THE ANDES MOUNTAIN RANGE UPLIFT AS A VICARIANT EVENT IN THE PIMELIINAE (COLEOPTERA: TENEBRIONIDAE) IN SOUTHERN SOUTH AMERICA

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ABSTRACT
The Andes mountain range extends over 8500 km along the Pacific coast of South America. Its medium altitude is 3500 m, reaching more than 6000 m at different latitudes. The uplift of the Andes split arid habitats creating very diverse ecosystems on both sides. The distribution of the Pimeliinae (Coleoptera: Tenebrionidae) south of parallel 15º South is analysed, where the Andean mountain range separates xeric habitats both eastward and westward. The genera of Pimeliinae show four distribution patterns: endemic taxa east of the Andes, endemic taxa west of the Andes, taxa widely distributed on both sides of the Andes, and taxa inhabiting high altitudes in the Andes. Known phylogenies of genera and species of Pimeliinae are examined in terms of the Andean mountain uplift creating a vicariant event. A biogeographical track exhibited by certain genera of Pimeliinae connecting central Chile and southern Argentina is examined.

Keywords : South America, Andes mountain range uplift, distribution patterns, Tenebrionidae, Pimeliinae, vicariance.

RÉSUMÉ
La vaste étendue des Andes couvre plus que 8500 km le long de la côte pacifique de l'Amérique du sud. L'altitude moyenne est de 3500 m mais elle dépasse plus que 6000 m avec des écosystemes très variés des deux côtés. La distribution des Pimeliinae (Coleoptera : Tenebrionidae) est examinée au sud du 15eme parallèlle où la formation des Andes a séparé des habitats désertiques à la fois vers l'est et vers l'ouest. Les genres de Pimeliinae montrent quatre modèles de distribution : espèces endémiques à l'ouest des Andes ; espèces endémiques à l'est des Andes ; espèces largement répandues les deux côtés des Andes et espèces habitant les hautes altitudes des Andes. La phylogénie connue de certaines espèces et genres est examinée pour événement vicariant à la suite de la formation des montagnes andines. Un chemin biogeographique démontré par quelques genres de Pimeliinae liant le Chile central et l'Argentine du sud est analysé.

Mots-clés : Amérique du sud, formation des Andes, modèles de distribution, Tenebrionidae, Pimeliinae, vicariance.

INTRODUCTION

The Andes mountain range extends over 8500 km along the Pacific coast of South America from Venezuela down south to Tierra del Fuego. Its medium altitude is 3500 m, reaching more than 6000 m at different latitudes and splitting very diverse ecosystems on both sides. South of parallel 15º South the Andean mountain range separates xeric habitats both eastward (due to the Humboldt current) and westward (due to the Andean mountain range, which acts as an orographic barrier to the winds of the Pacific Ocean) (HARTLEY, 2003). This area is named the "arid corredor of southern South America". Pimeliinae (Coleoptera: Tenebrionidae), are rich in number of species in this xeric area: many being apterous, and restricted in distribution. These are of particular interest in biogeographic studies (ROIG JUÑENT & FLORES, 2001, ROIG JUÑENT *et al.*, 2003, PIZARRO ARAYA & JEREZ, 2004).

The objectives of this study are to analyse the distributional patterns of the Pimeliinae in southern South America in relation to the Andean mountain range and to examine if the uplift of these mountains created a vicariant event for elements of the pimeliine fauna.

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METHODS

We analyzed the distribution of 669 species of Pimeliinae belonging to 15 tribes in 74 genera and subgenera in Southern South America (Table I). The arrangement of genera in tribes follow DOYEN (1993) while the distributional data of the genera and species follow PEÑA (1966), FLORES (1998), and other recent revisions. We then examine the known phylogenies of selected genera of Pimeliinae in relationship to their distribution to the Andean mountains to see if the uplift acted as a vicariant event. This uplift event is also examined in other groups of arthropods. Finally, we made a panbiogeographic approach (MORRONE & CRISCI, 1995) using individual tracks of five genera of Pimeliinae and two genera of Carabidae distributed in central Chile and southern Argentina between parallels 37º-41º South, where the mountain range is of low altitudes.

