

Biogeography of *Palpibracus* (Diptera: Muscidae): An integrative study using panbiogeography, parsimony analysis of endemism, and component analysis

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Palpibracus Rondani is a monophyletic genus of Muscidae (Soares and Carvalho, in press), endemic to southern South America, which occurs between 30–60° S in Chile and western Argentina (Carvalho, 1989; Carvalho *et al.*, 2003). These areas belong to the Andean region (Crisci *et al.*, 1991; Amorim and Tozoni, 1994; Morrone, 1996, 2001; Roig-Juñent and Coscarón, 2001) and comprise the Central Chilean, Subantarctic, and Patagonian subregions (Fig. 1). Central Chile comprises two provinces: Coquimbo and Santiago. The Subantarctic subregion comprises the Malvinas Islands, Juan Fernández Islands, Maule, Valdivian Forest, Magellanic Forest, and Magellanic Moorland provinces (Morrone, 2001). The Patagonian region lies in southern Argentina.

Palpibracus comprises 16 species with a recently proposed phylogeny (Soares and Carvalho, in press) and a recent biogeographic study (Carvalho *et al.*, 2003). In the latter study, parsimony analysis of endemism was used with no *a priori* phylogenetic knowledge. Two areas of endemism were found: one in Chile, between 30° and 45° S; and another in Tierra del Fuego. Since *P. pilosus* Macquart and *P. reynoldsi* Malloch are synonyms, in fact only one area of endemism exists (see Carvalho *et al.*, 1993, 2003). The biology and habits of *Palpibracus* species are unknown (Malloch, 1934; Carvalho, 1989).

We describe herein the areas of endemism of *Palpibracus* and analyze their relationships applying three historical biogeographical methods.

Material and Methods

Species distributions were compiled from the literature (Malloch, 1934; Séguy, 1937; Albuquerque, 1951; Carvalho, 1989; Carvalho *et al.*, 1993; Lopes and Khou-

ri, 1996; Soares and Carvalho, in press; see Appendix for a species list). For the biogeographical analysis of *Palpibracus* the following methods were used: panbiogeography (Craw, 1988; Morrone and Crisci, 1995; Craw *et al.*, 1999), parsimony analysis of endemism (Rosen, 1988; Morrone, 1994b; Morrone and Crisci, 1995), and component analysis (Page, 1993). Quadrats of five degrees of latitude by five degrees of longitude were used as biogeographical units for the parsimony analysis of endemism. This analysis, based on the data matrix presented in Table I, was carried out with NONA version 2.0 (Goloboff, 1993) and WinClada version 0.9.9 beta (Nixon, 1999), using the following options: heuristic search, maximum trees to keep = 1000, number of replications (mult*N) = 1000, starting trees per rep (hold/) = 100, random seed = 1224, and unconstrained search and search strategy Multiple TBR (default). A strict consensus cladogram was obtained. Provinces of the Andean region (*sensu* Morrone, 2001: Fig. 1) were used as units for component analysis. Phylogenetic and distributional data of *Palpibracus* Rondani (Soares and Carvalho, in press: Fig. 2), *Germainiellus* Morrone (Morrone, 1993: Fig. 3), and *Apsil* Malloch and *Reynoldsia* Malloch (Carvalho and Couri, 2002b: Figs. 4 and 5) were used to perform this analysis. The area cladogram was built using the program Component 2.0 (Page, 1993) with the following options: heuristic search, nearest-neighbor interchanges, and criterion to minimize: leaves added. A strict consensus cladogram was obtained.

Results

Panbiogeography. Eleven generalized tracks were found among the 15 individual tracks (Figs. 6–20):

(a) *P. veneris* + *P. similis* + *P. confusus* from Ñuble to Chiloé; (b) *P. separatus* + *P. chilensis* + *P. trivittatus* and (c) *P. confusus* + *P. peruvianus* from Santiago to Concepción; (d) *P. peruvianus* + *P. trivittatus* from Concepción to Chiloé; (e) *P. albuquerquei* + *P. confusus* around Bío Bío; (f) *P. fasciculatus* + *P. lancifer* + *P. nigri-ventris*, (g) *P. spicatus* + *P. nigri-ventris* + *P. veneris*;

(h) *P. fasciculatus* + *P. nigri-ventris* from Chiloé to Lago Argentino; (i) *P. nigri-ventris* + *P. spicatus* from Malleco to Chiloé; (j) *P. separatus* + *P. spicatus* and (k) *P. nigri-ventris* + *P. confusus* around Chiloé; (Fig. 21). Six nodes were detected: node (1) in the intersection of the tracks a+b in Santiago province; (2) b+c+d+i around Bío Bío; (3) e+i in Malleco; and nodes (4) a+e+d+f+g, (5) g+k, and (6) k+f+j+h on Chiloé Island (Fig. 21).

