Quaternary paleobiogeography of northern and central Chile

Paleobiogeografía cuaternaria del norte y centro de Chile

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ABSTRACT

A striking feature of the Pleistocene land mammal record from northern and central Chile is the high similarity in taxonomic composition over 25° of latitude, an area that encompasses contrastings environments such as the Atacama Desert in the north, and the temperate rainforests in the Lake District and Isla Grande de Chiloé in the south. The fossil-bearing sites are clustered in two disjunct faunistic nuclei separated by a record-free area between 23°S and 29°S. The presence of a northern nucleus in the area of current maximum eastward penetration of the hyperarid Atacama Desert (18°-24°S), and the hiatus of land mammal records between 23°S and 29°S, rises questions about the role of Quaternary climate changes on the past and modern biogeographic patterns of the biota. We propose a model to account for the geographic distribution of Pleistocene land mammals, modern vascular plants, and some rodent taxa from northern and central Chile. We propose that glacial climates affected the patterns of geographic distribution of the biota by means of the openning and closing of corridors along the Andes.

Key words: Pleistocene land mammals, Quaternary glaciations, barriers to dispersal, salars, paleolakes.

RESUMEN

Un rasgo notable del registro de mamíferos terrestres Pleistocénicos del norte y centro de Chile es la alta similitud taxonómica a lo largo de 25° de latitud, en un área que abarca ambientes tan contrastantes como el Desierto de Atacama en el norte, y los bosques templados lluviosos de la Región de los Lagos e Isla de Chiloé en el sur. Los sitios fosilíferos se encuentran agrupados en dos núcleos faunísticos disjuntos separados por un área carente de registros entre 23°S y 29°S. La presencia del núcleo norte en el área de máxima penetración actual del Desierto de Atacama (18°-24°S), y el hiato de registros de mamíferos terrestres entre 23°S y 29°S, plantea interrogantes respecto al rol de los cambios climáticos Cuaternarios en los patrones biogeográficos actuales y pasados de la biota. Proponemos un modelo para dar cuenta de la distribución geográfica de mamíferos terrestres Pleistocénicos, plantas vasculares y algunos roedores actuales del norte y centro de Chile. Nosotros proponemos que los climas cuaternarios afectaron los patrones de distribución geográfica de la biota mediante la apertura y cierre de corredores, a lo largo de los Andes.

Palabras claves: Mamíferos terrestres Pleistocénicos, glaciaciones cuaternarias, barreras para la dispersión, salares, paleolagos.

INTRODUCTION

Pleistocene mammalian records

Pleistocene land mammals have been described from 79 sites in northern and central Chile (18°-43° S Lat.) (Fig.1), most of the findings are located in the Valle Longitudinal (graben or semigraben) limited by the Costal range to the west, and by the Andes Cordillera to the east. The altitude of these sites range from sea level up to 4290 masl (Quebrada de Lipiche; ca.19°30'S, 70°W). Based on the patterns of geographic distribution of the sites, Moreno & Marshall (in prep.) distinguished two disjunct faunistic nuclei: the northern (14 sites, ca. 18°-23° S Lat) and the central nucleus (65 sites, ca. 29°-43°S Lat). These nuclei are separated by a record-free area between 23°35'S and 29°43'S.

The available chronology for the fossil findings is meager due mainly to the lack of stratigraphic control in most sites, and the scarcity of studies on the Quaternary geology of these areas. Most of the mammal-bearing sites (71) have been assigned to the Late Pleistocene, and 8

sites to the Early-Middle Pleistocene (Fig.1) (Moreno & Marshall in prep.). Six localities have ^{14}C chronologies (Table 1), three of which are paleoindian sites (Quereo, Tagua Tagua, Monte Verde [Núñez et al. 1983, Casamiquela 1976, Casamiquela & Dillehay 1989]), indicating that humans and Pleistocene mammals coexisted for more than 1000 years.
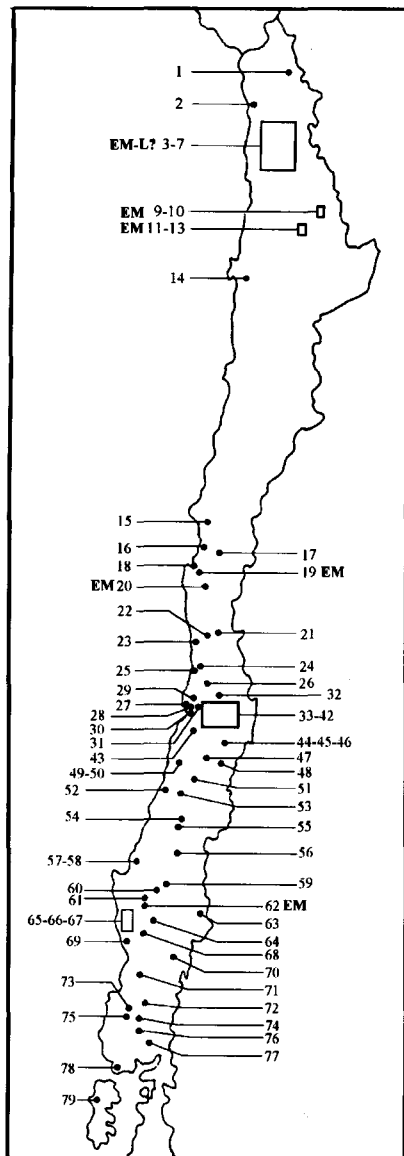

Fig. 1: Sites containing Pleistocene land mammals from northern and central Chile (E-M= Early-Middle Pleistocene).

Sitios con registros de mamíferos terrestres Pleistocénicos del norte y centro de Chile (E-M= Pleistoceno Inferior-Medio).

The mammalian fossil-record includes 22 genera and 11 families, belonging to the three Land-Mammal strata recognized in South America (Fig.2, Tables 2 and 3) (e.g. Webb 1976, Simpson 1980, Webb & Marshall 1982, Marshall et al. 1984, Marshall 1988, Marshall & Cifelli 1990, Marshall & Sempere 1992). The disparity on the stratigraphic distribution of the South American mammals is related to different dispersal events during the Late Cretaceous-Cenozoic (e.g. Simpson 1980, Marshall et al. 1984, Marshall 1988, Marshall & Cifelli 1990). Knowledge on the South American Land Mammal ages has been constructed mainly on the fossil mammal records from Bolivia and Argentina, the most exhaustively studied in South America. They include the best reference collections and type specimens, and corresponding chronologies for the tropical Andes and southern South America.

In order to decipher the biogeographic patterns of the taxa under analysis, and the processes which account for them, proper comparisons should be made among taxa with similar histories. Although there are marked differences in the biochrons of the taxa recorded in northern and central Chile at the level of orders and families (Table 3), there is uniformity on their biochrons at the generic level (with the exception of rodents, Lama sp., and Hippocamelus bisulcus which have persisted until recent times), a factor that warrants comparisons among them.