RESULTS

The Table I summarizes the distributional information of Pimeliinae inhabiting southern South America in relation to the Andes mountain range. Genera and subgenera of Pimeliinae exhibit four distribution patterns: taxa endemic to east of the Andes, taxa endemic to west of the Andes, taxa widely distributed on both sides of the Andes, and taxa inhabiting Andean high altitudes.

Known phylogenies of tribes and genera of Pimeliinae in South America include: 1) at generic level, the phylogeny of Nycteliini (FLORES, 2000) (Fig. 1) indicating as a oval node where the uplift of the Andes split the original populations creating: the genera *Epipedonota* Solier and *Patagonogenius* Flores (east) and *Callyntra* Solier and *Auladera* Solier (west); at specific level: 2) the phylogeny of *Mitragenius* Solier, *Auladera* and *Patagonogenius* (FLORES, 1999) (Fig. 2), in which the uplift of the Andes split the original populations into two species of *Mitragenius* in central Chile (west) while the rest remained in central Argentina and Patagonia; 3) the phylogeny of *Platesthes* Waterhouse (Praocini) (FLORES, 2004) (Fig. 3) shows one species (*P. vidali* Peña) inhabiting central Chile (west) and the remaining species in Patagonian steppes (east); 4) the phylogeny of *Discopleurus* Lacordaire (Stenosini) (AALBU & ANDREWS, 1996) (Fig. 4) in which the uplift of the Andes split the original populations into two species, *D. baloghi* Kaszab and *D. argentinensis* Aalbu & Andrews west and east of the Andes; and 5) the phylogeny of *Caenocrypticoides* Kaszab (Caenocrypticini) (FLORES & PIZARRO ARAYA, 2004) (Fig. 5) in which the uplift of the Andes also split the original populations into two species, *C. translucidus* Kaszab and *C. triplehorni* Flores & Pizarro Araya west and east of the Andes. This vicariant event leaving species both east and west of the Andes originating by the uplift of the Andes is also found in the phylogeny of other groups of arthropods such as *Acanthogonatus* Karsch (Araneae, Mygalomorphae) (GOLOBOFF, 1995), Tristiridae Rehn (Orthoptera, Acridoidea) (CIGLIANO, 1989), *Barypus* Dejean and *Cnemalobus* Guérin-Méneville (Coleoptera, Carabidae) (ROIG JUÑENT, 1995, 2002).

A panbiogeographic approach using individual tracks of five genera of Pimeliinae and two genera of Carabidae distributed in central Chile and southern Argentina between parallels 37º-41º South resulted in a generalized track connecting xeric and mesic areas in central Chile with arid Patagonian steppes in southern Argentina (Fig. 6). This track crosses the Andes between parallels 37º-41º South, where the mountain range is of low altitude (1500-2000 msl). This track is found in genera of Pimeliinae with different dispersion capacities such as *Nyctopetus* Guérin-Ménéville (winged) and *Platesthes* Waterhouse, *Peltolobus* Lacordaire, *Nyctelia* Latreille, and *Mitragenius* Solier (flightless). This track has been named Patagonic by ROIG JUÑENT *et al.* (2003) and also show a branch connecting Patagonian steppes with high altitudes of the Precordilera mountain range in western Argentina (Fig. 6).