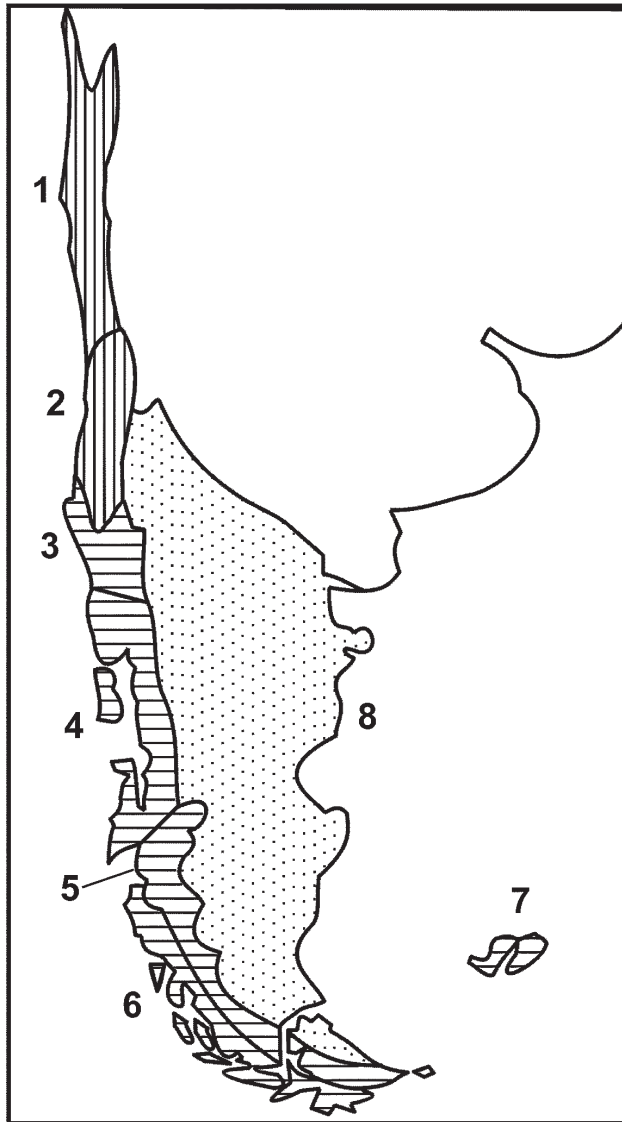


Fig. 1. Biogeography of the Andean region (adapted from Morrone, 2001a). Central Chilean subregion (vertical lines): (1) Coquimbo; (2) Santiago. Subantarctic subregion (horizontal lines): (3) Maule; (4) Valdivian Forest; (5) Magellanic Forest; (6) Magellanic Moorland; (7) Malvinas Islands (Falklands). Patagonian subregion (8, stippled).

Parsimony analysis of endemism. The parsimony analysis resulted in 10 most parsimonious trees, with length 26, consistency index of 0.61, and retention index of 0.41. A strict consensus cladogram (Fig. 22) showed a major area of endemism (Fig. 23) in Chile, between 33 and 42° S, based on *Palpi- bracus chilensis*, *P. peruvianus*, *P. separatus*, *P. spicatus*, and *P. trivittatus*. There are two subdivisions of this area: (1) from Linares to Osorno between 36 and 38° S, defined by the presence of *P. albuquerquei*, *P. carvalhoi* and

Table 1. Data matrix for *Palpi- bracus* species in 5° latitude by 5° longitude quadrats (0 – absence, 1 – presence). Area codes: (A) 25–30° S/70–75° W; (B) 30–35° S/70–75° W; (C) 30–35° S/65–70° W; (D) 35–40° S/70–75° W; (E) 35–40° S/65–70° W; (F) 40–45° S/70–75° W; (G) 40–45° S/65–70° W; (H) 45–50° S/75–80° W; (J) 45–50° S/70–75° W; (K) 45–50° S/65–70° W; (L) 50–55° S/70–75° W; (M) 50–55° S/65–70° W. Taxa code: (hyp) hypothetical area; (1) *Palpi- bracus albuquerquei*; (2) *P. carvalhoi*; (3) *P. chilensis*; (4) *P. confusus*; (5) *P. fasci- culatus*; (6) *P. lancifer*; (7) *Palpi- bracus* sp. n.; (8) *P. nigri- ventris*; (9) *P. peruvianus*; (10) *P. pilosus*; (11) *P. sepa- ratus*; (12) *P. similis*; (13) *P. spicatus*; (14) *P. trivittatus*; (15) *P. univittatus*; (16) *P. veneris*.

	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
hyp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
B	0	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0
D	1	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0
E	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
F	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1
J	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
L	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0

