congruence analysis based on similar parsimony analyses of endemicity from other taxa of the area;

(2) a cladistic biogeographic analysis based on taxon-area cladograms of Andean taxa, which would allow the precise estimation of the contribution that vicariance and dispersal have had.

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