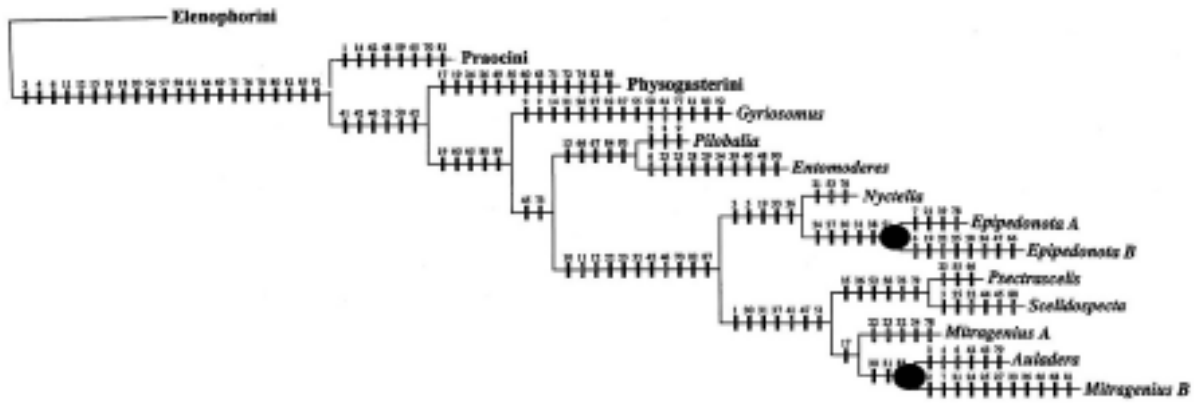

Fig. 1 - Cladogram of genera of Nycteliini (Flores, 2000). The black circle at the branch node indicates the uplift of the Andes. *Epipedonota* B currently includes the restored genus *Callyntra* and *Mitragenius* B currently is the genus *Patagonogenius.*

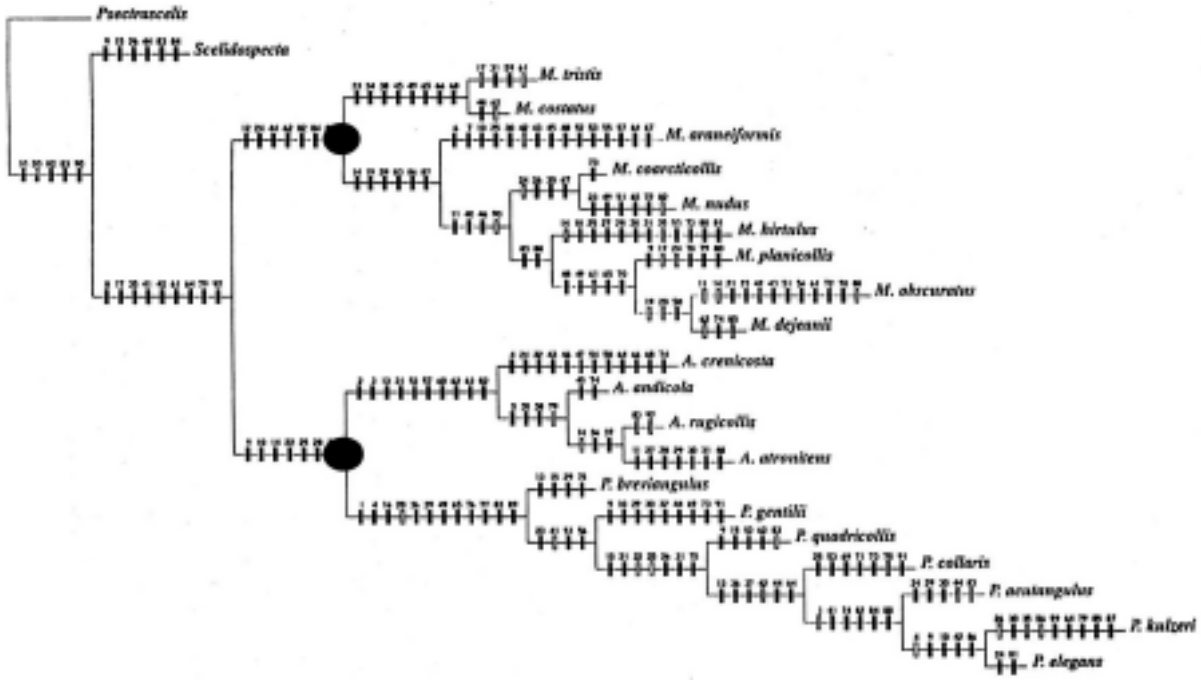

Fig. 2 - Cladogram of species of three genera of Nycteliini (Flores, 1999). The black circle at the branch node indicates the uplift of the Andes.