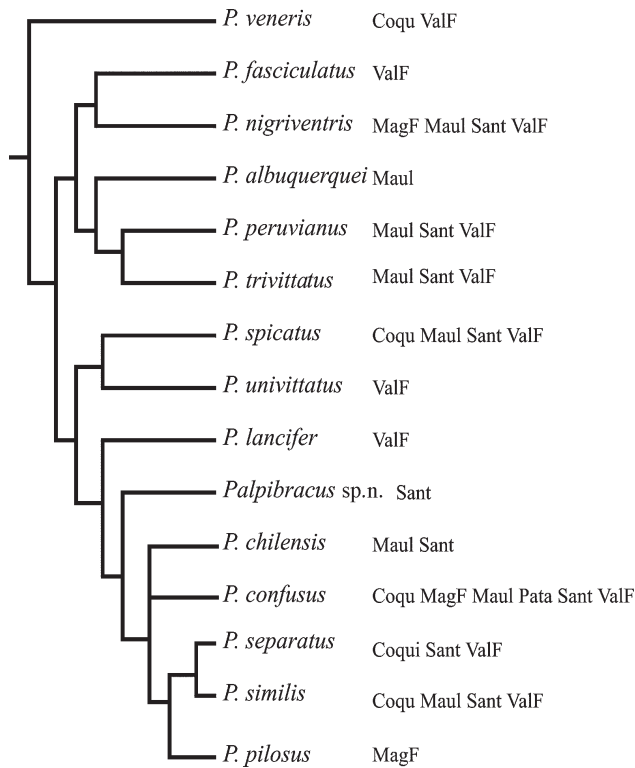


Fig. 2. *Palpibracus* phylogeny (adapted from Soares and Carvalho, in press) showing the species distribution in the subregions and provinces. Subregions: Central Chilean (CHI); Subantarctic (SUB); Patagonian (PAT). Provinces: Coquimbo (Coqu), Magellanic Forest (MagF), Maule (Maul), Patagonia (Pata), Santiago (Sant), and Valdivian Forest (ValF).

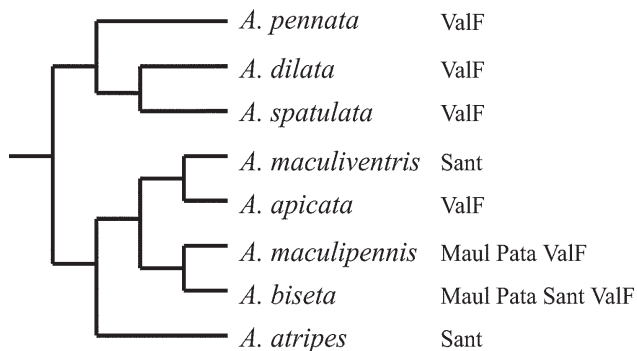


Fig. 4. *Apsil* phylogeny (adapted from Carvalho and Couri, 2002b), showing the species distribution in the subregions: Central Chilean (CHI); Subantarctic (SUB); Patagonian (PAT). Provinces: Maule (Maul), Patagonia (Pata), Santiago (Sant), and Valdivian Forest (ValF).

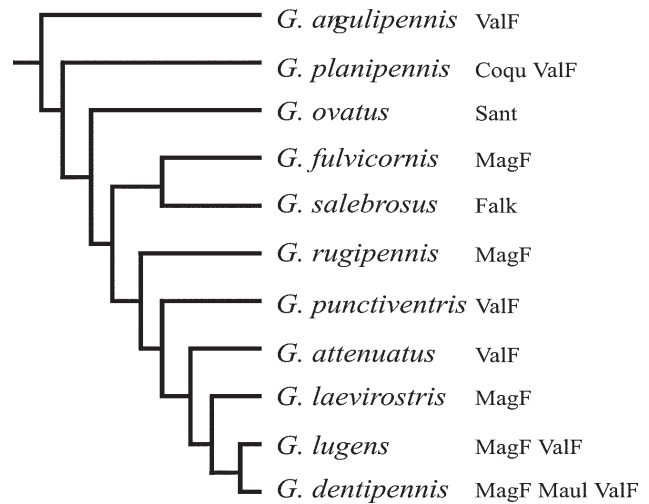


Fig. 3. *Germainiellus* phylogeny (adapted from Morroni, 1993), showing the species distribution in the subregions: Central Chilean (CHI); Subantarctic (SUB); Patagonian (PAT). And provinces Magellanic Forest (MagF), Valdivian Forest (ValF), Coquimbo (Coqu), Falkland Island (Falk), Maule (Maul), Patagonia (Pata), and Santiago (Sant).

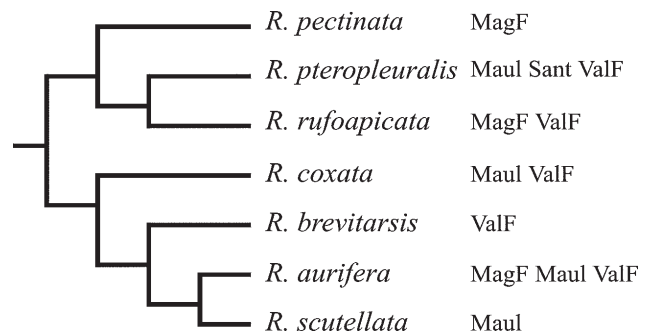


Fig. 5. *Reynoldsia* phylogenetic tree (adapted from Carvalho and Couri, 2002b) with the species distributions in the provinces of the Subantarctic (SUB) subregion: Magellanic forest (MagF), Maule (Maul), Santiago (Sant), and Valdivian Forest (ValF).

Palpibracus sp. n.; and (2) based on *P. lancifer* and *P. univittatus* (Fig. 23).