A striking feature of the Chilean paleomastozoological record is the high similarity in taxonomic composition between the two biogeographic nuclei over 25° of latitude (Moreno & Marshall in prep.). All the taxa recorded in the northern nucleus are present in the central nucleus (Table 4), the former being a depauperated subset of the latter. The fauna recorded in the northern and central nuclei exhibit close affinities with the Pleistocene mammalian records from Perú and Bolivia at the generic level, and even at the species level (Table 4). This close relationship has been recognized by several authors (Philippi 1893a,b; Schneider 1927). Casamiquela (1970c) concluded that northern and cen-

tral Chile constituted a single zoogeographic province during the Pleistocene, strictly linked to the Peruvian and Bolivian faunas (Casamiquela 1969a). In this work we will assess the biogeographic patterns of the Pleistocene land-mammals from northern and central Chile, through the light of the Quaternary environmental changes, and the modern patterns of distribution of vascular plants and sigmodontine rodents.

Pleistocene paleoenvironmental records

North of 24°S, the precipitation regime is controlled by the southwest shift of the Altiplanic low pressure cell during summer months determining the «invierno Boliviano» in the high Andes. The great width and height of the Andes massiff in this region exherts a formidable barrier to the westward penetration of moist air masses; as a consequence, the longitudinal valley remains arid all year-round under the

TABLE I

^{14}C dates from sites containing Pleistocene land mammals from northern and central Chile. Taken from Moreno & Marshall (in prep.) and references therein.

Dataciones ^{14}C provenientes de sitios con registro de mamíferos terrestres Pleistocénicos del norte y centro de Chile. Tomado de Moreno & Marshall (in prep.) y referencias citadas.

Site	Level ID#	Sample Dated	Material	Date (yr BP)
Salar de Bellavista	?	WSU 1986-1987	bone	4399 ± 90
Quereo	QR#1 member 2	N-2965	wood	1,600 ± 190
	QR#1 member 2	N-2966k	woodk	11,400 ± 145
	QR#1 top of member 2	N-2963-	wood-	11,100 ± 150
	QR#1 top of member 2	N-2962	wood	11,100 ± 150
	?	GAK-2984	?	9100 ± 300
	QR#1 member 3	N-2964	charred woodk	11,400 ± 155
	QR#1 member 3	N-2483	peat	9370 ± 180
	QR#1 member 3	N-2484	peat	9370 ± 180
Tagua	TT-1lower layer	GX-1205	charred wood	11,380 ± 320
Tagua	TT-1 lower layer		charred wood 1	1,320 ± 300
	TT-1 lower layer		charred wood	11,000 ± 170
	TT-1 upper layer	I-3987	charred wood	6130 ± 155
	TT-2	Beta-45520	charred wood	10,120 ± 130
	TT-2	Beta-45519	charred wood	9900 ± 100
	TT-2	Beta-45518	harred wood	9700 ± 90
Mulpulmo	?	?	bone	18,700 ± 900
Nochaco	?	?	bone	16,150 ± 750
Monte Verde	MV-6	TX-3760	bone	12,230 ± 200
	MV-6	Beta-6755	ivory artefact	12,600 ± 140
	MV-6	OXA-105	collagen of ivory artefact	12,360 ± 250
	MV-6	OXA-381	ivory artefact!	12,825 ± 150
	top of MV	TX-4437	ivory artefact	13,030 ± 130
	top of MV-7	TX-5375	ivory artefact	13,120 ± 440P

influence of the Subtropical High Pressure
Belt (Pacific Anticyclone). This factor,
along with the dessication effect of the
cold Humboldt Current, accounts for the
presence of the hyperarid Atacama desert
in the western coasts of South America
between 18°S and 26°S. Between 27°S and
30°S inland penetration of moist air masses
is favoured by the reduction in size and
continuity of the Coastal Range, deter-
mining the presence of transversal valleys
which dissect the central depression
(longitudinal valley), connecting the
lowlands with the Andean foothills. South
of 30°S, the winter rain regime is determined

TABLE 2

Chronology of the South American Land
Mammal ages and the dispersion events
during the Cenozoic (After Marshall &
Sempere 1992).

Cronología de las edades mamalíferas Sudamericanas y
eventos de dispersión durante el Cenozoico (según
Marshall & Sempere 1992).

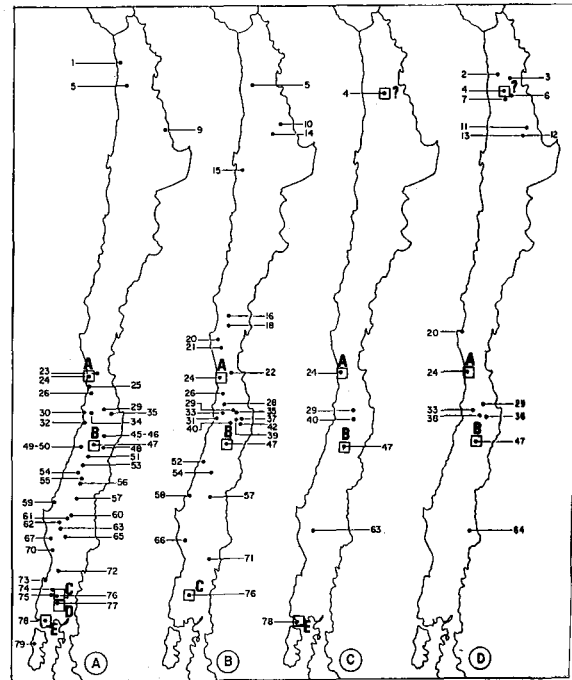| AGE (Ma)	EPOCH	SOUTH AMERICAN LAND MAMMAL AGE	FAUNISTIC STRATA
0	PLEISTOCENE	Lujanian	
	1.6	Ensenadan	
	PLIOCENE	Chapadmalalan	
5	5.3	Montehermosan	Stratum 3
		Huayquerian	
10		Chasicoan	
15	MIOCENE	Colloncuran	
		Santacrucian	
20		Colhuehuapian	
	23.7		
25		Deseadan	
30	OLIGOCENE		Stratum 2
		Divisaderan	
35	36.6		
40			
45			
	EOCENE	Mustersan	
50			
55		Casamayoran	
	57.8		
60		Riochican	
	PALEOCENE	Itaboraian	
65		Tiupampan	Stratum 1
	66.4		

Fig. 2:   A= Sites containnig Gomphotherd
remains in northern and central Chile (Cuvieronus,
Stegomastodon S); B= sites containnig Equidae
(horses) remains, Equus E, Hippidiun H,
Onohippidium O, Equidae undetermined; C= sites
containnig Cervidae (Antifer A, Hippocamelus ; D=
sites containnig Megatheridae (Megatherium M),
Mylodontd (GlossotheriumG, Scelidodon S)
remains

