THE TINGUIRIRICA FAUNA OF CHILE AND THE EARLY STAGES OF "MODERNIZATION" OF SOUTH AMERICAN MAMMAL FAUNAS[1]

(With 7 figures)

DARIN A. CROFT[2]
JOHN J. FLYNN[3]
ANDRÉ R. WYSS[4]

ABSTRACT: The evolution of South American Cenozoic mammal communities is generally seen as encompassing three distinct "faunal strata". The recently formalized Tinguiririca South American Land Mammal "Age" (SALMA) represents the earliest interval within Simpson's second faunal stratum and presents an exceptional opportunity to investigate a remarkable period of faunal "modernization" in South America. Of the 25 species currently recognized from the Tinguiririca Fauna, 17 are notoungulates, illustrating the group's diversity and abundance during this interval. Two-thirds of notoungulate species are hypsodont, in marked contrast with earlier faunas, indicating the nearly simultaneous convergent appearance of this feature in several notoungulate clades. The most diverse and abundant notoungulates at Tinguiririca are archaeohyracids (six species, the highest diversity for any locality known to date), notohippids (four species), and interatheriids (two species). Large, brachydont notoungulates are scarce. In addition to the fauna from the type locality in central Chile, several Patagonian faunas of Tinguiririran age provide important complementary taxonomic and biogeographic data. Hegetotheriids are absent from the Tinguiririca Fauna but are reported from Tinguiririran faunules in Patagonia. Trachytheriine mesotheriids are uncommon during the Tinguiririran; they have previously been reported only from Rocas Bayas in Rio Negro, though a recently prepared Chilean specimen indicates presence of the group just north of Tinguiririca during this SALMA. Faunal hypsodonty, cenograms, and rainfall estimates have previously been used to suggest that the Tinguiririca Fauna is the earliest open-habitat community in South America. This conclusion is corroborated herein through an ecological diversity analysis (EDA) that consolidates browsers and grazers into a single dietary category, to counter potential errors in hypsodonty-based dietary interpretations of extinct taxa. The statistically significant results of a multivariate discriminant model based on this EDA confirm the resemblance of the Tinguiririca Fauna to modern open habitat communities, further supporting the presence of open habitats in high latitude South America by earliest Oligocene time, despite the apparent lack of a substantial regional climatic shift across the Eocene-Oligocene Transition in Argentine Patagonia.

Key words: South American Land Mammal "Age". Notoungulate. Ecological diversity analysis. Tinguiririca Fauna. Chile.

RESUMO: A Fauna de Tinguiririca do Chile e os primeiros estágios de "modernização" das faunas de mamíferos sul-americanos.

A evolução das comunidades de mamíferos cenozóicos sul-americanos é geralmente vista como abrangendo três "estratos faunísticos" distintos. A recentemente formalizada "Idade" Tinguiririquense de Mamíferos Terrestres Sul-americanos representa o intervalo mais antigo do segundo estrato faunístico de Simpson e fornece uma oportunidade excepcional para se investigar um período notável de "modernização" faunística na América do Sul. Das 25 espécies atualmente reconhecidas para a Fauna de Tinguiririca, 17 são de notoungulados, ilustrando a diversidade e a abundância do grupo durante este intervalo. Dois terços das espécies de notoungulados são hipsodontes, em contraste marcante com as faunas mais antigas, indicando um surgimento convergente quase simultâneo desta característica em vários clados de notoungulados. Os mais diversos e abundantes notoungulados em Tinguiririca são os representantes de Archaeohyracidae (seis espécies, a mais alta diversidade para qualquer localidade conhecida), de Notohippidae (quatro espécies), e de Interatheriidae (duas espécies). Notoungulados de grande porte braquiodontes são raros. Além da fauna da localidade tipo no centro Chile, várias faunas da Patagônia, de idade Tinguiririquense, fornecem importantes dados taxonômicos e biogeográficos complementares. Os representantes de Hegetotheriidae estão ausentes

da Fauna de Tinguiririca, mas são reportados para a fáunula Tinguiririquense na Patagônia. Os Trachytheriinae, representantes dos Mesotheriidae, não são comuns no Tinguiririquense; eles foram previamente registrados apenas para Rocas Bayas em Rio Negro, embora um espécime recentemente preparado indique a presença do grupo apenas ao norte de Tinguiririca durante a "Idade" de Mamíferos Terrestres Sul-americanos. A hipsodontia faunística, os cenogramas e as chuvas estimadas foram previamente utilizados para sugerir que a Fauna de Tinguiririca é a mais antiga comunidade de habitat aberto na América do Sul. Esta conclusão é aqui corroborada através de uma análise de diversidade ecológica (ADE), que consolida pastadores e ramoneadores em uma única categoria de dieta alimentar, indo contra erros potenciais de interpretação de uma dieta com base na hipsodontia de táxons extintos. Os resultados estatisticamente significantes de um modelo discriminante multivariado nesta ADE confirmam a semelhança da Fauna de Tinguiririca com as comunidades de habitat aberto, suportando, além disso, a existência de habitats abertos em altas latitudes na América do Sul durante o início do Oligoceno, apesar da aparente ausência de mudanças climáticas regionais substanciais durante a transição Eoceno-Oligoceno na Patagônia Argentina.

Palavras-chave: "Idade" Mamíferos Terrestres Sul-americanos. Notoungulados. Análise de diversidade ecológica. Fauna de Tinguiririca. Chile.

INTRODUCTION

The evolution of South American Cenozoic mammal communities is generally described as a succession of three "faunal strata" (SIMPSON, 1980; FLYNN & WYSS, 1998; Fig.1). The oldest of these – spanning roughly the Paleocene-Eocene –, consists of communities dominated by the continent's "original inhabitants" (e.g., endemic ungulates, marsupials, xenarthrans) (MARSHALL & MUIZON, 1988). The second stratum is marked by the arrival of rodents (WYSS et al., 1993) and primates (HOFFSTETTER, 1969) and the appearance of notable morphological advances within many of the original endemic clades. The final stratum is marked by extensive late Cenozoic interchange with North America and the extinction of many of the last remaining endemic clades (WEBB, 1976; MARSHALL et al., 1982). The recently formalized Tinguiririan South American Land Mammal "Age" (SALMA) represents the earliest interval within Simpson's second faunal stratum (WYSS et al., 1994; FLYNN et al., 2003). As such, the Tinguiririca Fauna of central Chile (the best-sampled and most diverse fauna of Tinguiririan age) presents an exceptional opportunity to investigate the transition from Stratum 1 to 2, a remarkable period of faunal "modernization" in South America (PASCUAL et al., 1985; FLYNN & WYSS, 1998; FLYNN et al., 2007).

In addition to the fauna from the type locality in central Chile, a handful of Tinguiririan SALMA faunas occur in Patagonia (see FLYNN et al., 2003); although most of these faunas remain poorly sampled, they provide important, complementary taxonomic and biogeographic data. One of these, Cañadón Blanco in Chubut, Argentina, discovered by Santiago Roth (ROTH, 1901, 1903), was long mistakenly considered a temporally mixed fauna

(e.g., SIMPSON, 1967). In light of our findings in Chile, most of the fossils from Cañadón Blanco are now seen as pertaining to the Tinguiririan (WYSS et al., 1994; FLYNN et al., 2003), but the locality has yet to be relocated. Ameghino (AMEGHINO, 1901, 1902a) designated a faunally distinctive interval at the Gran Barranca south of Lago Colhué Huapí in Chubut as the "Astraponotéen plus supérieure" (APS) level; he later subsumed the APS within the Mustersan SALMA, but this post-Mustersan/pre-Deseadan faunal interval is now recognized as pertaining to the Tinguiririan as well (WYSS et al., 1994; BOND et al., 1996; FLYNN et al., 2003; see also KAY et al., 1999; CARLINI et al., 2005). Other smaller Argentine faunules of Tinguiririan age include Rocas Bayas in Río Negro province and a variety of others in Chubut (e.g., Laguna La Bombilla, Lomas Blancas/La Curandera, Campo de Velázquez/Paso de Indios, and Laguna Seca) (BOND et al., 1997; HITZ et al., 2000; FLYNN et al., 2003). The new Chilean locality of Cachapoal may also be of Tinguiririan age (FLYNN & WYSS, 2004; HITZ et al., 2006) as might other recently discovered central Chilean localities yielding characteristic Tinguiririan taxa (e.g., various archaeohyracid and interatheriid species).

The purpose of the present brief report is twofold: to provide an overview of Tinguiririan ungulates in a biogeographic context and to apply a new ecomorphological method of paleohabitat reconstruction to the Tinguiririca Fauna. We recognize that the names Notohippidae, Notopithecinae, Trachytheriinae, Archaeohyracidae, and Hegetotheriinae likely refer to paraphyletic groups, but we continue to use them in their traditional sense until phylogenetically based names of the relevant clades are formally defined.
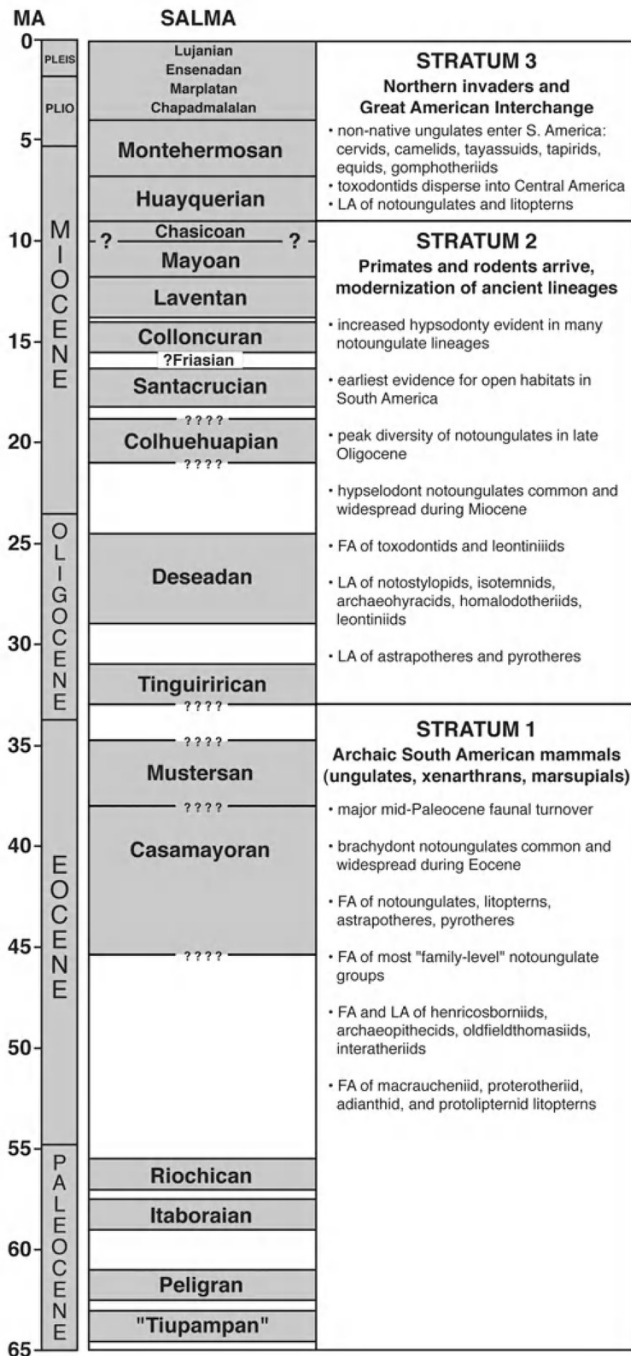
Figure 1 chart