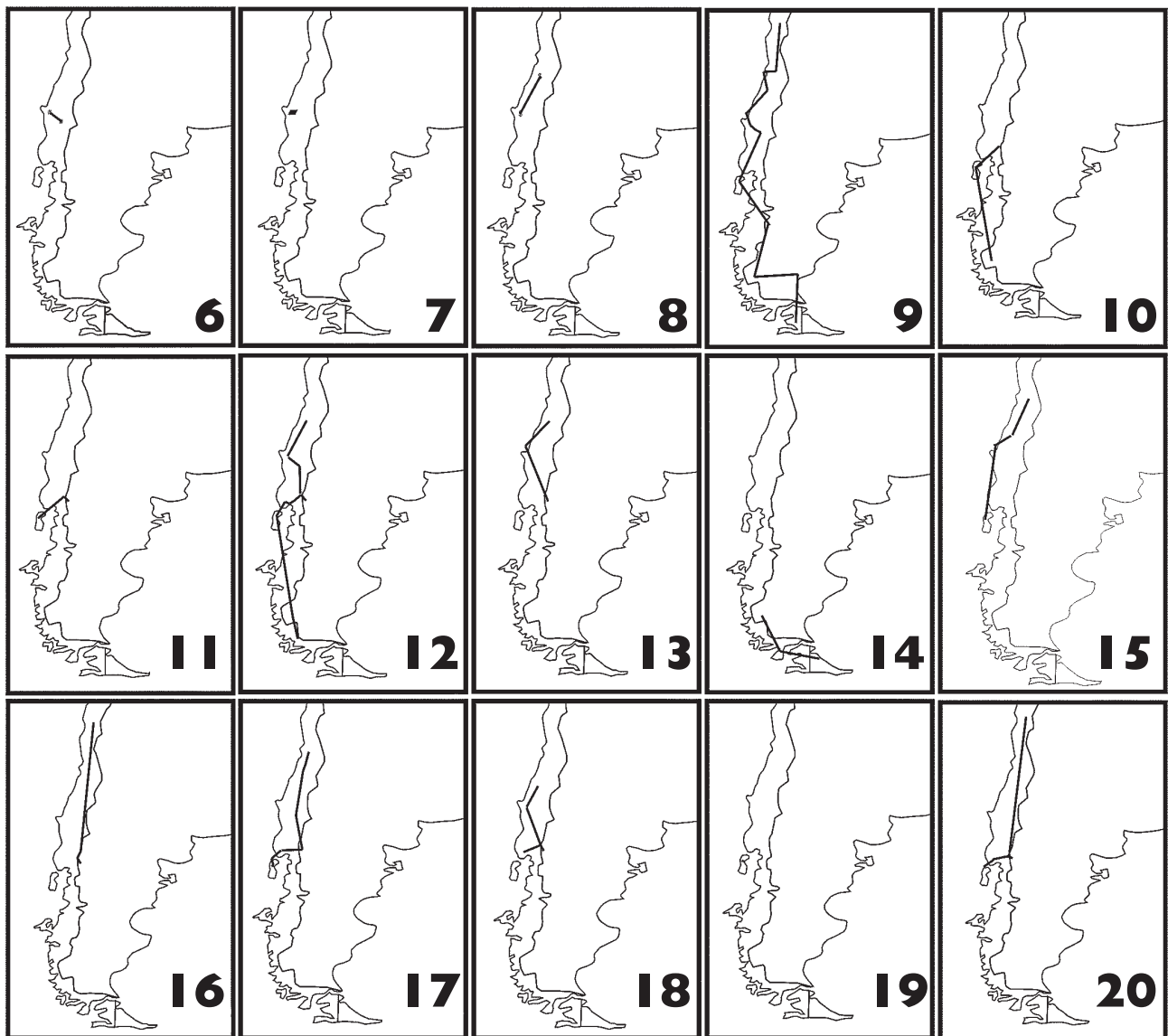
Component analysis. Three cladograms were found, each one showing different relationships among Maule, Valdivian Forest, and Magellanic Forest. In the first Maule is closer to the Valdivian Forest, in the second to the Magellanic Forest, and in the third the Magellanic Forest is closely related to the Valdivian

Forest. In the consensus cladogram the relationship among these areas is represented by a polytomy. Santiago province is the sister-group to this clade, Coquimbo is related to this group, and Patagonia is basal to them (Fig. 24).

Discussion

The distribution of *Palpibracus* shows a high degree of sympatry, except for *P. pilosus* whose distribution

is not congruent with none of the other species. *Palpibracus* diversification probably took place in the southern endemism area that was indicated by the parsimony analysis of endemism (Figs. 22 and 23), which corresponds to the northern part of the Valdivian Forest and has been considered an endemism area for *Apsil* and *Reynoldsia* (Carvalho *et al.*, 2003). Phylogenetic analysis of *Palpibracus* in association with individual and generalized tracks indicates that the distribution of the species in the clade (*P. fasciculatus*, *P. nigriventris*), (*P. albuquerquei*, (*P. peruvia-*



Figs. 6-20. Individual species tracks for *Palpibracus* Rondani: 6, *P. albuquerquei*; 7, *P. carvalhoi*; 8, *P. chilensis*; 9, *P. confusus*; 10, *P. fasciculatus*; 11, *P. lancifer*; 12, *P. nigriventris*; 13, *P. peruvianus*; 14, *P. pilosus*; 15, *P. separatus*; 16, *P. similis*; 17, *P. spicatus*; 18, *P. trivittatus*; 19, *P. univittatus*; and 20, *P. veneris*.