A= sitios con restos de Gomphotheriidae (mastodontes) en el
norte centro de Chile (Cuvieronus, Stegomastodon S); B=
sitios con restos de Equidae (caballos), Equus E, Hippidiun
H, Onohippidium O, Equidae indeterminado; C= sitios con
restos de Cervidae (Antifer A, Hippocamelus D= sitios con
restos de Megatheridae (Megatherium M), Mylodontd
(GlossotheriumG, Sceldodon S)

TABLE 3

Biochrons of South American land mammal orders (above), families (center) and genera (below) recorded in the Pleistocene of northern and central Chile (modified from Marshall & Sempere 1992 and references therein). X's represent known occurrences, dash lines are inferred occurrences. Abbreviations: T, Tiupampian; I, Itaboraian; R, Riochican; Ca, Casamayoran; M, Mustersan; Di, Divisaderan; De, Deseadan; C, Colhuehupian; S, Santacrucian; Co, Colloncuran; Ch, Chasicoan; H, Huayquerian; M, Montehermosan; Cp, Chapadmalalan; E, Ensenadan; L, Lujanian; and R, Recent.

Biocrones de ordenes (arriba), familias (centro) y géneros (abajo) de los mamíferos terrestres Sudamericanos registrados en el norte y centro de Chile (modificado de Marshall & Sempere 1992 y referencias ahí citadas. X representa ocurrencias documentadas, - representa ocurrencias inferidas. Abreviaciones: T, Tiupampense; I, Itaboraiense; R, Riochiquense; Ca, Casamayorense; M, Mustersan; Di, Divisaderense; De, Deseadense; C, Colhuehupiense; S, Santacrucense; Co, Colloncurense; Ch, Chasicoense; H, Huayqueriense; M, Montehermosense; Cp, Chapadmalalense; E, Ensenadense; L, Lujaniense; y R, Reciente.

		T	I	R	Ca	M	Di	De	C	S	Co	Ch	H	M	Cp	E	L	R
STRATUM 1	Xenarthra	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Litoptern	X	X	X	X	-	X	X	X	X	X	X	X	X	X	X	X	X
STRATUM 2	Rodentia						X	X	X	X	X	X	X	X	X	X	X	X
STRATUM 3	Rodentia													X	X	X	X	X
	Carnivora												X	X	X	X	X	X
	Proboscidea														X	X	X	
	Perissodactyla														X	X	X	X
	Artiodactyla														X	X	X	X
Xenarthra	Megalonychidae							X	X	X	X	X	X	X	X	X	X	
	Megatheriidae									X	X	X	X	X	X	X	X	
	Mylodontidae									X	X	X	X	X	X	X	X	
Litopterna	Macraucheniidae				X	-	X	X	X	X	X	X	X	X	X	X	X	
Rodentia	Myocastoriidae Capromyidae													X	X	X	X	X
	Octodontidae								X	X	X	X	X	X	X	X	X	X
	Cricetidae														X	X	X	X
Carnivora	Canidae														X	X	X	X
	Felidae														X	X	X	X
Proboscidea	Gomphotheriidae														X	X	X	
Peryssodactyla	Equidae														X	X	X	
Artiodactyla	Camelidae														X	X	X	X
	Cervidae														X	X	X	X
Megatheriidae	Megatherium														X	X	X	
Mylodontidae	Glossotherium														X	X	X	
	Mylodon															X	X	
	Scelidodon														X	X	X	
Macraucheniidae	Macrauchenia														X	X	X	
Myocastoriidae	Myocastor															X	X	X
Octodontd	Aconaemys																	X
	Spalacopus																	X
	Ctenomys														X	X	X	X
	Octodon																	X
Cricetidae	Phyllotis															X	X	X
Canidae	Canis															X	X	
	Pseudalopex														X	X	X	X
Gomphotheriidae	Cuvieronius														X	X	X	
	Stegomastodon															X	X	
Equidae	Equus															X	X	
	Hippidon														X	X	X	
	Onohippidium														X	X	X	
Camelidae	Lama														X	X	X	X
Palaeolama															X	X	X	
Cervidae	Antifer														X	X	X	X
	Hippocamelus															X	X	X

by the seasonal migration of the westerlies' stormtracks (Miller 1976); north of 30°S, the westerlies' influence is expressed as occasional snowfall in the highlands. The gradual transition between the zones of regular winter rains (34°-38°S), and episodic dry winters (30°-34°S), is caused by the northward weakening of cyclonic activity in the vecinities of the Pacific Subtropical High (van Husen 1967), determining maximum rain seasonality between 30°S and 34°S. The Coastal Range reaches its highest altitudes in this zone, continentality increases eastward as a consequence of its strong rain shadow effect.

Little is known about the effect of the Quaternary climate changes in the terrestrial communities in the Norte Grande and Norte Chico area. The current state of knowledge can be summarized as follows.

An increase in the intensity of upwelling in the eastern equatorial Pacific has been inferrred associated to the Quaternary glaciations (Arrhenius 1952, Luz 1973, Hays et al. 1969), suggesting that the Humboldt Current was greatly strengthened. A colder ocean may have further depressed the rates of evaporation, causing increased aridity in the coastal environments and nearby areas (Longitudinal Valley).

The limiting factor for glacier growth in the central Andes area (Altiplano) is the availability of precipitation, whereas at mid-latitudes the lowering of temperature seems to be the controlling factor, since enough precipitation is brought in by westerly flow (Clapperton 1991). The combination of lower air temperatures, and the intensification of easterly flow (Clapperton 1991, Setzer 1990 Grosjean et al. 1991, Veit 1991, Messerli *et al.* 1993) elicited snowline depression, triggering glacial advances in the high Andes, and high lake levels in the Altiplano (Kessler 1985, Hastenrath & Kutzbach 1985, Wirrman & Mouguiart 1987), and the chilean Andes at 24°S (Grosjean et al. 1991, Messerli et al. 1993). The chronology of these events shows an out-of-phase relationship with similar phenomena at southern latitudes (Chilean Lake District

[ca. 40°S]) (Mercer 1972, 1976; Porter 1981; Denton *et al.* unpublished data), analogous to the modern patterns of seasonal change of atmospheric and oceanic circulation in the southeastern Pacific.

Because of the great width and altitude of the Andes, and its strong rain shadow effect, the higher effective moisture was not manifested as rainfall in the Longitudinal Valley due to increased aridity (as a consequence of intensified coastal upwelling), but rather as increased ground- and streamwater flow. It is possible that the leeward slopes of the High Andes experienced increased precipitation, but this posssibility cannot be tested at the present time.