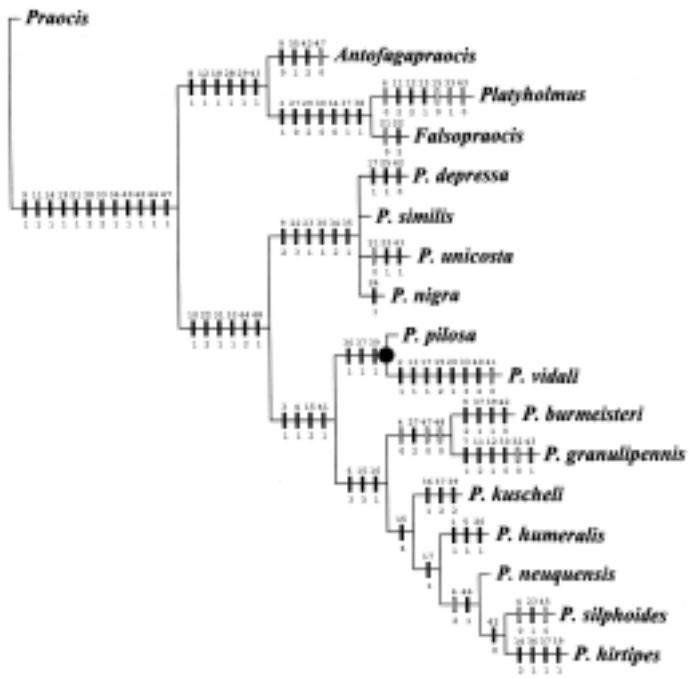

Fig. 3 - Cladogram of species of *Platesthes* (Flores, 2004). The black circle at the branch node indicates the uplift of the Andes.

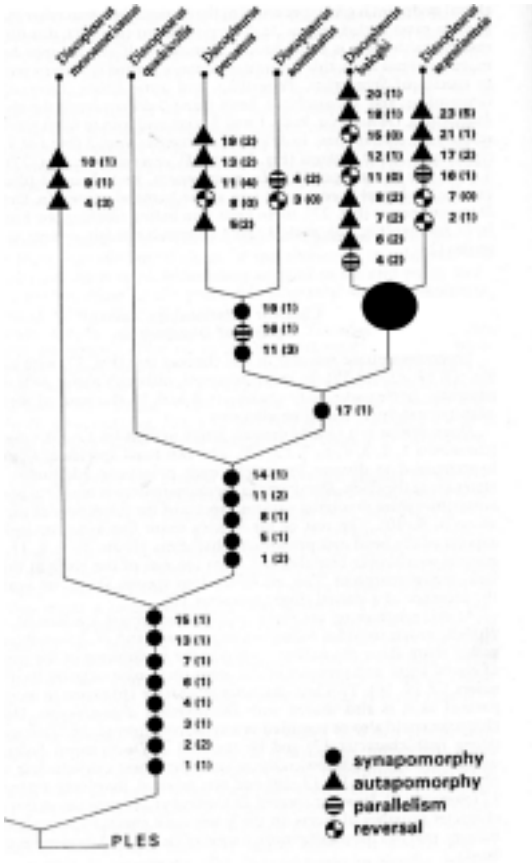

Fig. 4 - Cladogram of species of *Discopleurus* (Aalbu & Andrews, 1996). The black circle at the branch node indicates the uplift of the Andes.