MA (left axis): 0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65

Epochs: PLEIS, PLIO, MIOCENE, OLIGOCENE, EOCENE, PALEOCENE

SALMA

Lujanian
Ensenadan
Marplatan
Chapadmalalan
Montehermosan
Huayquerian
? Chasicoan ?
Mayoan
Laventan
Colloncuran
?Friasian
Santacrucian
????
Colhuehuapian
????
Deseadan
Tinguiririan
????
????
Mustersan
????
Casamayoran
????
Riochican
Itaboraian
Peligran
"Tiupampan"

STRATUM 3
Northern invaders and
Great American Interchange
• non-native ungulates enter S. America: cervids, camelids, tayassuids, tapirids, equids, gomphotheriids
• toxodontids disperse into Central America
• LA of notoungulates and litopterns

STRATUM 2
Primates and rodents arrive, modernization of ancient lineages
• increased hypsodonty evident in many notoungulate lineages
• earliest evidence for open habitats in South America
• peak diversity of notoungulates in late Oligocene
• hypselodont notoungulates common and widespread during Miocene
• FA of toxodontids and leontiniids
• LA of notostylopids, isotemnids, archaeohyracids, homalodotheriids, leontiniids
• LA of astrapotheres and pyrotheres

STRATUM 1
Archaic South American mammals (ungulates, xenarthrans, marsupials)
• major mid-Paleocene faunal turnover
• brachydont notoungulates common and widespread during Eocene
• FA of notoungulates, litopterns, astrapotheres, pyrotheres
• FA of most "family-level" notoungulate groups
• FA and LA of henricosborniids, archaeopithecids, oldfieldthomasiids, interatheriids
• FA of macraucheniid, proterotheriid, adianthid, and protolipternid litopterns

Fig.1- "Three stratum" model of mammalian faunal succession in South America highlighting major events in ungulate evolution. The three strata are calibrated to the timescale on the left, but the events listed for each stratum are not. FA and LA represent First Appearance and Last Appearance, respectively. The SALMA sequence is based primarily on FLYNN & SWISHER (1995) and FLYNN et al. (2003); the four youngest SALMAs have been consolidated to increase legibility.

RESULTS AND DISCUSSION

UNGULATE DIVERSITY AND BIOGEOGRAPHY

Ungulates are the most conspicuous component of the Tinguiririca Fauna, accounting for more than two-thirds of alpha diversity (Tab.1). Nearly all of these are notoungulates (Fig.2), a group whose diversity peaked in the Oligocene (CIFELLI, 1985b; MARSHALL & CIFELLI, 1989; CROFT, 1999). Many of these ungulates are present in other Tinguiririran faunas and are important biochronologically, permitting the recognition of Tinguiririran faunas in other parts of the continent (HITZ et al., 2000, 2006; CROFT et al., 2003a; REGUERO et al., 2003a).

The following section provides an overview of the major groups of Tinguiririran ungulates in their biogeographic and temporal contexts. Figure 3 provides a map of the main Tinguiririran localities and other localities discussed in the text. Recent studies suggest that the peculiar "Divisadero Largo Fauna" of west-central Argentina – generally considered to be late Eocene (BOND, 1991; FLYNN & SWISHER, 1995; FLYNN et al., 2003) – is a mixed fauna including both ?early-middle Eocene specimens (from the Divisadero Largo Formation) and ?early Miocene specimens (from the overlying Mariño Formation) (CERDEÑO et al., 2005; LÓPEZ & MANASSERO, 2006). We therefore follow these authors in rejecting the "Divisaderan" SALMA, and below we treat specimens from this locality as either Eocene or Miocene in age.

NOTOSTYLOPIDAE

A single specimen from the type locality of the Tinguiririca Fauna marks the last appearance of the Notostylopidae (WYSS et al., 1994; FLYNN et al., 2003) but additional unprepared notostylopid specimens may be present in the Chilean collections. The Tinguiririca notostylopid most closely resembles Otronia muehlbergi from the Mustersan of Chubut (SIMPSON, 1967) and Boreastylops lumbrerensis from the Casamayoran of Salta Province (VUCETICH, 1980), but likely represents a new species (WYSS et al., 1994).

Notostylopids are first recorded from the Itaboraian and Riochican of Chubut (BOND, 1986). They are abundant and characteristic components of Patagonian Casamayoran faunas (SIMPSON, 1948, 1984; BOND, 1986) and are present in both subdivisions of that SALMA, the Vacan and Barrancan (CIFELLI, 1985a).

TABLE 1. Tinguiririca faunal list and corresponding ecomorphological variables for each taxon.

Taxon	Order	Family	Diet	Locomotion	Mass
Klohnia charrieri	Marsupialia	Groeberiidae	FR	A	I
Polydolops abanicoi	Marsupialia	Polydolopidae	FR	A	IV
Pascualdelphys fierroensis	Marsupialia	(Didelphimorphia)	I	A	I
gen. et sp. indet.	Xenarthra	Dasypodidae	O	T	V
Pseudoglyptodon chilensis	Xenarthra	Phyllophaga (i.s.)	FO	T	VI
Indaleciinae gen. et sp. nov.	*Incertae sedis*	*incertae sedis*	FO	T	III
gen. et sp. nov.	Rodentia	?Dasyproctidae	FR	T	IV
?Prolagostomus sp.	Rodentia	Chinchillidae	FO	T	III
gen. et sp. nov.	Notoungulata	Notostylopidae	FO	T	VI
Notopithecinae gen. et sp. nov.	Notoungulata	Interatheriidae	FO	T	I
Santiagorothia chiliensis	Notoungulata	Interatheriidae	FO	T	IV
Archaeotypotherium tinguiriricaense	Notoungulata	Archaeohyracidae	FO	T	V
Archaeotypotherium pattersoni	Notoungulata	Archaeohyracidae	FO	T	VI
Protarchaeohyrax gracilis	Notoungulata	Archaeohyracidae	FO	T	IV
Protarchaeohyrax intermedium	Notoungulata	Archaeohyracidae	FO	T	II
Pseudhyrax strangulatus	Notoungulata	Archaeohyracidae	FO	T	V
Pseudhyrax eutrachytheroides	Notoungulata	Archaeohyracidae	FO	T	V
cf. *Rhyphodon* sp.	Notoungulata	Isotemnidae	FO	T	XI
Trigonolophodon cf. *elegans*	Notoungulata	Homalodotheriidae	FO	T	IX
Periphragnis sp.	Notoungulata	Homalodotheriidae	FO	T	IX
Eomorphippus sp. nov.	Notoungulata	Notohippidae	FO	T	VIII
"*Eomorphippus*" cf. *pascuali*	Notoungulata	Notohippidae	FO	T	VII
gen. et sp. nov. A (large)	Notoungulata	Notohippidae	FO	T	VIII
gen. et sp. nov. B (small)	Notoungulata	Notohippidae	FO	T	VI
incertae sedis	Notoungulata	Leontiniidae	FO	T	X

Dietary abbreviations: FR, frugivore; FO, folivore; I, insectivore; O, omnivore. Locomotor abbreviations: A, arboreal; T, terrestrial. Body mass categories: I, 1-200 g; II, 201-400 g; III, 401-800 g; IV, 801-1600 g; V, 1.6-3.2 kg; VI, 3.2-6.4 kg; VII, 6.4-12.8 kg; VIII, 12.8-25.6 kg; IX, 25.6-51.2 kg; X, 51.2-102.4 kg; XI, 102.4-204.8 kg; XII, 204.8+ kg.

Notostylops itself is especially well-represented in Casamayoran assemblages (*e.g.*, SIMPSON, 1932a, 1948; RIGGS & PATTERSON, 1935), forming the basis for Ameghino's original designation for these faunas, the "*Notostylops* beds" (SIMPSON, 1984). *Otronia* is the only described Mustersan notostylopid (SIMPSON, 1948; BOND, 1986), although LÓPEZ (1997) has noted a new notostylopid species from Antofagasta de la Sierra, an Eocene fauna of uncertain SALMA assignation.

The Tapado Fauna documents the presence of notostylopids in central Chile during the late Eocene, probably during the Casamayoran (WYSS *et al.*, 1996; FLYNN *et al.*, 2005a). Notostylopids have not been recorded from the Divisadero Largo Fauna of Mendoza province (SIMPSON *et al.*, 1962). This absence is likely an artifact of sampling given that notostylopids were present throughout Patagonia, northwest Argentina, and central Chile during this interval.