Numerous salars (salt-encrusted playas) occur in Northern Chile at different altitudes in basins with centrypetal drainage (Fig.3). Most of these salars were lakes formed during the Pleistocene by ground- and streamwater flow originating from the Andes, associated with increases in meltwater and/or precipitation during the Quaternary glaciations (Stoertz & Ericksen 1974, Ericksen 1983).
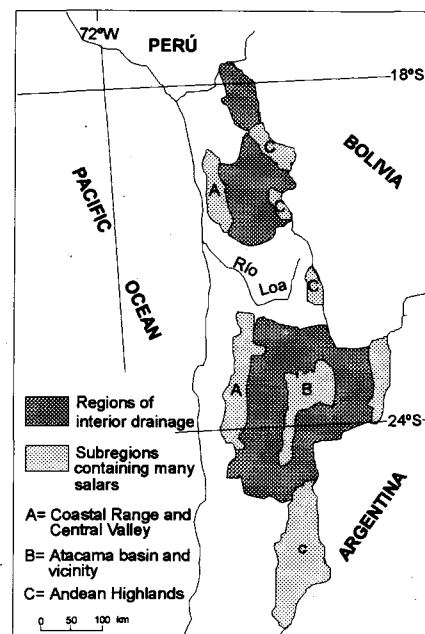

Fig. 3: Geographic distribution of salars in northern Chile (modified from Stoertz & Erícksen 1974).

Distribución geográfica de los salares del norte de Chile (modificado de Stoertz & Ericksen 1974).

Vascular plant biogeography

In order to assess the possibility of modern and past floristic exchanges along the Andes of northern and central Chile, we analyzed the patterns of species richness, endemism, and floristic similarities of the native vascular plant species between 18°S and 38°S. The data stems from nine altitudinal transects summarized in Table 5 and depicted in Fig. 5a.

Maximum species richness is observed at 18°S (372 spp.), decreasing abruptly towards the south (77 spp. at 24°S, 96 spp. at 26°S) (Fig. 4a, Table 5). This trend coincides with the decrease in summer rainfall towards the south, ranging from 300 at 18°S to 50 mm at 26°S (Huber 1975), and the progressive altitudinal penetration of the hyperarid Atacama desert (Villagrán et al. 1983). A marked increase in species richness towards mediterranean latitudes becomes evident south of 26°S, reaching maximum values at 38°S (312 spp) (Fig. 4a, Table 5), consistent with the southward increase in winter precipitation (1500 mm at 38°S, Huber 1975) brought by the westerly winds. Although both zonal and azonal floras depict high values of endemism at 18°S and 33°S, and subsequent south- and northward decreases, the bog (azonal) flora shows relatively higher levels of endemism at intermediate latitudes with maximum aridity (22°-26°S), whereas the

TABLE 4

Summary of the Pleistocene mammalian records from northern and central Chile, and comparisons with Perú and Boliva and Argentine Patagonia. Between brackets is expressed the number of sites in which the taxa have been reported in northern/central Chile.

Resumen de los registros de mamíferos terrestres Pleistocénicos del norte y centro de Chile, y comparaciones con Perú, Bolivia y la Patagonia Argentina. Entre paréntesis se expresa el número de sitios en el norte/centro de Chile.

Taxa	Perú and Bolivia	Northern nucleus	Central nucleus	Argentine Patagonia
Megatherium medinae (5/2)	X	X	X	X
Glossotherium and undet. Mylodontinae (0/3)	X		X	
Scelidodon chiliense (2/3)	X	X	X	
Macrauchenia (1/2)	X	X	X	
Myocastor sp.(0/1)	X		X	
Aconaemys sp. (0/1)	X		X	
Spalacopus sp.(0/1)	X		X	
Ctenomys sp. (1/1)	X	X	X	X
Octodon sp. (0/2)	X		X	X
Phyllotis sp. (0/2)	X		X	X
Canis sp. (0/1)	X		X	X
Pseudalopex sp. (1/1)	X	X	X	X
Cuvieronius hyodon (2/5)	X	X	?	
Stegomastodon humboldtii (0/6)			X	X
Equus sp. (2/12)	X	X	X	X
Hippidion sp. (1/3)	X	?	X	X
Onohippidium sp. (0/2)	X		X	X
Lama sp. (1/2)	X	X	X	X
Palaeolama sp. (0/2)	X		X	X
Antifer sp. (0/5)			X	X
Hippocamelus bisulcus (0/3)		X	X	X
Equidae undetermined (1/7)			X	X
Gomphotheriidae undet. (0/41)			X	

zonal flora depicts low values and progressive southward increases at the same latitudes (Fig. 4b, Table 5). High levels of endemism of the zonal flora in the Altiplano and mediterranean Andes, suggest intense floristic differentiation in both areas. Contrastingly, the azonal bog vegetation has an out-of-phase maximum species endemism in the area of current maximum aridity (22°-26°S), suggesting high degrees of conservatism under harsh climatic conditions. The floristic distinctivity of the
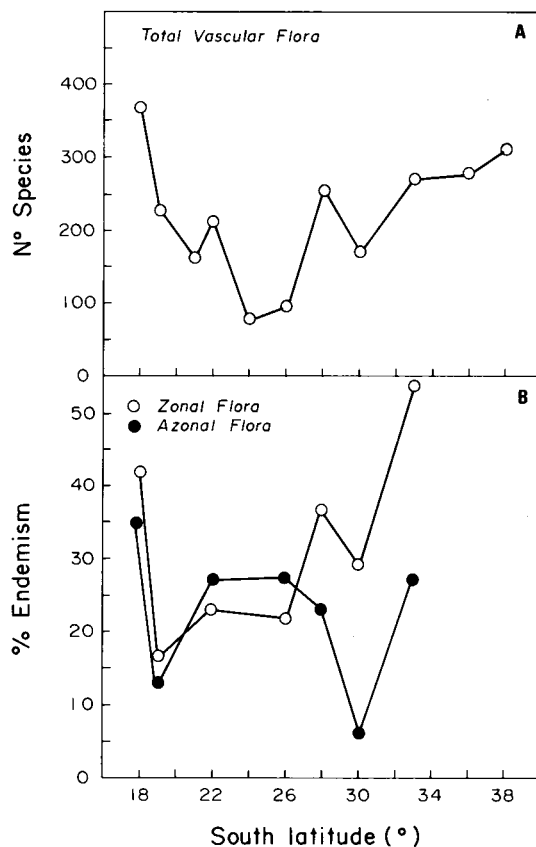

Fig. 4: A) Latitudinal variation of vascular plant species richness. The data stems from eleven altitudinal transects between 18° and 38°S (the data from latitudes 21°S and 24°S was taken Kalin et al. 1988). B) Latitudinal variation of the percentage of zonal and azonal (bog) vascular plant species endemic to the altitudinal transects between 18° and 33°S.