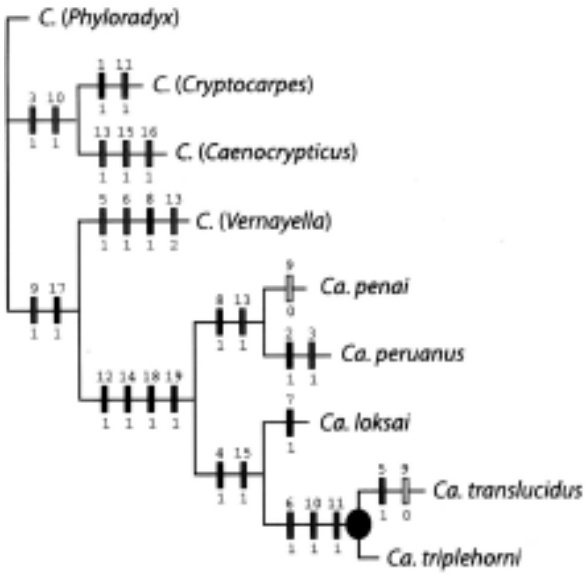

Fig. 5 - Cladogram of species of *Caenocrypticoides* (Flores & Pizarro Araya, 2004). The black circle at the branch node indicates the uplift of the Andes. *C.*= *Caenocrypticus; Ca* = *Caenocrypticoides.*

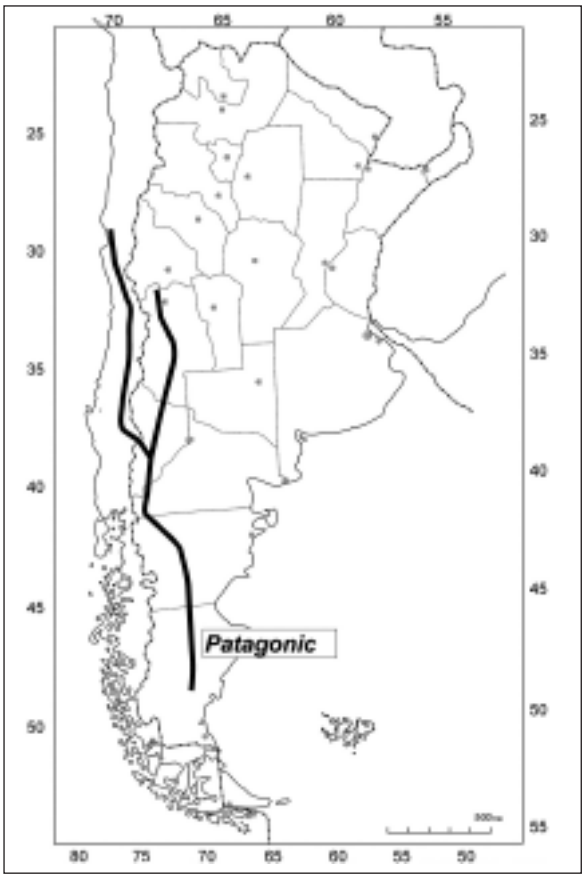

Fig. 6 - Patagonic generalized track.

CONCLUSIONS

1) There are four distribution patterns in Pimeliinae in Southern South America in relation to the Andes mountain range: a) taxa endemic to east of the Andes, b) taxa endemic to west of the Andes, c) taxa widely distributed on both sides of the Andes, and d) taxa inhabiting high altitudes in the Andes.
2) The Andes is vicariant at different taxonomic levels: genera and species. The Andean uplift affected most of the genera and subgenera of Pimeliinae: 49 of 74 analysed are endemic to east or to west of the Andes.
3) Among the genera widely distributed east and west of the Andes (13), the Andean uplift affected most of its species (only very few species inhabit both sides of the Andes).
4) Species of genera with different capacities of dispersion (winged or flightless) show the same distribution pattern (i.e.: endemic east or west of the Andes).
5) Only three apterous genera inhabit exclusively high altitudes in the Andes (up to 3000 msl), suggesting that these species evolved together with the Andean uplift and became adapted to the new ecological and climatic conditions created by the uplift.
6) The "Patagonic" biogeographic track connecting arid lands east and west of the Andes is reflected by five genera of Pimeliinae with different capacity of dispersion (winged or flightless) and two genera of Carabidae.