INTERATHERIIDAE

The Tinguiririan is unique among SALMAs in documenting the co-occurrence of both traditional subfamilies of interatheriids: low-crowned notopithecines and higher crowned interatheriines (WYSS *et al.*, 1994; HITZ *et al.*, 2000, 2006; FLYNN *et al.*, 2003). In this regard, the interatheriids mimic the Tinguirirican SALMA as a whole, in that various "archaic" taxa co-occur with members of clades marked by more derived morphologies (WYSS *et al.*, 1993, 1994; FLYNN *et al.*, 2003).
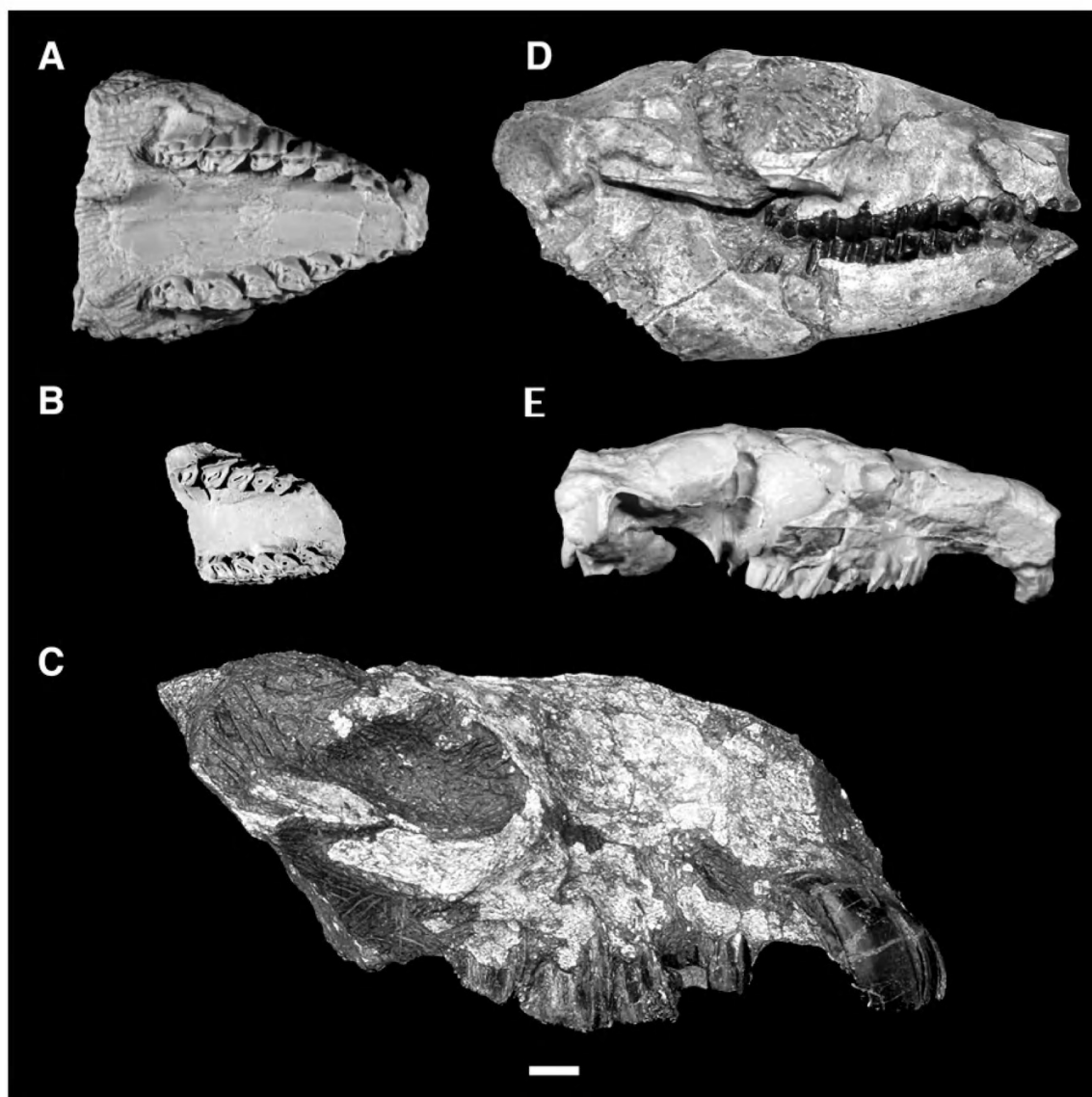
Fig.2- Representative notoungulate specimens from the Tinguiririca Fauna of central Chile. A, SGO PV 2923, holotype palate of *Archaeotypotherium tinguiriricaense*, occlusal view (cast); B, SGO PV 2998, palate referred to *Protarchaeohyrax intermedium*, occlusal view (cast); C, SGO PV 3046, skull of *Eomorphippus* sp. nov.; D, SGO PV 2914, holotype skull and mandibles of *Santiagorothia chiliensis* (left lateral view, reversed); E, SGO PV 2900, skull referred to *Archaeotypotherium tinguiriricaense*, right lateral view. Scale bar = 1cm.

The Tinguiririca Fauna itself includes two interatheriids: *Santiagorothia* (a basal interatheriine; Fig.2D) and a new species of basal interatheriid (HITZ *et al.*, 2000, 2006; FLYNN *et al.*, 2003). Besides in the Tinguiririca Valley, *Santiagorothia* occurs at virtually every Tinguiririca locality in Patagonia with the exception of Cañadón Blanco (HITZ *et al.*, 2000), whereas the new basal interatheriid appears to be endemic to central Chile (HITZ *et al.*, 2006). The interatheriine *Eopachyrucos* occurs in the Tinguirirican APS level of Gran Barranca, Cañadón Blanco, and Rocas Bayas; the interatheriine *Proargyrohyrax* has been reported from the Gran Barranca (LÓPEZ *et al.*, 2005) and Lomas Blancas (HITZ *et al.*, 2000). Outside of Chile, basal interatheriids of Tinguirirican age have only been reported from the Gran Barranca (*e.g.*, La Cancha; LÓPEZ *et al.*, 2005). Interestingly, a basal interatheriid distinct from that

of the Tinguiririca Fauna occurs at the more recently discovered locality of Cachapoal (HITZ *et al.*, 2006); at least one currently unidentified species of interatheriine is also present in that fauna.

The only interatheriids present prior to the Tinguiriri鈴can are basal members of the clade (*i.e.*, notopithecines or non-interatheriines), the earliest occurrence of which is in the Riochican of Patagonia (SIMPSON, 1935b, 1967; BOND, 1986). *Notopithecus* and similar forms are abundant and characteristic of Casamayoran faunas (SIMPSON, 1967), although they are apparently restricted to the Barrancan (younger) subdivision in Patagonia (CIFELLI, 1985a).

Guilielmoscottia occurs in the Mustersan of Patagonia (SIMPSON, 1967; MARSHALL *et al.*, 1983), and may also occur in the Tinguirirican (LÓPEZ *et al.*, 2005). A diminutive basal interatheriid, *Punapithecus*, has been described from the indeterminate Eocene fauna of Antofagasta de la Sierra (LÓPEZ & BOND, 1995; LÓPEZ, 1997). Two other small basal interatheriids are now known from Eocene deposits in Chile, a new diminutive taxon from the Tapado Fauna and *Antepithecus* from the Azufre Fauna (HITZ *et al.*, 2006). As is the case for notostylopids, interatheriids are absent from Divisadero Largo, probably due to small sample sizes.

Fig.3- Map of primary localities discussed in the text; localities with Tinguiririan-aged intervals are designated by a star.

SHOCKEY *et al.* (2004) reported a small, indeterminate interatheriine from the Paleogene fauna of Santa Rosa in the lowland Peruvian Amazon. That locality has been considered late Eocene (possibly Mustersan) in age (CAMPBELL *et al.*, 1996, 2004; CAMPBELL, 2004), which would make this taxon the earliest known interatheriine. The interatheriine and the other notoungulates from Santa Rosa are more indicative of an Oligocene age for the fauna, however (SHOCKEY *et al.*, 2004), and given the general reliability of notoungulates for biochronologic correlation, this age assignment seems more likely. Regardless, Santa Rosa is the northernmost record of interatheriids in South America prior to the middle Miocene.

MESOTHERIIDAE

Mesotheriids are rare in Tinguiririran faunas; no specimens have been collected from the type locality in Chile, nor have any been reported from the APS level at Gran Barranca or Cañadón Blanco (FLYNN *et al.*, 2003). A trachytheriine specimen from Rocas Bayas in Río Negro, Argentina does record the presence of the clade in western Argentina during this interval, however (BOND *et al.*, 1997). Additionally, we have identified a trachytheriine upper molar from the Cachapoal Fauna of central Chile. Cachapoal may correlate with or predate a level preliminarily dated at 29.3 ± 0.1 Ma (*i.e.*, early Deseadan SALMA or older) and thus may be of Tinguiririran age (FLYNN & WYSS, 2004). This chronological assessment is supported by the occurrence of *Protarchaeohyrax* and *Archaeotypotherium* at Cachapoal, both typical Tinguiririran archaeohyracids (CROFT *et al.*, 2003a; FLYNN *et al.*, 2003; REGUERO *et al.*, 2003a; see also below). A relatively large mesotheriid (?trachytheriine) mandible from a third central Chilean fauna of potential Tinguiririran age further documents the presence of mesotheriids in central Chile at this time. The clade has long been reported from Divisadero Largo of Mendoza, Argentina (SIMPSON & MINOPRIO, 1949) and this was thought to be the oldest occurrence of mesotheriids (REGUERO & CASTRO, 2004). It appears these specimens more likely derive from the overlying Mariño Formation, however, and are therefore Miocene in age (CERDEÑO *et al.*, 2005).

Mesotheriids apparently increased in abundance after the Tinguiririran; *Trachytherus* is a characteristic component of Deseadan faunas and is arguably the best known late Oligocene typothere (MARSHALL *et al.*, 1986; REGUERO & ESCRIBANO, 1996). Specimens of *Trachytherus* (or closely related forms)

have been collected from Deseadan faunas in Patagonia (PATTERSON, 1934; MARSHALL *et al.*, 1986; REGUERO & ESCRIBANO, 1996), Bolivia (MACFADDEN *et al.*, 1985; SYDOW, 1988; SHOCKEY, 1997a, b; SHOCKEY *et al.*, 2007), Perú (SHOCKEY *et al.*, 2006), and Uruguay (BOND *et al.*, 1998) – essentially from all reasonably well-sampled Deseadan faunas. The absence of mesotheriids in the Tremembé Formation of Brazil (BERGQVIST & RIBEIRO, 1998; VUCETICH & RIBEIRO, 2003) and the Paleogene Santa Rosa Fauna of lowland Perú (CAMPBELL *et al.*, 2004; SHOCKEY *et al.*, 2004), if not attributable to small sample sizes, may reflect true absence (see below).

Until recently, mesotheriids were unknown from the earliest Miocene Colhuehuapian SALMA (MARSHALL *et al.*, 1983; CROFT *et al.*, 2003b, 2004; FLYNN *et al.*, 2005b; KRAMARZ *et al.*, 2004). Trachytheriines therefore became extinct between the Deseadan and Colhuehuapian SALMAs, and mesotheriines evidently originated. Based on the geographic and temporal distributions of the earliest diverging mesotheriines (Fig.4), it seems that this clade differentiated in the middle latitudes of South America (FLYNN *et al.*, 2002; CROFT *et al.*, 2003b, 2004). No mesotheriids are recorded from low latitudes (*i.e.*, north of 10° S; see KAY *et al.*, 1997; LINARES, 2004), however, suggesting the presence of a geographic or ecological barrier to their dispersal during much of the Cenozoic.

ARCHAEOHYRACIDAE

The Tinguiririran is the "Age of Archaeohyracids"; this assemblage – paraphyletic though it may be – exhibited greater species richness during this period of time than at any other point in its relatively short history (CROFT, 1999; CROFT *et al.*, 2003a). Not only did it achieve its own peak diversity during this period, archaeohyracid alpha diversity at Tinguiririca is among the highest exhibited by any "family-level" notoungulate group for any SALMA. The reasons for this short-lived species richness are unknown but may relate to the group's early acquisition of hypsodont cheek teeth (SIMPSON, 1967; CROFT *et al.*, 2003a). Archaeohyracids are quite abundant at Tinguiririca; in this regard, Tinguiririca is more similar to Salla, Bolivia than typical Patagonian faunas.

At least six archaeohyracids are known from Tinguiririca, two species each of *Archaeotypotherium* (Fig.2A, E), *Protarchaeohyrax* (Fig.2B), and *Pseudhyrax* (CROFT *et al.*, 2003a; FLYNN *et al.*, 2003, REGUERO *et al.*, 2003a). *Archaeotypotherium* and

Protarchaeohyrax are recorded from the APS level at Gran Barranca and from Cañadón Blanco (ROTH, 1903; SIMPSON, 1967; CROFT *et al.*, 2003a; REGUERO *et al.*, 2003a) and are characteristic of the Tinguiririran SALMA (FLYNN *et al.*, 2003). Tinguiririca is the only Tinguiriririan fauna yet known to record *Pseudhyrax*, a taxon otherwise typical of the Mustersan of Patagonia (SIMPSON, 1967).