nus, *P. trivittatus*)) suggests that the diversification of these taxa occurred in that region. *P. fasciculatus* and *P. nigriventris* share a generalized track (track h, Fig. 21), extended through the Valdivian Forest and the Magellanic Forest; *P. albuquerquei*, *P. peruvianus* and *P. trivittatus* are distributed mainly north of Chiloé Island, on the Valdivian Forest, and also in Maule and Santiago. The remaining species are more northerly

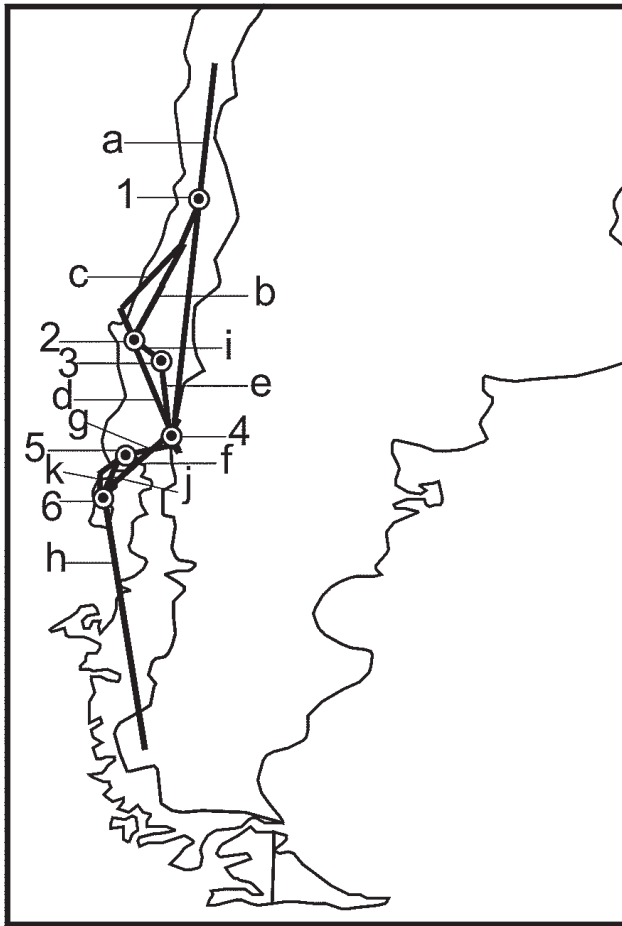


Fig. 21. *Palpibracus* Rondani generalized tracks: (a) *P. veneris* + *P. similis* + *P. confusus*; (b) *P. separatus* + *P. chilensis* + *P. trivittatus*; (c) *P. confusus* + *P. peruvianus*; (d) *P. peruvianus* + *P. trivittatus*; (e) *P. albuquerquei* + *P. confusus*; (f) *P. fasciculatus* + *P. lancifer* + *P. nigriventris*; (g) *P. spicatus* + *P. nigriventris* + *P. veneris*; (h) *P. fasciculatus* + *P. nigriventris*; (i) *P. nigriventris* + *P. spicatus*; (j) *P. separatus* + *P. spicatus*; (k) *P. nigriventris* + *P. confusus*. Geographic nodes: (1) a + b; (2) b + c + d + i; (3) e + i; (4) a + e + d + f + g; (5) g + k; (6) k + f + j + h.

distributed, mostly occurring north of 42° S, except for *P. pilosus* which is found on the southern extreme of the continent. These results suggest a connection between Central Chile and the Subantarctic subregion, which is supported by the major area of the parsimony analysis of endemism (Figs. 22 and 23), by the presence of two generalized tracks (*P. separatus*-*P. similis* and *P. peruvianus*-*P. trivittatus*: Fig. 21) and by Morrone (1994a: Fig. 25), Amorim and Pires (1996: Fig. 26), Roig-Juñent and Coscarón (2001), and Carvalho and Couri (2002b).

The parsimony analysis of endemism and the large number of generalized tracks and nodes near Chiloé Island indicate that this is an endemism area, com-