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Tribe	Genera	N° species and distribution
Asidini	*Cardigenius*	9 spp endemic to east of the Andes (Argentina, Brazil, Uruguay)
	Scotinus	10 spp endemic to east of the Andes (Brazil)
Caenocrypticini	*Caenocrypticoides*	1 sp endemic to east of the Andes (Argentina)
		4 spp endemic to west of the Andes (Chile, Peru)
Cnemeplatiini	*Lepidocnemeplatia*	3 spp endemic to east of the Andes (Argentina, Bolivia, Brazil)
		1 sp endemic to west of the Andes (Chile)
Elenophorini	*Megelenophorus*	1 sp endemic to east of the Andes (Argentina, Bolivia)
Epitragini	*Aspidolobus*	3 spp endemic to west of the Andes (Chile)
	Epitragella	1 sp endemic to east of the Andes (Argentina)
	Epitragopsis	1 sp endemic to west of the Andes (Chile)
		2 spp endemic to east of the Andes (Argentina, Bolivia)
	Epitragus	4 spp endemic to east of the Andes (Argentina, Paraguay)
	Eunotioides	3 spp endemic to east of the Andes (Argentina, Bolivia, Paraguay)
	Geoborus	2 spp endemic to west of the Andes (Chile)
	Hemasodes	5 spp endemic to east of the Andes (Argentina, Bolivia, Paraguay)
	Hypselops	1 sp endemic to west of the Andes (Chile)
	Nyctopetus	4 spp endemic to east of the Andes (Patagonian steppes Argentina)
		11 spp endemic to west of the Andes (Chile)
	Omopheres	17 spp endemic to east of the Andes (Argentina, Bolivia)
	Parepitragus	4 spp endemic to west of the Andes (Chile, Peru, Ecuador)
	Pectinepitragus	1 sp endemic to east of the Andes (Argentina)
	Penaus	1 sp endemic to west of the Andes (Chile)
	Pseudothinobatis	2 spp endemic to west of the Andes (Chile)
Eurymetopini	*Achanius*	6 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Peru)
		1 sp endemic to east of the Andes (Argentina)
	Ambigatus	1 sp inhabiting high altitudes in the Andes (Peru)
		4 sp endemic to east of the Andes (Argentina)
		1 sp endemic to west of the Andes (Chile)
	Arthroconus	1 sp endemic to east of the Andes (Argentina)
		2 spp endemic to west of the Andes (Chile)
	Hylithus	1 sp endemic to west of the Andes (Chile)
		6 spp endemic to east of the Andes (Argentina)
		6 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile, Peru)
Evaniosomini	*Aryenis*	2 spp endemic to west of the Andes (Chile, Peru)
		1 sp endemic to east of the Andes (Argentina)
		1 sp widely distributed on both sides of the Andes
	Melaphorus	2 spp endemic to west of the Andes (Chile, Peru)
Nycteliini	*Auladera*	4 spp endemic to west of the Andes (Chile)
	Callyntra	17 spp endemic to west of the Andes (Chile)
	Entomoderes	9 spp endemic to east of the Andes (Argentina, Bolivia)
	Epipedonota	23 spp endemic to east of the Andes (Argentina, Bolivia)
	Gyriosomus	38 spp endemic to west of the Andes (Chile)
	Mitragenius	7 spp endemic to east of the Andes (Argentina)
		2 spp endemic to west of the Andes (Chile)
	Nyctelia	2 spp endemic to west of the Andes (Chile)
		63 spp endemic to east of the Andes (western Argentina and Patagonian steppes Argentina, Chile)
	Patagonogenius	7 spp endemic to east of the Andes (Patagonian steppes Argentina)
	Pilobalia	46 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile, Peru)
	Psectrascelis	74 spp widely distributed on both sides of the Andes and inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile, Peru)
	Scelidospecta	5 spp endemic to east of the Andes (Argentina)
Phrynocarenini	*Phrynocarenum*	1 sp endemic to east of the Andes (Argentina)
Physogasterini	*Entomochilus*	19 spp endemic to west of the Andes (Chile)
	Philorea	22 spp endemic to west of the Andes (Chile, Peru)
	Physogaster	8 spp endemic to west of the Andes (Chile)
		3 spp endemic to east of the Andes (Argentina)
		4 spp inhabiting high altitudes in the Andes (Argentina, Chile)