Although SIMPSON (1967) viewed archaeohyracids as spanning the latest Riochican through Deseadan, he noted that their occurrence in the Riochican is doubtful. They are first definitively known from Casamayoran faunas, with all currently described species from this temporal interval being referred to *Eohyrax*. Of the dozen

Casamayoran localities reviewed by CIFELLI (1985a), *Eohyrax* occurs only in three (Gran Barranca, Río Chico oeste, and possibly in Cañadón Lobo), illustrating the scarcity of archaeohyracids at that time. Moreover, these three localities predominantly or exclusively represent the younger of CIFELLI's (1985a) two subdivisions of the Casamayoran, the Barrancan, suggesting that the oldest securely identified archaeohyracids may be substantially younger than once thought. The northernmost report of *Eohyrax* is from the Cosquín Formation in Córdoba, Argentina (LINARES *et al.*, 1960). Archaeohyracids have also been reported from Antofagasta de la Sierra in northwest Argentina, a locality of uncertain age that may pertain to the
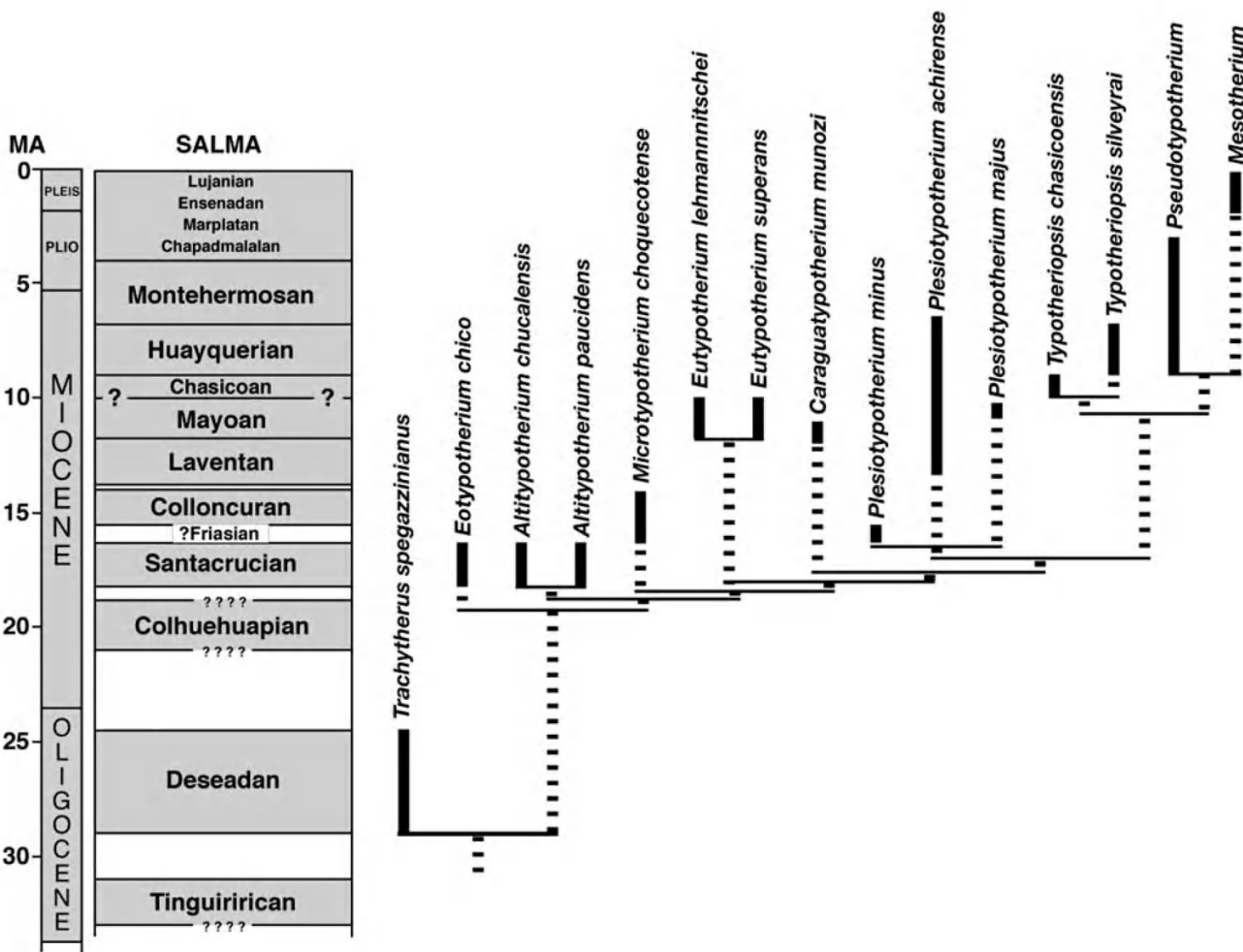

Fig.4- Time-calibrated phylogeny of mesotheriids based on the analysis of CROFT *et al.* (2004). Solid bars represent fossil occurrences, dashed lines represent inferred phylogenetic lineages. The four youngest SALMAs have been consolidated to increase legibility.

middle or even early Eocene (LÓPEZ, 1997; REGUERO & LÓPEZ, 1999; REGUERO *et al.*, in press). If this age assignment proves correct, it could represent the earliest occurrence of the group. A time calibrated phylogeny of archaeohyracids suggests that a major diversification took place at or just prior to the Tinguiririran, potentially coincident with the Eocene-Oligocene Transition (Fig.5).

Archaeohyracids are last recorded in the Deseadan where they are represented by species of *Archaeohyrax* (a primarily Deseadan taxon) and *Protarchaeohyrax* (known also from the Tinguiririran). Only *Archaeohyrax* occurs in Deseadan faunas of Patagonia (*e.g.*, CHAFFEE, 1952; MARSHALL *et al.*, 1986) and only *Protarchaeohyrax* occurs in the Fray Bentos Formation of Uruguay and northeastern Argentina (REGUERO *et al.*, 1995; BOND *et al.*, 1998; REGUERO *et al.*, 2003b). Both taxa occur in the Deseadan at Salla, Bolivia, but *Archaeohyrax* is much more abundant than *Protarchaeohyrax* there (REGUERO & CIFELLI, 1997). *Archaeohyrax* has also been reported preliminarily from the Tinguiririran Rocas Bayas locality (BOND *et al.*, 1997), which would be its oldest occurrence. Archaeohyracids have not yet been recorded from the late Oligocene Tremembé Formation of southeastern Brazil (BERGQVIST & RIBEIRO, 1998; VUCETICH & RIBEIRO, 2003) nor from the recently described Deseadan Moquegua Fauna of Perú (SHOCKEY *et al.*, 2006); neither have they been recorded from the Santa Rosa Fauna from the Amazonian lowlands of eastern Perú (CAMPBELL *et al.*, 2004; SHOCKEY *et al.*, 2004) nor Divisadero Largo in western Argentina (SIMPSON *et al.*, 1962). Given the sparse sampling at most of these localities and the scarcity of archaeohyracids in many faunas, these absences likely have little biogeographic significance.

HEGETOTHERIIDAE

Hegetotheriids are absent from the Tinguiririca Fauna and the APS level at Gran Barranca; their only Tinguiririran occurrence is at Cañadón Blanco (BOND, 1991; REGUERO, 1993; FLYNN *et al.*, 2003), although several hegetotheriids specimens are now
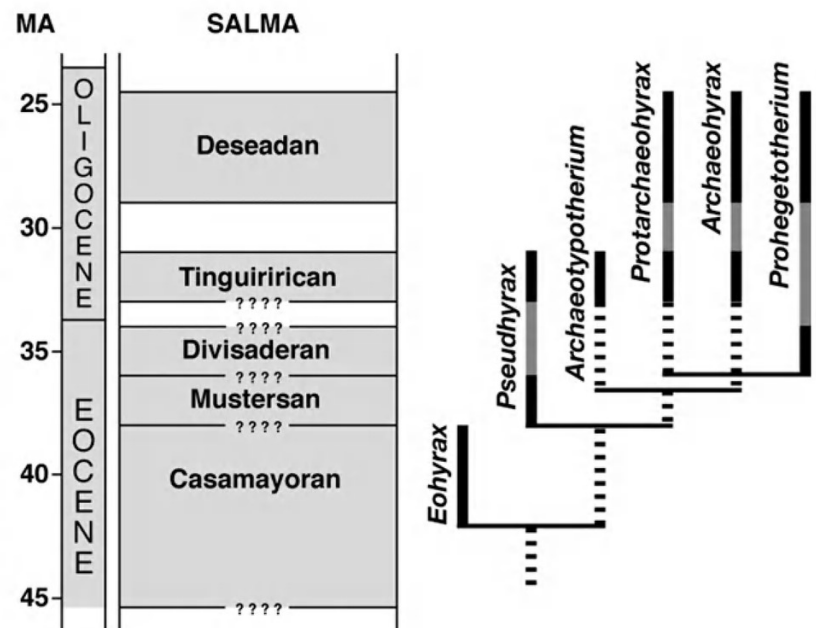

Fig.5- Time-calibrated phylogeny of archaeohyracids based on the analysis of CROFT *et al.* (2003a). Solid bars represent fossil occurrences; gray bars represent interpolated occurrences; dashed lines represent inferred phylogenetic lineages.

known from Cachapoal in central Chile, potentially also of Tinguiririran age. A skull and mandibles of a hegetotheriid from Divisadero Largo were previously thought to record the earliest Hegetotheriidae (SIMPSON & MINOPRIO, 1949; SIMPSON *et al.*, 1962), but this specimen likely comes from the Miocene Mariño Formation (LÓPEZ & MANASSERO, 2006).

Two hegetotheriid sub-groups are generally recognized (SIMPSON, 1945a; MCKENNA & BELL, 1997): Hegetotheriinae and Pachyrukhinae. Pachyrukhinae is universally considered monophyletic (CERDEÑO & BOND, 1998) and the clade is certainly recognizable as early as the Deseadan (LOOMIS, 1914; SIMPSON, 1945b; DOZO *et al.*, 2000) and potentially as early as the Tinguiririran (REGUERO, 1993). In contrast, Hegetotheriinae is likely paraphyletic, though it may include a monophyletic subset of Miocene taxa (CIFELLI, 1993; CROFT, 2000; CROFT *et al.*, 2004; CROFT & ANAYA, 2006). All Paleogene non-pachyrukhine hegetotheriids have been referred to *Prohegetotherium*, a taxon that occurs at Divisadero Largo, La Cantera, and various Deseadan localities in Patagonia (REGUERO & CERDEÑO, 2001, 2005; LÓPEZ *et al.*, 2005; but see LÓPEZ, 2002), and possibly in Oligocene faunas in Chile (*e.g.*, Cachapoal).

ISOTEMNIDAE

Large, low-crowned notoungulates are poorly represented at Tinguiririca, where only a single species of isotemnid, cf. *Rhyphodon*, has been identified. If this tentative identification is substantiated, it would represent a temporal and geographic range extension for the taxon, otherwise known only from the Mustersan of Lago Musters/ Cerro del Humo in Chubut (SIMPSON, 1967). *Anisotemnus*, *Periphragnis*, *Pleurostylodon*, and *Rhyphodon* are known from the Tinguirirican APS level of Gran Barranca (FLYNN *et al.*, 2003; LÓPEZ *et al.*, 2005), and an indeterminate isotemnid with affinities to *Periphragnis* has been reported from Rocas Bayas (BOND *et al.*, 1997). Both *Anisotemnus* and *Pleurostylodon* are known from the Casamayoran of Patagonia, with *Anisotemnus* previously restricted to the Barrancan (SIMPSON, 1967; CIFELLI, 1985a); *Pleurostylodon* has also recently been identified from the ?Casamayoran Tapado Fauna of central Chile (FLYNN *et al.*, 2005a). Besides various Tinguirirican localities, *Periphragnis* is known only from the Mustersan of Patagonia (WYSS *et al.*, 1994; FLYNN *et al.*, 2003; LÓPEZ *et al.*, 2005). Although isotemnids appear to be fairly diverse during the Tinguirirican, precise comparisons and identifications are hampered by the relatively poor material presently known.