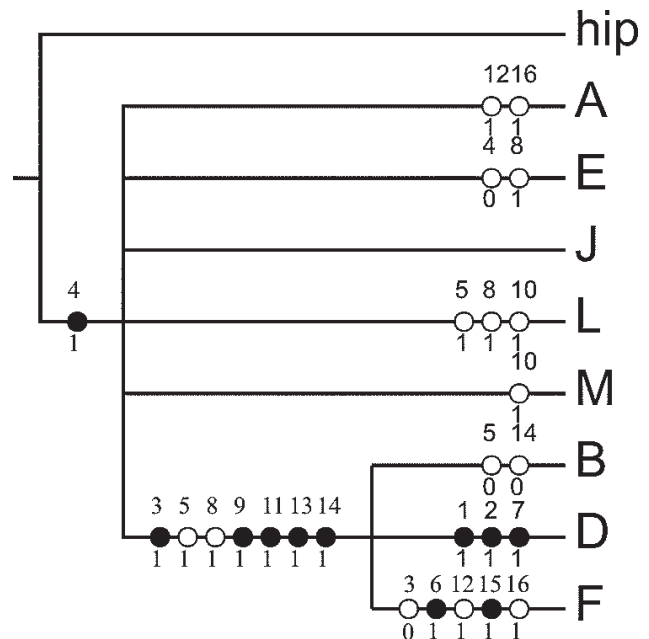


Fig. 22. Consensus area cladogram obtained by parsimony analysis of endemism. Quadrats: (A) 25-30° S/70-75° W; (B) 30-35° S/70-75° W; (C) 30-35° S/65-70° W; (D) 35-40° S/70-75° W; (E) 35-40° S/65-70° W; (F) 40-45° S/70-75° W; (G) 40-45° S/65-70° W; (H) 45-50° S/75-80° W; (J) 45-50° S/70-75° W; (K) 45-50° S/65-70° W; (L) 50-55° S/70-75° W; (M) 50-55° S/65-70° W. Taxa: (hyp) hypothetical area; (1) *P. albuquerquei*; (2) *P. carvalhoi*; (3) *P. chilensis*; (4) *P. confusus*; (5) *P. fasciculatus*; (6) *P. lancifer*; (7) *Palpibracus* sp. n.; (8) *P. nigriventris*; (9) *P. peruvianus*; (10) *P. pilosus*; (11) *P. separatus*; (12) *P. similis*; (13) *P. spicatus*; (14) *P. trivittatus*; (15) *P. univittatus*; (16) *P. veneris*.

prising the northern Valdivian Forest. The northern area recognized by PAE is also endemic and is supported by two generalized tracks (*P. separatus*, *P. chilensis*, *P. trivittatus* and *P. confusus*-*P. peruvianus*). These areas together constitute a major endemism region that has been considered one of the world's 25 hotspots of endemism (Myers *et al.*, 2000) and an endemism area for Muscidae (Carvalho *et al.*, 2003) and several other taxa (Morrone, 2001).

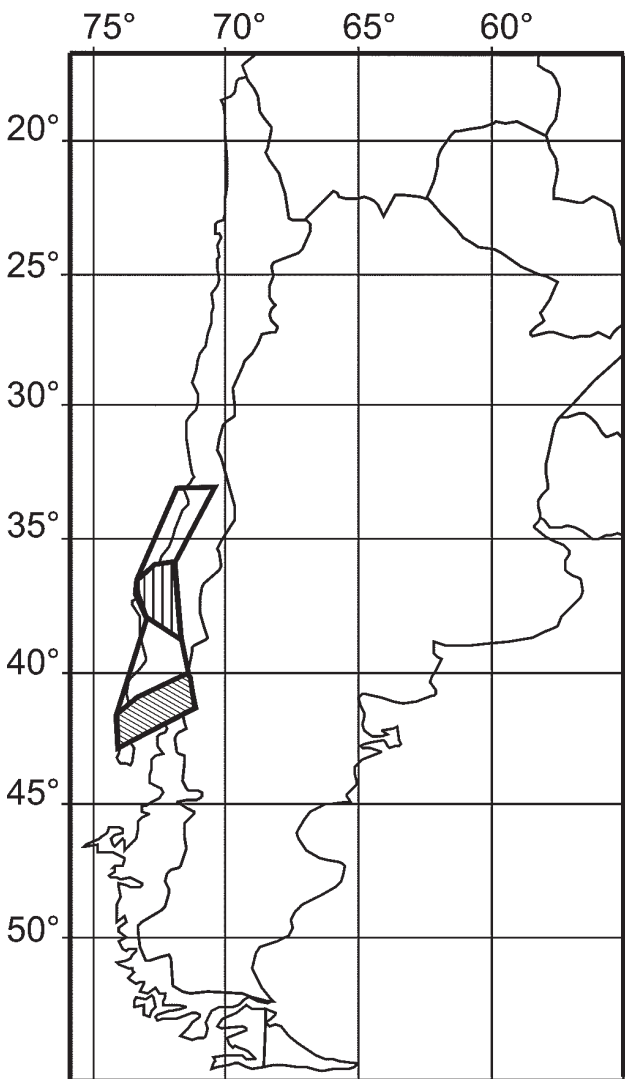


Fig. 23. Endemism areas determined by parsimony analysis of endemicity. Areas: Quadrats BDF (unfilled area): *Palpibracus chilensis*, *P. peruvianus*, *P. separatus*, *P. spicatus* and *P. trivittatus*; Quadrats D (vertical lines): *P. albuquerquei*, *P. carvalhoi* and *Palpibracus sp. n.*; Quadrats F (diagonal lines): *P. lancifer* and *P. univittatus*.