TABL. 1 - List of tribes (Doyen, 1993) and genera (Peña, 1966, Flores, 1998) of Pimeliinae in Southern South America

	Pimelosomus	4 spp endemic to east of the Andes (Argentina, Bolivia)
Praocini	*Antofagapraocis*	2 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile)
	Asidelia	1 sp endemic to east of the Andes (Argentina)
	Calymmophorus	5 spp endemic to east of the Andes (Argentina)
	Eutelocera	1 sp endemic to east of the Andes (Argentina)
	Falsopraocis	3 spp inhabiting high altitudes in the Andes (Argentina, Chile)
	Neopraocis	1 sp endemic to east of the Andes (Patagonian steppes Argentina, Chile)
	Afrasida (Gyrasida)	1 sp endemic to west of the Andes (Chile)
	Platesthes	12 spp endemic to east of the Andes (Patagonian steppes Argentina, Chile) 1 sp endemic to west of the Andes (Chile)
	Platyholmus	16 spp endemic to east of the Andes (Argentina, Bolivia, Peru)
	Praocis (Praocis)	18 spp endemic to west of the Andes (Chile)
	Praocis (Mesopraocis)	4 spp endemic to west of the Andes (Chile)
	Praocis (Postpraocis)	4 spp endemic to west of the Andes (Chile) 1 sp inhabiting high altitudes in the Andes (northwestern Argentina)
	Praocis (Anthrasomus)	4 spp endemic to west of the Andes (Chile)
	Praocis (Filotarsus)	6 spp endemic to west of the Andes (Chile) 8 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile, Peru)
	Praocis (Parapraocis)	3 spp inhabiting high altitudes in the Andes (Peru)
	Praocis (Hemipraocis)	7 spp endemic to east of the Andes (Patagonian steppes Argentina, Chile)
	Praocis (Praonoda)	2 spp endemic to east of the Andes (Patagonian steppes Argentina, Chile)
	Praocis (Orthogonoderus)	21 spp widely distributed on both sides of the Andes and inhabiting high altitudes in the Andes (Argentina, Bolivia, Chile, Peru)
	Praocis (Praocida)	1 sp endemic to east of the Andes (Argentina) 3 spp inhabiting high altitudes in the Andes (Argentina, Bolivia, Peru)
	Thylacoderes	4 spp endemic to east of the Andes (Argentina)
Psammetichini	*Psammetichus*	13 spp endemic to west of the Andes (Chile, Peru)
Stenosini	*Discopleurus*	4 spp endemic to west of the Andes (Chile, Peru) 1 sp endemic to east of the Andes (Argentina)
	Ecnomoderes	2 spp endemic to east of the Andes (Argentina)
	Grammicus	1 sp endemic to west of the Andes (Chile, Peru)
	Hexagonochilus	2 spp endemic to west of the Andes (Chile, Peru)
	Schizaraeus	1 sp endemic to east of the Andes (Argentina)
Thinobatini	*Cordibates*	7 sp endemic to west of the Andes (Chile)
	Thinobatis	13 spp endemic to west of the Andes (Chile)
Trilobocarini	*Derosalax*	1 spp endemic to east of the Andes (Argentina)
	Eremoecus	2 spp endemic to west of the Andes (Chile)
	Peltolobus	2 spp endemic to west of the Andes (Chile) 3 spp endemic to east of the Andes (Patagonian steppes Argentina, Chile)
	Salax	1 sp distributed on both sides of the Andes
	Trilobocara	2 spp endemic to east of the Andes (Argentina) 1 sp endemic to west of the Andes (Chile)
Total species		669

TABL. 1 (suite) - List of tribes (Doyen, 1993) and genera (Peña, 1966, Flores, 1998) of Pimeliinae in Southern South America