The Tinguirirican isotemnids are the youngest representatives of the group; the oldest are Riochican in age (SIMPSON, 1935a, 1967; MARSHALL *et al.*, 1983). Within this time interval, isotemnids are recorded at most Eocene localities from Patagonia and as far north as Jujuy (BOND & LÓPEZ, 1995).

HOMALODOTHERIIDAE

Homalodotheriids are relatively large, vaguely chalicothere-like notoungulates that were never very diverse or abundant (PATTERSON & PASCUAL, 1968; SIMPSON, 1980; COOMBS, 1983; CIFELLI, 1985b; CROFT, 1999). SIMPSON (1967) did not regard Mustersan *Periphragnis* as a homalodotheriid, but this may very well be the earliest member of the group (Bond, pers. comm.). During the Tinguirirican, *Trigonolophodon* is present at Tinguiririca, Cañadón Blanco, and the APS level at Gran Barranca (WYSS *et al.*, 1994; FLYNN *et al.*, 2003). The group persisted through the late Miocene (RINGUELET, 1957).

NOTOHIPPIDAE

The phylogenetic relationships among notohippids are only beginning to be resolved (SHOCKEY, 1997a, b), but the group's name (as traditionally conceived) almost certainly does not refer to a monophyletic entity. CIFELLI (1993) found support for a monophyletic subgroup of Deseadan and later notohippids, but his analysis positioned *Eomorphippus* as the outgroup to a clade formed by these later notohippids plus toxodontids. In contrast, SHOCKEY (1997a, b) found no such support for a monophyletic subclade, and in fact obtained very little resolution among notohippids; most notohippids were part of a six-way polytomy that included a clade formed by *Pascualihippus* plus toxodontids (Fig.6).

Isotemnidae
Pamphippus arenalei
Plexotemnus complicatissimus
Puelia coarctatus
Leontinia gaudryi
Scarrittia canquelensis
Eomorphippus obscurus
Eurygenium pacegnum
Eurygenium latirostris
Argyrohippus praecox
Argyrohippus fraterculus
Rhynchippus brasiliensis
Rhynchippus pumilus
Rhynchippus equinus
Pascualihippus boliviensis
Proadinotherium leptognathum
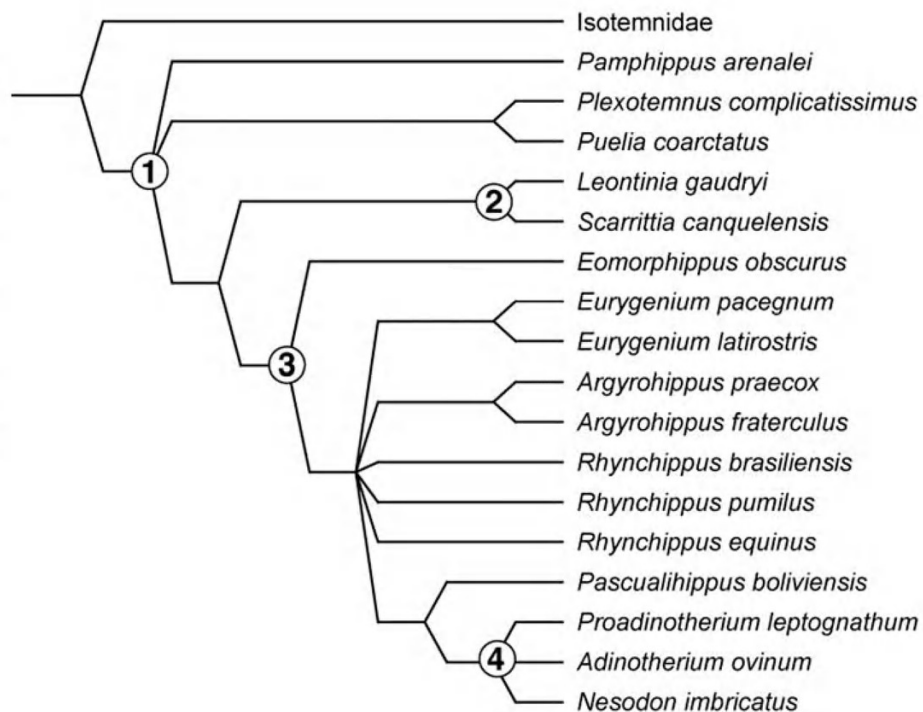*Adinotherium ovinum*
Nesodon imbricatus

Fig.6- Notohippid relationships based on the analyses of SHOCKEY (1997a, b). The following named nodes are indicated: 1, Notohippidae *sensu* BOND & LÓPEZ (1993); 2, Leontiniidae; 3, Notohippidae *sensu* SIMPSON (1967); 4, Toxodontidae.

The cladogram resembled CIFELLI's (1993), however, in that *Eomorphippus* (*E. obscurus*) was the nearest outgroup to this larger clade including some notohippids plus toxodontids. If taxa such as *Plexotemnus*, *Pampahippus*, and *Puelia* are included in the Notohippidae, as advocated by BOND & LÓPEZ (1993), these taxa are positioned as outgroups to a clade formed by leontiniids plus traditionally recognized notohippids and toxodontids (SHOCKEY, 1997a, b). In other words, notohippids are distributed across a variety of anatomically advanced toxodontian groups (Fig.6). Our research group is working to clarify relationships among these later diverging toxodontians, but for the purposes of the current discussion we employ BOND & LÓPEZ's (1993) broader conception of Notohippidae.

After archaeohyracids, notohippids are the most diverse group at Tinguiririca, with at least four species present (WYSS *et al.*, 1994, 2005; FLYNN *et al.*, 2003). These include two relatively basal notohippids (an undescribed species (Fig.2C) and cf. "*Eomorphippus*" *pascuali*) and two more advanced notohippids (both new species of *Eomorphippus*, one close to *E. obscurus*) (WYSS *et al.*, 1994, 2005). *E. obscurus* occurs at Cañadón Blanco (SIMPSON, 1967; FLYNN *et al.*, 2003) and both "*E.*" *pascuali* and *E. obscurus* have been collected from the APS level at Gran Barranca (BOND *et al.*, 1996). *Puelia*, an otherwise Mustersan taxon, possibly occurs at Rocas Bayas along with another indeterminate notohippid (BOND *et al.*, 1997). Species of *Eomorphippus* share the derived presence of hypsodont molars and incisors and are useful taxa for recognition of Tinguiririan faunas (WYSS *et al.*, 1994, 2005; FLYNN *et al.*, 2003).

The earliest notohippids are Casamayoran in age and include *Pampahippus* from the lower part of the Lumbrera Formation of Salta, Argentina (BOND & LÓPEZ, 1993) and *Plexotemnus* from the Gran Barranca (SIMPSON, 1967). More refined age estimates for these taxa are lacking since the Lumbrera Formation is poorly constrained (BABOT *et al.*, 2002; HONGN *et al.*, 2007) and the stratigraphic position of *Plexotemnus* at the Gran Barranca is unknown (CIFELLI, 1985a). According to BOND & LÓPEZ (1993), *Pampahippus*, *Plexotemnus*, and *Puelia* appear to represent a structural lineage between basal toxodontians and later-occurring notohippids such as *Eomorphippus*; accordingly, northwest Argentina has been proposed as the center of diversification for the group.

Notohippids are diverse and abundant in Deseadan faunas (CIFELLI, 1985b); besides the classic localities in Patagonia, they also occur in the Fray Bentos Formation, Uruguay (REGUERO *et al.*, 2003b); Salla, Bolivia (SHOCKEY, 1997a, b); new sites in the Abanico Formation, central Chile; and the Tremembé Formation, southeast Brazil (SORIA & ALVARENGA, 1989). They have not been reported from Moquegua or Santa Rosa in Perú (SHOCKEY *et al.*, 2004, 2006) but this may be attributable to sparse sampling.

LEONTINIIDAE

Leontiniids are rare during the Tinguiririan; only a single specimen has been collected from the type locality, and it has not yet been identified more precisely (FLYNN *et al.*, 2003). The Tinguiririan leontiniid represented the earliest record of the group until the recent report of a new species (*Coquenia bondi*) from the ?Mustersan upper part of the Lumbrera Formation of northwest Argentina (POWELL & DERACO, 2003; DERACO *et al.*, in press). A specimen from a new pre-Tinguiririan Chilean locality may comparably extend the group's range in Chile. Leontiniids are more diverse and apparently much more abundant in the Deseadan, having been reported from Bolivia (SHOCKEY, 1997a, 2005), southeast Brazil (PAULA COUTO, 1983), and Uruguay/northeast Argentina (REGUERO *et al.*, 2003b), in addition to Patagonia (LOOMIS, 1914; CHAFFEE, 1952; MARSHALL *et al.*, 1986). Some of these Deseadan specimens even include complete skeletons (SIMPSON, 1934; CHAFFEE, 1952). Leontiniids also are diverse and abundant at the locality of La Cantera at Gran Barranca, but the precise age of this Oligocene fauna is unclear (LÓPEZ *et al.*, 2005). Fragmentary material from the Paleogene locality of Santa Rosa, Perú, may pertain to a leontiniid (SHOCKEY *et al.*, 2004); as noted above, this likely represents an Oligocene occurrence.

In the Neogene, the record of leontiniids is much patchier. Although *Colpodon* is characteristic of the early Miocene Colhuehuapian SALMA (AMEGHINO, 1902b; SIMPSON, 1932b, 1935b; BORDAS, 1939; MARSHALL *et al.*, 1983) the group is thereafter absent from the Patagonian record. The last occurrence is in the middle Miocene La Venta Fauna of Colombia (VILLARROEL & COLWELL DANIS, 1997). Based on this distribution, it appears that leontiniids experienced a significant contraction and/or shift in their geographic range by the late early Miocene. Testing this hypothesis will require additional low and middle latitude faunas, especially from the early and middle Miocene. Moderately well-sampled later Cenozoic faunas from the middle latitudes of Chile

and Bolivia appear to lack evidence of leontiniids (CROFT *et al.*, 2004, 2007; CROFT, 2007). A recently identified leontiniid from the Miocene Laguna del Laja region of south-central Chile (WYSS *et al.*, 2003; WERTHEIM *et al.*, 2004, 2005; FLYNN *et al.*, in press) may provide important information on the geographic and temporal distribution of leontiniids, depending on resolution of its precise age and stratigraphic position.

OTHER UNGULATE GROUPS

In addition to the groups discussed above, the presence or absence of several less diverse groups from the Tinguirirican merit comment. Among notoungulates, no henricosborniids, archaeopithecids, or oldfieldthomasiids have been reported from this interval; all of these groups are restricted to Eocene and older localities (SIMPSON, 1948, 1967; MARSHALL *et al.*, 1983). Given the abundance and diversity of oldfieldthomasiids at Divisadero Largo and the number of Tinguiririan faunas that have been sampled, it seems likely that those from Divisadero Largo predate the Tinguiririan (WYSS *et al.*, 1994; FLYNN *et al.*, 2003). No toxodontids occur in the Tinguiririan, apparently constraining their origin to the small interval of time between the Tinguiririan and the Deseadan.