Variación latitudinal de la riqueza de especies de plantas vasculares. Los datos se derivan de once transectos altitudinales entre 18° y 38°S (los datos de las latitudes 21°S y 24°S fueron tomados de Kalin et al. 1988). B) Variación latitudinal de los porcentajes de especies zonales y azonales (bofedal) endémicas a los transectos altitudinales entre 18° y 33°S.

vegetation in the northern (18°-30°S) and mediterranean Andes (33°-39°S), is further supported by the low similarity values obtained (6.7%, Fig.5) using Sorensen's similarity index. High values of species richness and endemism, and low floristic relationship of the Altiplano and mediterranean floras, suggest long-term differentiation in isolation implying that severe barriers to dispersal have precluded the north-south exchange of flora. When analyzing by separate the zonal and azonal vegetation, low similarity values are replicated by the zonal vegetation (5.7%); however, the azonal vegetation shows relatively high similarity values (25.1%) between the northern and mediterranean Andes, and between the Norte Chico and central Chile (31.3%) (Fig.5). This close relationship highlights the possibility of dispersion along a wide and climatically heterogeneous geographic area, when these habitats expanded and coaslesced during the Quaternary.

Small mammals biogeography

Small mammals by virtue of being poor dispersers are useful indicator taxa of biogeographic barriers (e.g. Brown & Gibson 1983). We will illustrate current biogeographic patterns of species richness of South American Sigmodontine cricetid rodents (subfamily Sigmodontine), along northern and central Chile.

The latitudinal pattern of species richness along the Pacific slope of the Andean mountain range agrees with the biogeographic statement outlined above. Small mammal species richness reaches a maximum of 18 species at latitude 17°S, and decreases towards southern latitudes (Fig.6). This decline in diversity is steep. Species number drops from 18 down to 3 species at 24°S. This trend coincides with the progressive altitudinal penetration of the Atacama desert, causing the near disappearance of the Prepuna vegetation belt, and the shrinking of the Puna, High-Andean, and Subnival belts (Villagrán et al. 1983). An additional factor involved in the steep decrease in species richness at

24°S is the decrease in areal extent of the Puna or Altiplano which can potentially cause a peninsular effect.

Sigmodontine rodents had potential access to the Puna (Altiplano) area and to the Pacific coastal desert through most of the Pleistocene (Marquet in press). The paleoclimatic evidence, and current patterns of diversity characterize the Puna area as a major center of diversification for both birds and sigmodontine rodents (Reig 1986, Vuilleumier & Simberloff 1980). From this area small mammals migrated into the lowland desert and also dispersed along the Andes.

Migrants into the lowland desert found a favorable habitat along the deeply cut and vegetated valleys that traverse the currently arid depression in northern Chile, connecting the high altitude Puna area with the lowlands (Marquet 1989, Meserve & Kelt 1990). This factor explains the existence of typically high altitude species such as *Eligmodontia typus, Abrothrix andinus, Phyllotis xanthophygus,* and *Phyllotis magister* in lowland habitats within the Atacama desert (Marquet 1989, Contreras pers. comm.). Interestingly, some of these species developed physiological adaptations to cope with the hyperarid lowland environment (Bozinovic & Marquet 1991). Southward migration along the western flank of the Andes might have occurred along a narrow vegetated area between 23°S and 24°S, especially during high lake levels in the Pleistocene. Some species such as *Abrothrix andinus* and *Phyllotis xanthophygus,* could have dispersed through this corridor. This corridor must have represented a strong filter to dispersal, since other species either shifted their distribution toward the east side of the Andes (e.g. *Eligmodontia typus, Akodon albiventer*) and migrated south along the Argentinian highlands, or stopped altogether (e.g., *Calomys lepidus*).

The pattern of distribution of sigmodontine rodents south of 35° S suggest the existence of favorable conditions for dispersal across the Andes (see the transandean corridor section below, and Meserve & Glanz 1977, Contreras 1990). This is reflected in a higher overall similarity (using Jaccard's similarity index) between chilean and argentinean altitudinal transects at the same latitude (Fig. 7d). Similarity is lower between chilean and argentinean transects further north (Fig. 7c).

TABLE 5

Geographic data and detailed information on species richness and endemisms of the total, zonal, and azonal vascular plant species, along nine altitudinal transects in northern and central Chile. For the theree last colums, the first figure is the numbre of species present only in each transect, and the second figure is the total number os species.

Datos geográficos e informacón detallada acerca de la riqueza de especies y endemismos de las especies vasculares totales, zonales y azonales a lo largo de transectos de vegetación zonal, and azonal en el norte y centro de Chile. En las tres últimas columnas, la primera cifra indica el número de especies exclusivas de cada transecto y la segunda el número total.

Latitudinal range	Altitudinal range(m)	Zonal vegetation	Azonal vegetation	Total	References
18°-19°S	1540-5200	136/321	18/51	154/372	A,B
19°-20°S	1600-4800	32/194	4/30	36/224	A,B
22°-23°S	2400-4500	37/160	15/56	52/216	A
26°S	730-5100	14/63	9/33	23/96	B,C
28°30′-29°S	1600-4100	73/193	13/57	86/254	D
30°-31°S	2100-4000	40/136	2/33	42/169	A
33°-34°S	220-3800	123/226	12/45	135/271	A
35°-36°S	1000-2450	-	-	119/227	E
38°-39°S	850-1850	-	-	164/312	E