Component analysis shows that Central Chile is paraphyletic (Fig. 24), and the southern component, Santiago, is closer to Subantarctic elements than to Coquimbo. Santiago and the provinces of the Subantarctic subregion share many taxa whereas Coquimbo has mainly endemic taxa (Morrone, 2000). Amorim and Pires (1996) also showed the paraphyly of Central Chile, with Santiago and Maule as sister groups to the Subantarctic subregion, with Coquimbo as the basal province (Fig. 24). Indeed, the separation of Magellanic Forest, Maule and Valdivian Forest is a recent event and their biotas are very similar (Morrone *et al.*, 1994). The relationship found in component analysis (Fig. 24) disagrees with the proposition of Posadas and Morrone (2001), which states that the Subantarctic subregion is paraphyletic, joining Maule, Valdivian Forest, and Central Chile (Fig. 27). The paraphyly of the Subantarctic subregion was also found in the parsimony analysis of endemicity and the analysis of individual tracks and phylogeny of *Palpibracus* together. The northern part of the Valdivian Forest presents two different patterns, suggesting a vicariant event around 42° S. The first associates this area with Maule and Santiago, linked by generalized tracks a and d (Fig. 21). A second pattern links Valdivian Forest and Magellanic Forest, track h (Fig. 21). Menu-Marque *et al.* (2000) also found a generalized track joining Valdivian Forest, Maule and Santiago, and another grouping Valdivian Forest, Magellanic Forest, and Magellanic Moorland.

The different patterns of relationship found can be explained by the geological history of the area. Events of marine introgression changed the continent conformation between 26-20 million years ago (mya) in the areas today comprising Chiloé Island, Concepción, and Valparaíso, which were islands isolated from the continent (Donato *et al.*, 2003: Fig. 28). Three successive marine introgressions happened between 15-11 mya, separating the Andean region (*sensu* Morrone, 2001) from the Neotropical region (Donato *et al.*, 2003). Fossil records suggest that 15-20 mya (Miocene) is the minimum age for Muscidae (Pont and Carvalho, 1997). *Palpibracus* could have diversified under the influence of these vicariance events associated with several concurrent glacial periods. These events changed the distributional boundaries of the biota of this region several times (Crisci

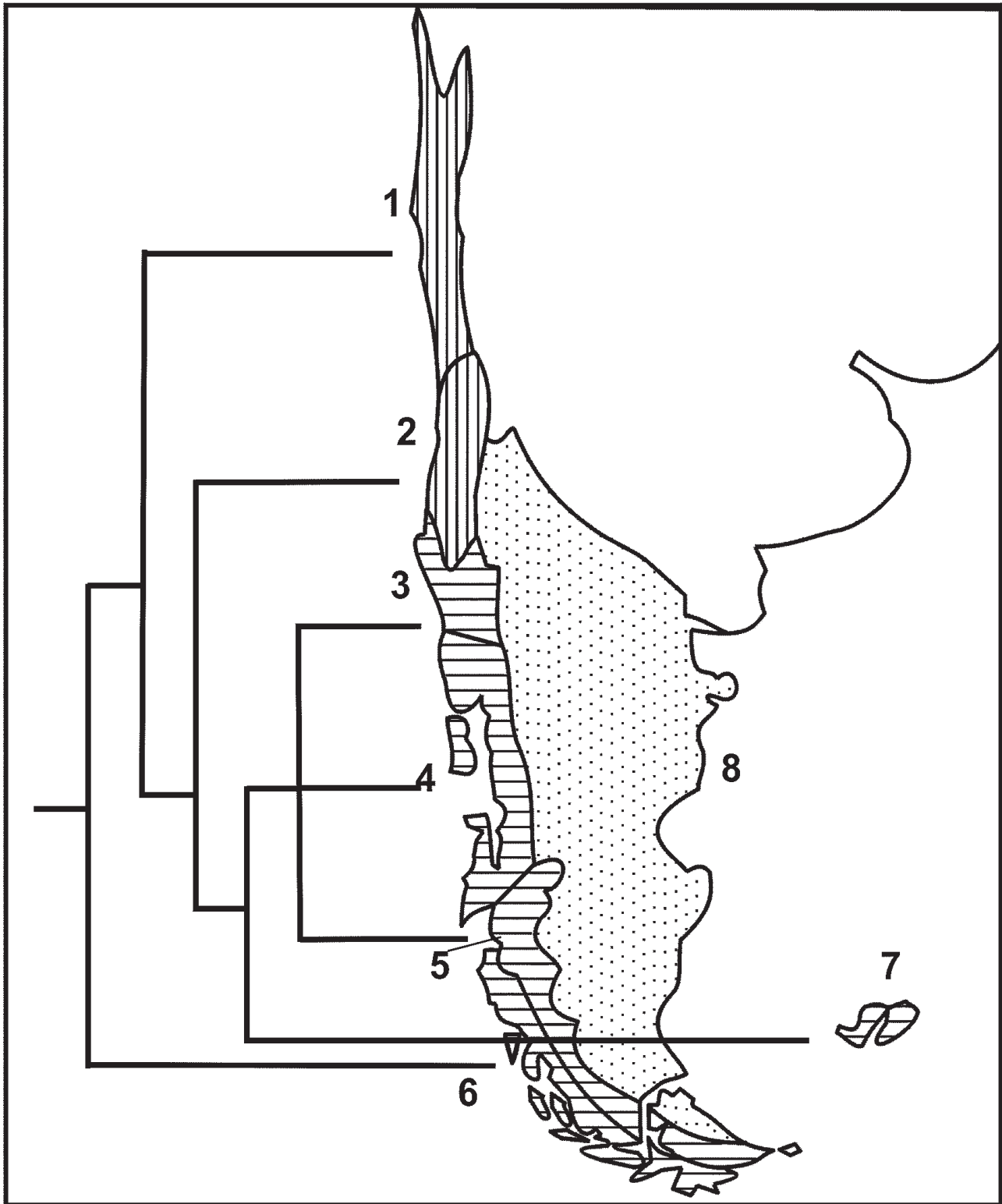


Fig. 24. Area cladogram for the provinces of the Andean region using component analysis for *Apsil*, *Germaniellus*, *Palpibracus* and *Reynoldsia*. Central Chilean subregion (vertical lines): (1) Coquimbo; (2) Santiago. Subantarctic subregion (horizontal lines): (3) Maule; (4) Valdivian Forest; (5) Magellanic Forest; (6) Magellanic Moorland; (7) Malvinas Islands. Patagonian subregion (8, stippled).