Ungulates other than notoungulates constitute only a minor component of Tinguiririan faunas. Astrapotheres (including trigonostylopids) range from the Riochican through the middle Miocene (SIMPSON, 1935b, 1967; CIFELLI, 1985b) and are only represented during the Tinguiririan by *Isolophodon* at Cañadón Blanco (ROTH, 1903; FLYNN *et al.*, 2003). Litopterns exhibit a pattern similar to that of astrapotheres; the sole representative of the clade during the Tinguiririan is the proterotheriid *Anisolambda* from Cañadón Blanco (ROTH, 1903). *Anisolambda* is a particularly long-ranging taxon, occurring in Riochican through Deseadan faunas (CIFELLI, 1983).

A single indaleciine has been reported from Tinguiririca (WYSS *et al.*, 1994; FLYNN *et al.*, 2003); although traditionally allied with litopterns, several analyses have cast doubt on this taxonomic affiliation (CIFELLI, 1983, 1993; CIFELLI & SORIA, 1983; WYSS *et al.*, 1994). Regardless of its proper higher-level relationships, the form from Tinguiririca is most similar to *Indalecia grandis* from the Casamayoran lower part of the Lumbrera Formation of Salta, Argentina (BOND & VUCETICH, 1983; WYSS *et al.*, 1994). The close similarity of this taxon to a species from

northwest Argentina parallels geographic patterns seen other Tinguirirican ungulate groups such as basal interatheriids and notostylopids (see above).

TINGUIRIRICA PALEOENVIRONMENT

Multiple lines of evidence (faunal hypsodonty, cenograms, rainfall estimates via ecological diversity analysis) have previously been used to suggest that the Tinguiririca Fauna represents the earliest 'open' habitat (likely grassland/wooded grassland) community in South America (FLYNN *et al.*, 2003). Although these lines of evidence are not entirely independent (*e.g.*, diet and body mass factor into ecological diversity analyses), their congruence increases confidence in the resultant habitat reconstruction. An open question, however, is the degree to which unusual aspects of the Tinguiririca Fauna (and/or South American mammalian paleofaunas in general, relative to those on other continents) might be driving these patterns. For example, is it possible that the high proportion of hypsodont ungulates at Tinguiririca reflects not the consumption of siliceous phytolith-bearing open habitat vegetation (*i.e.*, grasses), but rather exogenous grit produced by nearby volcanoes, as suggested by PASCUAL & ORTIZ JAUREGUIZAR (1990)? Or might notoungulates have had some intrinsic tendency to increase the height of their cheek teeth regardless of the environment, as implied by SIMPSON (1980)? With these questions in mind, we undertook an even more conservative ecological diversity analysis (EDA) in which the influence of hypsodonty would be minimized.

As in our previous ecological diversity analysis, we coded each Tinguiririca taxon for three variables: diet, locomotor style, and body mass (FLYNN *et al.*, 2003). For comparative purposes, we also coded mammals from sixteen modern Neotropical faunas (from KAY & MADDEN, 1997) for the same variables. In the present analysis, however, we coded these attributes differently. We used far broader, more conservative dietary categories than in our previous analysis, to minimize the chance of misinterpreting diet based on tooth crown height (hypsodonty); these five dietary categories included folivore (a combination of browser, grazer, and mixed feeder categories), frugivore, insectivore, omnivore, and carnivore. Our locomotor categories also were quite broad; species were classified as either terrestrial or arboreal, with the latter category including scansorial and semi-arboreal species. In contrast,

we used narrower body mass categories (following TOWNSEND, 2004) which permitted greater discrimination among taxa than the six categories used previously, but still buffered against small errors inherent in estimating body masses of extinct taxa (DAMUTH & MACFADDEN, 1990; CROFT, 2001). For details of paleobiological inferences, see FLYNN *et al.* (2003).

The proportion of taxa in each category noted above (*e.g.*, number of frugivores/total number of species) was calculated for Tinguiririca and each modern fauna. These proportions were then arcsine transformed to normalize the data (SOKAL & ROHLF, 1995) and seven of the original nineteen categories were used in a discriminant function analysis (DFA); the seven categories employed were those demonstrated by TOWNSEND (2004) to be statistically correlated with habitat type in her dataset of modern South American mammal faunas. The DFA was performed using SPSS (SPSS Inc.) on an Apple G4 computer; the prior probabilities for the three habitat types (open, mixed, closed) were considered equal. The resultant two functions correctly classified 15 of 16 modern faunas by habitat type and classified Tinguiririca as an open habitat fauna with 100% probability, thus strongly supporting previous habitat interpretations (WYSS *et al.*, 1994; FLYNN *et al.*, 2003). The raw percentages used in our analysis are provided in table 2 and the structure matrix of the two functions is provided in table 3.

TABLE 2. Structure coefficients (pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions) for DFA by habitat type.

	FUNCTION 1	FUNCTION 2
Frugivorous	-0.023	-0.256
Folivorous	0.106	0.252
Insectivorous	-0.148	0.423
Mass Class VII	0.332	-0.626
Mass Class VIII	-0.090	0.468
Arboreal	-0.147	-0.498

The proportion of terrestrial taxa was not used in either discriminant function.

TABLE 3. Percentages of mammal species in each of seven macroecological categories for Tinguiririca and sixteen modern Neotropical faunas from KAY & MADDEN (1997).

FAUNA	HABITAT	FRUGIVORES	FOLIVORES	INSECTIVORES	MASS CLASS VII	MASS CLASS VIII	ARBOREAL	TERRESTRIAL
Guatopo	Mixed	42.5	15.0	20.0	10.0	2.5	60.0	40.0
Masaguaral	Open	37.9	17.2	13.8	13.8	3.4	55.2	44.8
Puerto Páez	Open	45.8	20.8	4.2	12.5	0.0	45.8	54.2
Puerto Ayacuchi	Mixed	53.3	13.3	15.6	4.4	4.4	57.8	42.2
Esmeralda	Closed	60.6	9.1	13.6	6.1	3.0	69.7	30.3
Manaus	Closed	49.0	13.7	17.6	7.8	5.9	62.7	37.3
Belém	Closed	35.5	14.5	19.4	8.1	4.8	58.1	41.9
Caatingas	Mixed	19.0	23.8	28.6	4.8	4.8	38.1	61.9
Federal District	Mixed	39.4	19.7	19.7	3.0	4.5	37.9	62.1
Acurizal	Mixed	35.7	19.0	11.9	4.8	11.9	42.9	57.1
Chaco	Mixed	19.4	27.8	25.0	0.0	11.1	30.6	69.4
Transitional Forest	Closed	20.0	22.2	24.4	2.2	4.4	42.2	57.8
Low Montane	Closed	34.6	26.9	3.8	3.8	0.0	46.2	53.8
Cocha Cashu	Closed	52.9	14.3	14.3	8.6	5.7	67.1	32.9
Rio Cenapa	Closed	43.5	12.9	17.7	8.1	4.8	61.3	38.7
Ecuador Tropical	Closed	43.9	11.0	18.3	7.3	3.7	63.4	36.6
Tinguiririca	Unknown	12.0	80.0	4.0	4.0	8.0	12.0	88.0

Although the DFA unequivocally classifies Tinguiririca as an open habitat, the Mahalanobis distance between it and the open habitats centroid far exceeds that for any modern fauna (Fig.7). In other words, Tinguiririca is more similar to a modern savanna than a modern forest, but it still differs markedly from the sixteen modern faunas used in the DFA. This is best illustrated by the extremely high proportion of folivorous species at Tinguiririca (close to three times that of any modern fauna) and the equally low proportion of arboreal taxa (less than one third that of any modern fauna) (Tab.3). Given these numbers, it is obvious why the fauna is classified as open habitat, but the non-analog aspect of the fauna is also evident.

There are, of course, several potential explanations for the uniqueness of Tinguiririca. Given that Tinguiririca is a fossil fauna, the possibility of taphonomic bias cannot be ruled out. What such bias might include is unclear, however, since taxa of many sizes are present at Tinguiririca and the preservation of specimens is generally excellent. Moreover, the number of small arboreal frugivores missing from the fauna due to taphonomic bias would have to be quite large to result in a fauna similar to any existing today in South America. Perhaps most compelling is the great similarity between the results obtained in this study and those obtained by CROFT & TOWNSEND (2005) in their EDA of the late early Miocene Santa Cruz Fauna of Argentina; if taphonomic bias were at work, it would have to produce similar effects despite considerable temporal, geographic, and depositional differences between Santa Cruz and Tinguiririca. This seems implausible.

Errors in ecological interpretations of extinct taxa could also bias this type of analysis. Since we used very conservative ecomorphological categories, it is difficult to imagine systematic errors that would result in drastically different locomotor or dietary interpretations for the taxa under consideration. That is not to say that such errors are impossible; perhaps some of the smaller notoungulates (or even some of the larger ones) were less folivorous and more frugivorous. But as noted above, such misinterpretations would have to be prevalent to significantly alter habitat inferences.

The most reasonable conclusion is that middle Cenozoic South American faunas simply were structured very differently than modern South American communities (e.g., CROFT, 2001). This should not be surprising given the great differences in taxonomic composition (at high taxonomic levels) between most fossil and modern faunas, and the dramatic changes in endemism and interchange through the Cenozoic in South America. Such differences have also been observed in North American fossil faunas (JANIS et al., 2002), but not necessarily to the same degree. Even though the differences between modern and fossil faunas necessarily limit confidence in paleohabitat interpretations, the evidence presented here
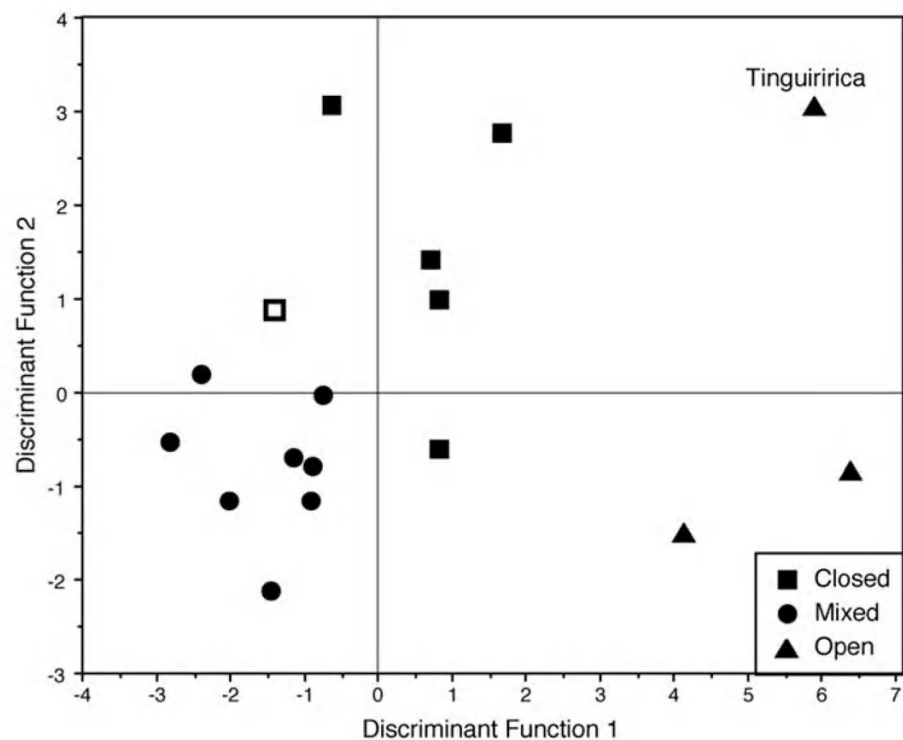

Fig.7- Bivariate plot of Tinguiririca and 16 modern Neotropical faunas based on the first two functions from the discriminant analysis described in the text. Habitats are plotted by predicted group membership (i.e., habitat type), with Tinguiririca identified. The open box represents Puerto Ayacucho, a mixed habitat misidentified as a closed habitat; this was the only misidentified modern habitat.

combined with that of FLYNN *et al.* (2003) provides compelling evidence for the presence of open habitats in South America by the earliest Oligocene.