A= Vllagrán et al. 1983; B= Kalin Arroyo et al.1988; C= Vllagrán & Arroyo, unpublished data; D= Kalin Arroyo et al.1984; E= Vllagrán et al. 1994.
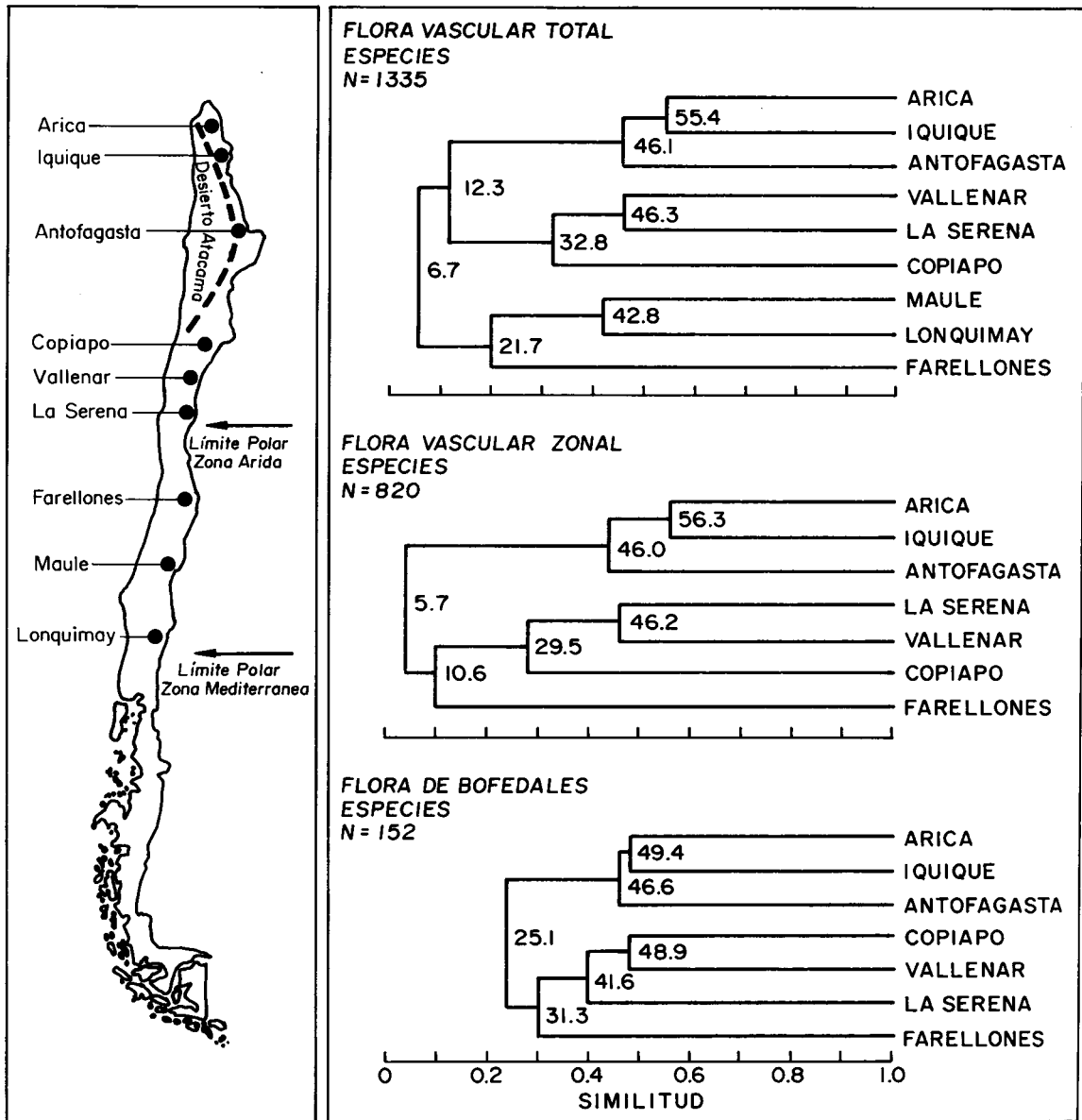
Fig. 5: Geographic location of the vegetation transects analyzed, and dendrograms showing floristic similarities among total, zonal, and azonal (bog) vascular plant species.

Ubicación geográfica de los transectos vegetacionales analizados y dendrogramas de silmilitud florística entre las especies vasculares totales, zonales y azonales.

Pleistocen corridors: a working hypothesis

In order to elucidate the patterns of migration of the fossil faunas into northern and central Chile it is necessary to choose the taxa that exhibit chronological and/or geographic polarities. The taxa selected must be recorded in several sites so as to yield representative samples, and must have a well known geographic and stratigraphic distribution in South America, in order to recognize spatial and chronological polarities. Table 6 lists the species that meet these requirements. We decided to exclude from the analysis *Macrauchenia patachonica, Equus curvidens,* and *Hippidion sp.* due to their wide distribution in southern South America.

The presence of *Megatherium medinae, Scelidodon chiliense,* and *Cuvieronius hyodon* (Table 4) in the Chilean northern and central nuclei can be explained by southwestward migration of the tropical Andean faunas (*sensu* Hoffstetter 1986) into the Norte Grande area, and a southward migration towards mid latitudes (Moreno & Marshall in prep.). The presence of *Stegomastodon humboldti* (sister species of the Argentinian *S. superbus), Glossotherium lettsomi, Hippocamelus bisulcus,* and *Antifer* sp. in the Chilean central nucleus and adjacent Argentine Patagonia (Table 4), and their absence from the northern nucleus (these taxa have not been found unequivocally in Perú nor Bolivia [Hoffstetter 1986, Hoffstetter in Marshall *et al.* 1984, Marshall & Sempere

1992]), suggest a westward migration path towards central Chile from Argentine Patagonia (Fig.8) (Moreno & Marshall in prep.).

In our mind, migration might have occurred through corridors linking areas separated by the arid barrier established by the maximum eastward penetration of the Atacama desert at 18°S and 23°S, and across the Andes Cordillera in central Chile.

The desertic corridor

We postulate a southward corridor along the western flank of the Andes in an area where the hyperarid Atacama desert imposes an important barrier on the biota (see above). In our mind, the most parsimonious route would coincide with the western edge of the salars between 18°S and 29°S. The crux of our argument is that hydrological and topographical constraints west of the Andes, permited the formation of paleolakes in basins with centrypetal drainage under a cold, hyperarid climate regime. The responsible mechanism would be a rise in groundwater level, due to increased fluvial and glaciofluvial flow originating from the high Andes between 18°S and 29°S. A rise in ground water depth in basins with centrypetal drainage may have favoured the expansion of phreatic plant species (e.g. leguminous plant taxa, such as *Prosopis, Schinus,* and
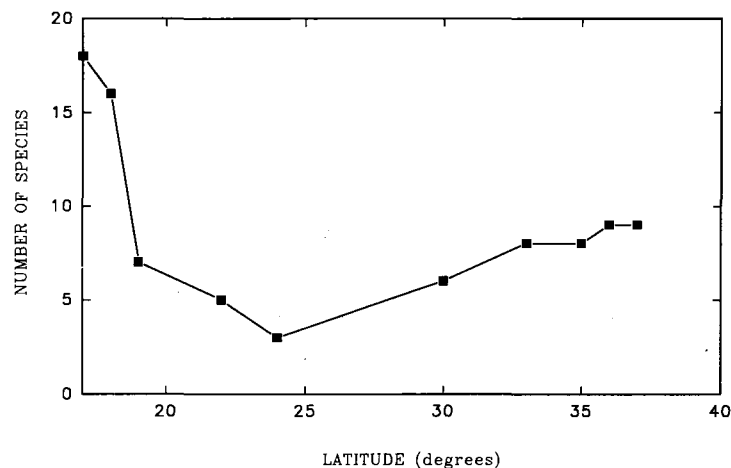

Fig. 6: Latitudinal variation in sigmodontine rodents species richness. Data represents number of species found in bands of one latitudinal degree in width, sources listed in Marquet (in press).

Variación en la riqueza de especies de roedores sigmodontinos. Los datos representan número de especies por banda latitudinal de un grado en ancho, fuentes en Marquet (in press).

Geoffroea) in the lowlands, and expansion of moorland (bofedales) environments in the highlands due to increased runoff . The proliferation of suitable habitats for phreatic species, converted a treeless, barren environment into a parkland/woodland in the basins containing the former lakes, present day salars.