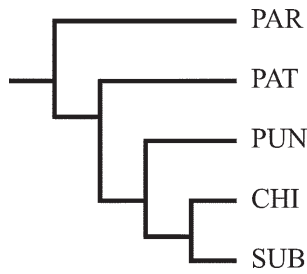


Fig. 25. Area cladogram of the South American subregions (adapted from Morrone, 1994a). Central Chilean (CHI); Subantarctic (SUB); Paramo (PAR); Patagonian (PAT); Puna (PUN).

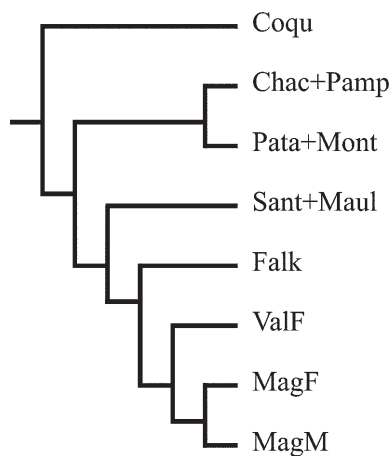


Fig. 26. Area cladogram of the Andean provinces (adapted from Amorim and Pires, 1996; based on Morrone, 1993 and Morrone *et al.*, 1994). Chaco (Chac); Coquimbo (Coqu); Malvinas Islands (Falk); Magellanic Forest (MagF); Magellanic Moorland (MagM); Maule (Maul); Monte (Mont); Pampa (Pamp); Patagonia (Pata); Santiago (Sant); Valdivian Forest (ValF).

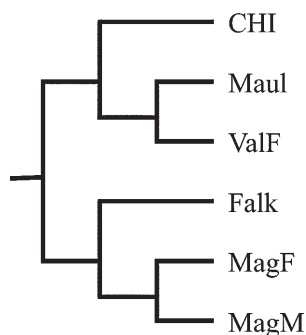


Fig. 27. Area cladogram adapted from Posadas and Morrone (2001). Central Chilean subregion (CHI); Malvinas Islands (Falk); Magellanic Forest (MagF); Magellanic Moorland (MagM); Maule (Maul); Valdivian Forest (ValF).

et al., 1991). *Palpibracus* diversification around 41–42° S is congruent with the marine introgressions of 26–20 mya (Fig. 28), that separated Chiloé Island from the southern Valdivian Forest and to the Maule (Donato *et al.*, 2003). The last glacial age covered the region south of 42°S with ice from 2 mya to 15 000 years ago, thereby imposing northern distributional limits for the biota (Donato *et al.*, 2003). The few records of *Palpibracus* south of 42° S suggest that its distributional patterns could have been influenced by the Quaternary glaciation events. Hence, *Palpibracus* species found in Patagonia and the southern extreme of Chile probably reached these areas by dispersion. *P. confusus* (Fig. 9) is widespread in this area and *P. nigriventris* (Fig. 12) probably appeared south of 41° S and subsequently extended its distribution north and south. Although *P. pilosus* (Fig. 14) has not been found further north, its distribution in the Magellanic Forest and the distribution of its sister-group in the north suggest that *P. pilosus* reached



Fig. 28. South America between 26–20 mya. Shaded areas illustrate marine introgressions (adapted from Donato *et al.*, 2003).

this region by dispersion. These patterns can be associated with the gradual migration of the biota that occurred following the retreat of the ice sheets and with the re-establishment of forests in the region (Posadas, 1996).

Acknowledgments

We are grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the support provided by grants to the authors (EDGS, 1310621/2002-6; CJBC, 304148/2002-4). To Márcia Souto Couri, Gabriel Augusto Rodrigues de Melo, and Guilherme Schnell Schulli for comments to the manuscript. This is the contribution number 1504 of the Departamento de Zoologia da Universidade Federal do Paraná.

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Appendix

List of species of *Palpibracus* Rondani.

- Palpibracus albuquerquei* Carvalho
P. carvalhoi Lopes and Khouri
P. chilensis (Bigot)
P. confusus (Malloch)
Palpibracus sp. n. Soares and Carvalho
P. fasciculatus (Malloch)
P. lancifer (Malloch)
P. nigriventris (Malloch)
P. peruvianus (Malloch)
P. pilosus (Macquart)
P. separatus (Malloch)
P. similis (Malloch)
P. spicatus (Malloch)
P. trivittatus (Malloch)
P. univittatus (Bigot)
P. veneris (Bigot)