CONCLUSIONS

Faunas dominated by hypsodont herbivores appear significantly earlier in South America than elsewhere in the world (WYSS *et al.*, 1994; FLYNN & WYSS, 1998; FLYNN *et al.*, 2003). This "precocious hypsodonty" has long been recognized for Deseadan faunas (*e.g.*, PATTERSON & PASCUAL, 1968) but has only recently been demonstrated to apply to the older Tinguiririan SALMA as well (WYSS *et al.*, 1990, 1993, 1994; FLYNN *et al.*, 2003). The high degree of hypsodonty seen in many Tinguiririan species reflects a dramatic "modernization" of South American mammal communities compared to those immediately preceding this time, and may reflect environmental effects of the Eocene-Oligocene Transition (WOLFE, 1971; PROTHERO & BERGGREN, 1992). The results of EDA provide additional evidence that open habitats prevailed at these latitudes in South America by earliest Oligocene time, this despite the intriguing recent proposal that regional climate (*i.e.*, continental temperatures) in Patagonia did not change substantially across the Eocene-Oligocene Transition (KOHN *et al.*, 2004).

In addition to documenting important changes in hypsodonty on a faunal level, Tinguiririan faunas have clarified other aspects of dental evolution in various notoungulate clades. A dramatic jump in hypsodonty (without the attainment of hypselodonty) is synchronous across several lineages of notoungulates (viz., notohippids, interatheriids, archaeohyracids) by the Tinguiririan. Hypselodonty (*i.e.*, "euhypsodonty"), in contrast, appears to have originated among notoungulates in two pulses: by the Tinguiririan in hegetotheriids and mesotheriids, and by the Deseadan (late Oligocene) in interatheriids and toxodontids. Although hypselodont taxa dominate Neogene faunas, it is the very hypsodont taxa that predominate during the Tinguiririan; early mesotheriids and hegetotheriids are represented by very limited material, and toxodontids and hypselodont interatheriines are not recorded until the Deseadan. Such a pattern suggests that these dentally advanced members of "primitive" lineages (*e.g.*, archaeohyracids, notohippids) enjoyed some type of competitive superiority and/or ecological incumbency during the early Oligocene and that the later success of

hypselodont taxa may be less attributable to tooth crown height than previously believed.

Biogeographic interpretations based on Tinguiririan faunas are limited by the lack of corresponding faunas from northern South America and by the uncertain age(s) of the species from Divisadero Largo. Still, some trends are worth noting. The ungulate fauna of Tinguiririca demonstrates affinities to both classical localities in Patagonia and more recently uncovered localities in northwest Argentina (WYSS *et al.*, 1994; FLYNN *et al.*, 2003). This mixed pattern thus provides evidence for a mild degree of faunal provinciality during this interval, but not one reflecting dramatic ecological or geographic barriers. Absences of certain Tinguiririan-aged ungulates at Tinguiririca stem either from sampling or regional differences; study of additional new Tinguiririan faunas in central Chile (*e.g.*, Cachapoal) should help discriminate between these two alternatives. Given the small size of collections from most Patagonian localities, absences of various Tinguiririan ungulates at Cañadón Blanco and the APS level of the Gran Barranca should be accorded little biogeographic significance at this time. Increased sampling of these faunas promises to clarify biogeographic patterns during this important interval of mammal evolution.

In contrast to the overall resemblance among Chilean and Patagonian Tinguiririan faunas, the faunal differences between Tinguiririca and Divisadero Largo are striking, especially given their close geographic proximity (Fig.3). This disparity is evident in both ecomorphological and taxonomic contexts; Tinguiririca is dominated by hypsodont taxa such as archaeohyracids, interatheriids, and notohippids, whereas brachydont taxa such as oldfieldthomasiids predominate at Divisadero Largo (SIMPSON *et al.*, 1962). No taxon is shared at the specific or generic level between the two faunas, and none of the most abundant families (*i.e.*, the four noted above) is recorded at both. The marked disparity between Divisadero Largo and earliest Oligocene Tinguiririan localities from central Chile is consistent with the recent suggestion that the former is a temporally mixed assemblage (CERDEÑO *et al.*, 2005; LÓPEZ & MANASSERO, 2006). Our review of Tinguiririan notoungulates suggests that Divisadero Largo does not sample the Tinguiririan, but rather includes many pre-Tinguiririan species and two likely post-Tinguiririan ones.

ACKNOWLEDGMENTS

REFERENCES

AMEGHINO, F., 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de Patagonie. **Boletín de la Academia Nacional de Ciencias de Córdoba**, **16**:350-426.

AMEGHINO, F., 1902a. Notices préliminaires sur des mamifères nouveaux des terrains crétacés de Patagonie. **Boletín de la Academia Nacional de Ciencias de Córdoba**, **17**:5-70.

AMEGHINO, F., 1902b. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. **Boletín de la Academia Nacional de Ciencias de Córdoba**, **17**:71-138.

BABOT, M.J.; POWELL, J.E. & MUIZON, C.D., 2002. *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the Early Eocene of Argentina. **Geobios**, **35**:615-629.

BERGQVIST, L.P. & RIBEIRO, A.M., 1998. A paleomastofauna das bacias Eoterciárias brasileiras e sua importância na datação das bacias de Itaboraí e Taubaté. In: CASADÍO, S. (Ed.) **Paleógeno de América del Sur y de la Península Antártica**. Buenos Aires: Publicación Especial 5, Asociación Paleontológica Argentina. p.19-34.

BOND, M., 1986. Los ungulados fósiles de Argentina: evolución y paleoambientes. In: CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, 4., 1986, Mendoza. **Actas...**, 2. Mendoza. p.173-185.

BOND, M., 1991. Sobre las capas de supuesta edad Divisaderense en los "Estratos de Salla," Bolivia. In: SUÁREZ-SORUCO, R. (Ed.) **Fósiles y Facies de Bolivia - Vol. I Vertebrados**. Santa Cruz: Yacimientos Petrolíferos Fiscales Bolivianos. p.701-705.

BOND, M. & LÓPEZ, G., 1993. El primer Notohippidae (Mammalia, Notoungulata) de la Formación Lumbrera (Grupo Salta) del noroeste Argentino. Consideraciones sobre la sistemática de la familia Notohippidae. **Ameghiniana**, **30**:59-68.

BOND, M. & LÓPEZ, G., 1995. Los mamíferos de la Formación Casa Grande (Eoceno) de la provincia de Jujuy, Argentina. **Ameghiniana**, **32**:301-309.

BOND, M.; LÓPEZ, G. & REGUERO, M., 1996. "Astraponoteén plus supérieur" of Ameghino: another interval in the Paleogene record of South America. **Journal of Vertebrate Paleontology**, **16**:23A.

BOND, M.; LÓPEZ, G. & REGUERO, M., 1997. Rocas Bayas, una localidad fosilífera Paleógena de la Provincia de Río Negro, República Argentina. **Ameghiniana**, **34**:533.

BOND, M.; LÓPEZ, G.; REGUERO, M.A.; SCILLATO-YANÉ, G.J. & VUCETICH, M.G., 1998. Los mamíferos de la Formación Fray Bentos (edad mamífero Deseadenese, Oligocene superior?) de las provincias de Corrientes y Entre Ríos, Argentina. In: CASADÍO, S. (Ed.) **Paleógeno de América del Sur y de la Península Antártica**. Buenos Aires: Publicación Especial 5, Asociación Paleontológica Argentina. p.41-50.

BOND, M. & VUCETICH, M.G., 1983. *Indalecia grandensis* gen. et sp. nov. del Eoceno temprano del noroeste argentino, tipo de una nueva Subfamilia de los Adianthidae (Mammalia, Litopterna). **Revista de la Asociación Geológica Argentina**, **38**:107-117.

BORDAS, A.F., 1939. Diagnosis sobre algunos mamíferos de las capas con *Colpodon* del Valle del Río Chubut (República Argentina). **Physis**, **14**:413-433.

CAMPBELL, K.E., JR. (Ed.), 2004. **The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru**. Los Angeles: Natural History Museum of Los Angeles County. 163p.

CAMPBELL, K.E.; FRAILEY, C.D. & ROMERO-PITTMAN, L., 1996. The first Paleogene fauna from the Amazon Basin and its bearing on the first occurrence of rodents in South America. **Journal of Vertebrate Paleontology**, **16**:25A.

CAMPBELL, K.E.; FRAILEY, C.D. & ROMERO-PITTMAN, L., 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: geographic and geologic setting. **Natural History Museum of Los Angeles County, Science Series**, **40**:3-14.

CARLINI, A.A.; MADDEN, R.H.; VUCETICH, M.G.; BOND, M.; LÓPEZ, G.; REGUERO, M. & SCARANO, A., 2005. Mammalian biostratigraphy and biochronology at Gran Barranca: the standard reference section for the continental middle Cenozoic of South America. In: CONGRESO GEOLÓGICO ARGENTINO, 15., 2005, El Calafate. **Actas...** El Calafate. CD-ROM, Artículo Nº 807, 2p.

CERDEÑO, E. & BOND, M., 1998. Taxonomic revision and phylogeny of *Paedotherium* and *Tremacyllus* (Pachyrukhinae, Hegetotheriidae, Notoungulata) from the late Miocene to Pleistocene of Argentina. **Journal of Vertebrate Paleontology**, **18**:799-811.

CERDEÑO, E.; LÓPEZ, G. & REGUERO, M., 2005. Sobre un Mesotheriidae (Mammalia, Notoungulata) de la Formación Mariño y sus implicancias sobre la identidad de la "Edad Mamífero" Divisaderense. **Ameghiniana**, **42**:21R.

CHAFFEE, R.G., 1952. The Deseadan vertebrate fauna of the Scarritt Pocket, Patagonia. **Bulletin of the American Museum of Natural History**, **98**:509-562.

CIFELLI, R.L., 1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). **American Museum Novitates, 2772**:1-49.

CIFELLI, R.L., 1985a. Biostratigraphy of the Casamayoran, Early Eocene, of Patagonia. **American Museum Novitates, 2820**:1-26.