The high similarity values between the northern and the mediterranean bog vegetation, suggest a high-altitude corridor between 23°S and 29°S in the area were no fossil records are available. Migration might have continued downvalley at ca. 27°S, possibly through the Transversal Valleys, which connect the Andes with the lowlands. Southward migration may have continued through coastal and inland (Longitudinal Valley) environments, favoured by the southward increase of westerly precipitation.

The desertic corridor may have remained open during glacial periods, as the lowering of temperature, and the increase of easterly flow brought enough effective moisture to produce glacial advances, and high lake levels in the Altiplano area and the western flank of the Andes between 18°S and 29°S.

The transandean corridor

The presence of *Stegomastodon humboldti, Glossotherium lettsomi, Hippocamelus bisulcus,* and *Antifer* sp. in the Chilean central nucleus, suggest close affinities with the Pleistocene land-mammal faunas from the Argentinian Patagonia (these taxa have not been found unequivocally in Perú nor Bolivia; Hoffstetter 1986, Hoffstetter in Marshall *et al.* 1984, Marshall & Sempere 1992) (Table 4). According to Casamiquela (1969), the species *Glossotherium lettsomi* should not be considered as an integrant of the land mammal faunas of central Chile, since the single finding of this species is located very close to the Argentinian border in the Valle de Lonquimay (ca. 38°S). In his view, the habitat of this species is restricted to the Patagonian steppe, therefore, the differences in the vegetation of the eastern and western flanks of the Andes should have acted as an ecological barrier to dispersal, impeding a trans-Andean faunal exchange.

The modern andean vegetation between 30°S and 39°S occurs along a marked west-east gradient with an eastward decrease in

TABLE 6

Indicator fossil-mammal taxa used in this study to determine possible routes and directions of migration

Mamíferos fósiles indicadores usados en este estudio para determinar posibles rutas y direcciones de migración

Taxa	Latitudinal range
Megatherium medinae	13°30'(ca.20°00'-33°30'S)
Scelidodon chiliense	13°30'(ca.20°00'-33°30'S)
Macrauchenia patachonica	10°50'(ca.22°20'-33°10'S)
Cuvieronius hyodon	19°20'(ca.19°40'-39°00'S)
Equus curvidens	16°25'(ca.22°20'-38°45'S)
Hippidiun sp.	6°00'(ca.28°30'-34°30'S)
Glossotherium and dermal oscicles (undet. *Mylodontinae*)	6°31'(ca.31°55'-38¿¿26S)
Hippocamelus bisulcus	2°35'(31°55'-34°30S)
Antifer sp.	2°35'(31°55'-34°30S)
Stegomastodon humboldti	9°00'(ca.32°30'-41°30'S)

precipitation, and slight increase in continentality. The average altitude of the Andes and the Coastal Range decreases progressively south of 35°S, causing similar degrees of continentality at both sides of the Andes. This factor has favoured floristic interchange, as inferred from relatively high similaritiy percentages across the Andes (28.4%) at 36°S and 38°S, compared to low values (19.4%) at 35°S (Fig.7b) (Villagrán et al. 1994). The Lonquimay area is characterized by a narrowing and significant lowering of the Andes Cordillera, and westward penetration of the Patagonian steppe towards the Alto Biobio river area.

We propose a trans-Andean migration path of a fraction of the Patagonian faunas to central Chile through the low-altitude areas at 38°S during interstades and/or interglacials of the Pleistocene, when ice-free conditions permitted the exchange of flora and fauna. Findings of *Hippocamelus bisulcus, Antifer,* and mylodontine dermal oscicles (that may well represent *Glossotherium lettsomi,* or at least *Glossotherium* sp.) in Quereo (30°S) and Tagua Tagua (34°S) (Moreno & Marshall in prep.), support a westward and (later) northward migration of these taxa in central Chile. The existence of the Chilean
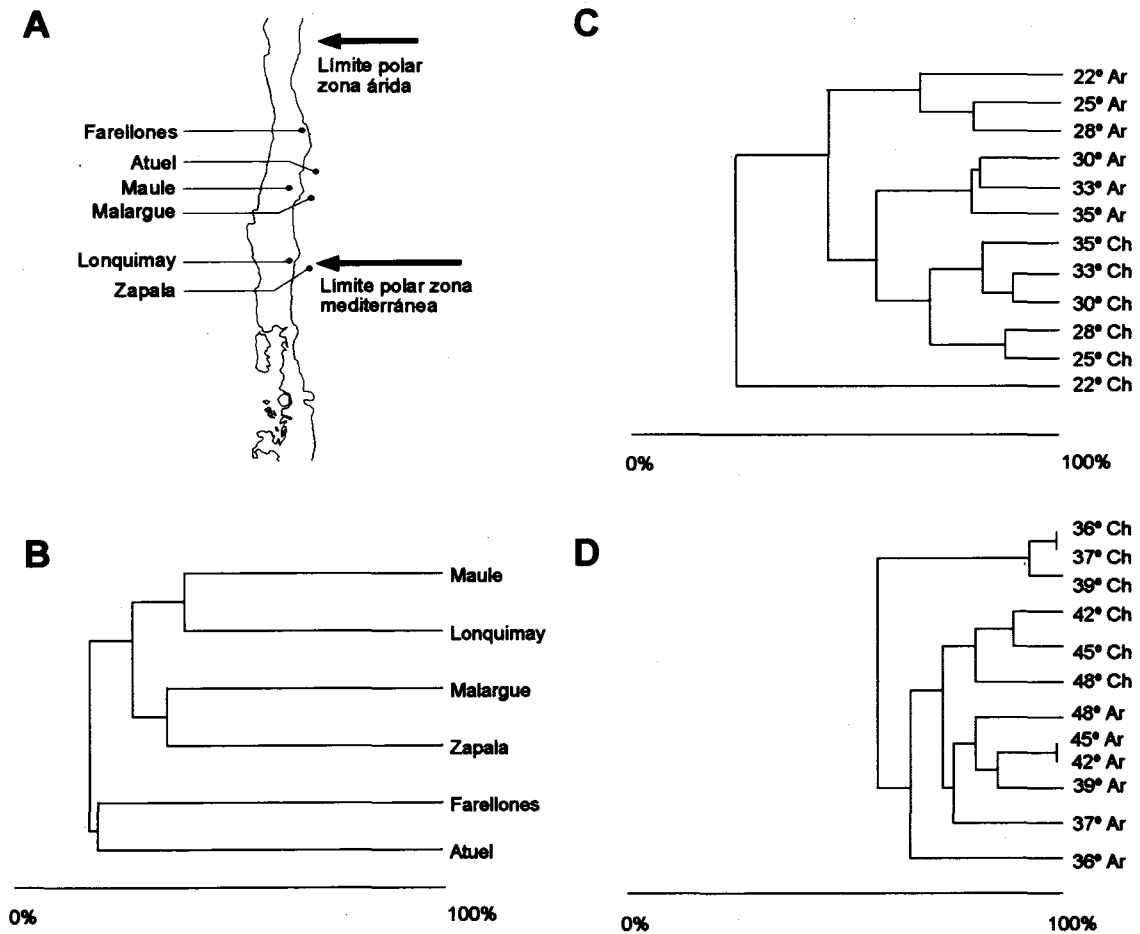

Fig. 7: Dendrograms showing floristic (a,b) and faunistic (c,d) similarities at both sides of the Andes of central Chile and Argentina. Faunistic data represent species of sigmodontine rodents found at altitudinal transects encompassing similar areal extent in Chile and Argentina.

Dendrogramas de similitud florística (a,b) y faunística (c,d) a ambos lados de los Andes en Chile central y Argentina. Los datos de fauna representan especies de roedores sigmodontinos registrados en transectos altitudinales de abarcan una extensión areal similar en Chile y Argentina.

mastodon species *Stegomastodon humboldti* in central Chile, further supports a trans-Andean corridor, since its sister (ancestral?) species *Stegomastodon superbus* is restricted to Argentine Patagonia.

Land bridges and vicariant patterns in central Chile

Tamayo & Frassinetti (1980) reported mastodon findings in the western side of Cordillera de Piuchué in Isla Grande de Chiloé. The biogeograhic significance of this finding (the southernmost finding of mastodons in Chile) lies in the fact that, nowadays, this island is separated from the mainland by the Canal de Chacao, a natural barrier to dispersal.

Interestingly, the existence of *Pseudalopex fulvipes* (a modern species of fox) and other land mammals (Osgood 1943) endemic to Chiloé, attest for a former connection of this island with the mainland. Medel *et al.* (1990) and Jiménez *et al.* (1991) have reported findings of living specimens of *P. fulvipes* in the Cordillera de Nahuelbuta (37°45'S 72°44'W). The coincidence of these findings with the presence of outliers of Magellanic Moorland on the mountaintops of Cordillera de Piuchué and Nahuelbuta (Ruthsanz & Villagrán 1991), suggests that the Quaternary glaciations exherted significant shifts in the distribution of plant and animal taxa characteristic of southern latitudes and high elevations (northward and downvalley migrations; Villagrán 1988, Moreno in prep., Heusser in prep.), and that the Coastal Range acted as a refuge as climate changed rapidly (Ashworth & Hoganson1993, Moreno in prep.) during the last deglaciation.
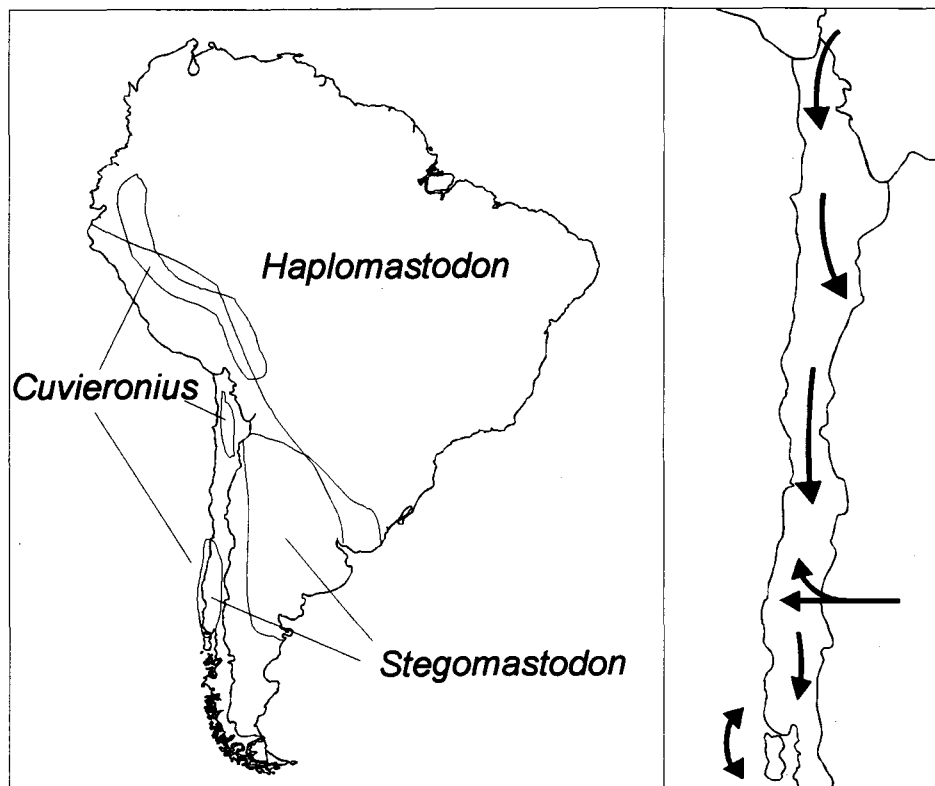

Fig. 8: Map showing distribution ranges of mastodont genera in South America (modified from Paula Couto 1979). (*Haplomastodon* H, *Stegomastodon* S, and *Cuvieronius* C). The arrows indicate the corridors postulated in this study through which migration might have occured during the Pleistocene.

Mapa de los rangos de distribución de los génros de mastodontes Sudamericanos (modificado de Paula Couto 1979) (*Haplomastodon* H, *Stegomastodon* S, y *Cuvieronius* C). Las flechas muestran los corredores postulados en este trabajo a través de los cuales las migraciones pudieron haber ocurrido durante el Pleistoceno.

Climap (1981) proposed a lowering of ca.150 m in sea level at the height of the Last Glacial Maximum (LGM, 18,000 yr BP) as a consequence of glacioeustatism. As sea level dropped, significant portions of the continental shelf were exposed worldwide. The 150 m. depth around the modern coasts of the Canal de Chacao area lies at a significant distance off the coast of Golfo Coronados (Instituto Hidrográfico de la Armada de Chile 1974), distant enough to have established a wide land bridge connecting Chiloé and the mainland during the LGM.

Considering the geographic distribution of *Stegomastodon humboldti* and *Pseudalopex fulvipes* and their relationship to their sister species *S. superbus, and P. culpaeus* and *P. griseus,* respectively, it is possible to explain their speciation in terms of the fragmentation of a former wide distribution. The Quaternary climate changes had a primordial role in the establishment of ecological and physical barriers to dispersal. In the case of *Stegomastodon humboldti*, cladogenesis must have occurred during glacial periods as glacial ice blocked trans-Andean corridors, producing isolation of disjunct populations and promoting differentiation. Conversely, the cladogenesis of *Pseudalopex fulvipes* must have occurred during interglacials, when the rise in sea level closed land bridges through the continental shelf, producing geographic isolation in Isla de Chiloé.

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