CIFELLI, R.L., 1985b. South American ungulate evolution and extinction. In: STEHLI, F.G. & WEBB, S.D. (Eds.) **The Great American Biotic Interchange**. New York: Plenum Press. p.249-266.

CIFELLI, R.L., 1993. The phylogeny of the native South American ungulates. In: SZALAY, F.S.; NOVACEK, M.J. & MCKENNA, M.C. (Eds.) **Mammal Phylogeny: Placentals**. New York: Springer-Verlag. p.195-216.

CIFELLI, R.L. & SORIA, M.F., 1983. Systematics of the Adianthidae (Litopterna, Mammalia). **American Museum Novitates, 2771**:1-25.

COOMBS, M.C., 1983. Large mammalian clawed herbivores: a comparative study. **Transactions of the American Philosophical Society**, New Series, **73**:1-96.

CROFT, D.A., 1999. Placentals: South American ungulates. In: SINGER, R. (Ed.) **Encyclopedia of Paleontology**. Chicago: Fitzroy-Dearborn Publishers. p.890-906.

CROFT, D.A., 2000. **Archaeohyracidae (Mammalia, Notoungulata) from the Tinguiririca Fauna, central Chile, and the evolution and paleoecology of South American mammalian herbivores**. Dissertation (Ph.D.), The University of Chicago, Chicago. Unpublished.

CROFT, D.A., 2001. Cenozoic environmental change in South American as indicated by mammalian body size distributions (cenograms). **Diversity and Distributions**, **7**:271-287.

CROFT, D.A., 2007. The middle Miocene (Laventan) Quebrada Honda Fauna, southern Bolivia, and a description of its notoungulates. **Palaeontology, 50**:277-303.

CROFT, D.A. & ANAYA, F., 2006. A new middle Miocene hegetotheriid (Notoungulata: Typotheria) and a phylogeny of the Hegetotheriidae. **Journal of Vertebrate Paleontology**, **26**:387-399.

CROFT, D.A.; BOND, M.; FLYNN, J.J.; REGUERO, M.A. & WYSS, A.R., 2003a. Large archaeohyracids (Typotheria, Notoungulata) from central Chile and Patagonia including a revision of *Archaeotypotherium*. **Fieldiana, 49**:1-38.

CROFT, D.A.; FLYNN, J.J. & WYSS, A.R., 2003b. Diversification of mesotheriids (Mammalia: Notoungulata: Typotheria) in the middle latitudes of South America. **Journal of Vertebrate Paleontology**, **23**:43A.

CROFT, D.A.; FLYNN, J.J. & WYSS, A.R., 2004. Notoungulata and Litopterna of the early Miocene Chucal Fauna, northern Chile. **Fieldiana, 50**:1-52.

CROFT, D.A.; FLYNN, J.J. & WYSS, A.R., 2007. A new basal glyptodontid and other Xenarthra of the early Miocene Chucal Fauna, northern Chile. **Journal of Vertebrate Paleontology**, **27**:780-796.

CROFT, D.A. & TOWNSEND, K.A., 2005. Inferring habitat for the late early Miocene Santa Cruz Fauna (Santa Cruz Province, Argentina) using ecological diversity analysis. **Journal of Vertebrate Paleontology**, **25**:48A.

DAMUTH, J. & MACFADDEN, B.J. (Eds.), 1990. **Body Size in Mammalian Paleobiology: Estimation and Biological Implications**. Cambridge: Cambridge University Press. 409p.

DERACO, M.V.; POWELL, J.E. & LÓPEZ, G., in press. Primer leontínido (Mammalia, Notoungulata) de la Formación Lumbrera (Subgrupo Santa Bárbara, Grupo Salta – Paleógeno) del Noroeste Argentino. **Ameghiniana**.

DOZO, M.T.; REGUERO, M. & CERDEÑO, E., 2000. *Medistylus dorsatus* (Ameghino, 1903), un Hegetotheriidae Pachyrukhinae (Mammalia, Notoungulata) del Deseadense de la provincia de Chubut, Argentina. **Ameghiniana, 37**:24R.

FLYNN, J.J.; CHARRIER, R.; CROFT, D.A.; GANS, P.B.; HERRIOTT, T.M.; WERTHEIM, J.A. & WYSS, A.R., in press. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa formations, Laguna del Laja area, south central Chile. **Journal of South American Earth Sciences**.

FLYNN, J.J.; CROFT, D.A.; CHARRIER, R.; HÉRAIL, G. & WYSS, A.R., 2002. The first Cenozoic mammal fauna from the Chilean Altiplano. **Journal of Vertebrate Paleontology**, **22**:200-206.

FLYNN, J.J.; CROFT, D.A.; CHARRIER, R. & WYSS, A.R., 2005b. New Mesotheriidae (Mammalia, Notoungulata, Typotheria), geochronology and tectonics of the Caragua area, northernmost Chile. **Journal of South American Earth Sciences**, **19**:55-74.

FLYNN, J.J.; CROFT, D.A.; HITZ, R. & WYSS, A.R., 2005a. The Tapado Fauna (Casamayoran SALMA), Abanico Formation, Tinguiririca Valley, central Chile. **Journal of Vertebrate Paleontology**, **25**:57A.

FLYNN, J.J. & SWISHER, C.C., III, 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. In: BERGGREN, W.A., KENT, D.V., AUBRY, M.-P. & HARDENBOL, J. (Eds.) **Geochronology, Time Scales, and Global Stratigraphic Correlation**. Tulsa: SEPM (Society for Sedimentary Geology) Special Publication No. 54. p.317-333.

FLYNN, J.J. & WYSS, A.R., 1998. Recent advances in South American mammalian paleontology. **Trends in Ecology and Evolution**, **13**:449-454.

FLYNN, J.J. & WYSS, A.R., 2004. A polydolopine marsupial skull from the Cachapoal Valley, Andean Main Range, Chile. **Bulletin of the American Museum of Natural History**, **285**:80-92.

FLYNN, J.J.; WYSS, A.R. & CHARRIER, R., 2007. South America's missing mammals. **Scientific American**, **5**:68-75.

FLYNN, J.J.; WYSS, A.R.; CROFT, D.A. & CHARRIER, R., 2003. The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age". **Palaeogeography, Palaeoclimatology, Palaeoecology**, **195**:229-259.

HITZ, R.; FLYNN, J.J. & WYSS, A.R., 2006. New Basal Interatheriidae (Typotheria, Notoungulata, Mammalia) from the Paleogene of Central Chile. **American Museum Novitates**, **3520**:1-32.

HITZ, R.; REGUERO, M.; WYSS, A.R. & FLYNN, J.J., 2000. New interatheriines (Interatheriidae, Notoungulata) from the Paleogene of central Chile and southern Argentina. **Fieldiana**, **42**:1-26.

HOFFSTETTER, R., 1969. Un primate de l'Oligocène inférieurran sudamerica: *Branisella boliviana* gen. et sp. nov. **Comptes Rendus de la Académie des Sciences**, **269**:434-437.

HONGN, F.; DEL PAPA, C.; POWELL, J.; PETRINOVIC, I.; MON, R. & DERACO, V., 2007. Middle Eocene deformation and sedimentation in the Puna-Eastern Cordillera transition (23°–26°S): control by preexisting heterogeneities on the pattern of initial Andean shortening. **Geology**, **35**:271-274.

JANIS, C.M.; DAMUTH, J. & THEODOR, J.M., 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. **Palaeogeography, Palaeoclimatology, Palaeoecology**, **177**:183-198.

KAY, R.F. & MADDEN, R.H., 1997. Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). **Journal of Human Evolution**, **32**:161-199.

KAY, R.F.; MADDEN, R.H.; CIFELLI, R.L. & FLYNN, J.J. (Eds.), 1997. **Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia**. Washington, D.C.: Smithsonian Institution Press. 592p.

KAY, R.F.; MADDEN, R.H.; VUCETICH, M.G.; CARLINI, A.A.; MAZZONI, M.M.; RE, G.H.; HEIZLER, M. & SANDEMAN, H., 1999. Revised geochronology of the Casamayoran South American land mammal age: climatic and biotic implications. **Proceedings of the National Academy of Sciences of the United States of America**, **96**:13235-13240.

KOHN, M.J.; CARLINI, A.A.; JOSEF, J.A.; KAY, R.F.; MADDEN, R.H. & VUCETICH, M.G., 2004. Climate stability across the Eocene-Oligocene transition, southern Argentina. **Geology**, **32**:621-624.

KRAMARZ, A.; GARRIDO, A.C.; RIBEIRO, A.M. & ORTIZ, R., 2004. Nuevos registros de vertebrados fósiles de la Formación Chichinales, Mioceno Temprano de la provincia de Río Negro. **Ameghiniana**, **41**:53R.

LINARES, O.J., 2004. Bioestratigrafía de la fauna de mamíferos de las formaciones Socorro, Urumaco y Codore (Miocene medio - Plioceno temprano) de la región de Urumaco, Falcon, Venezuela. **Paleobiología Neotropical**, 1:1-26.

LINARES, E.; PASCUAL, R. & TIMONIERI, A.J., 1960. La edad de los sedimentos terciarios del valle de Punilla, provincia de Córdoba, y la presencia de *'Eohyrax rusticus'* Ameghino en los mismos. **Revista de la Asociación Geológica Argentina**, **15**:191-212.

LOOMIS, F.B., 1914. **The Deseado Formation of Patagonia**. Concord: Runford Press. 232p.

LÓPEZ, G.M., 1997. Paleogene faunal assemblage from Antofagasta de la Sierra (Catamarca Province, Argentina). **Palaeovertebrata**, **26**:61-81.

LÓPEZ, G.M., 2002. Redescripción de *Ethegotherium carettei* (Notoungulata, Hegetotheriidae) de la Formación Divisadero Largo de la provincia de Mendoza, Argentina. **Ameghiniana**, **39**:295-306.

LÓPEZ, G. & BOND, M., 1995. Un nuevo Notopithecinae (Notoungulata, Typotheria) del Terciario Inferior de la Puna, Argentina. **Studia Geológica Salmanticensia**, **31**:87-99.

LÓPEZ, G. & MANASSERO, M., 2006. Determinación de la procedência estratigráfica de *Ethegotherium carettei* Minoprio, 1947 (Notoungulata, Hegetotheriidae) a partir de un análisis de petrografía sedimentaria. **Ameghiniana**, **43**:44-45R.

LÓPEZ, G.; BOND, M.; REGUERO, M.; GELFO, J. & KRAMARZ, A., 2005. Los ungulados del Eoceno-Oligoceno de la Gran Barranca, Chubut. In: CONGRESO GEOLÓGICO ARGENTINO, 15., 2005, El Calafate. **Actas...** El Calafate. CD-ROM, Artículo N° 805, 5p.

MACFADDEN, B.J.; CAMPBELL, K.E., JR.; CIFELLI, R.L.; SILES, O.; JOHNSON, N.M.; NAESER, C.W. & ZEITLER, P.K., 1985. Magnetic polarity stratigraphy and mammalian fauna of the Deseadan (Late Oligocene-Early Miocene) Salla Beds of northern Bolivia. **Journal of Geology**, **93**:223-250.

MARSHALL, L.G. & CIFELLI, R.L., 1989. Analysis of changing diversity patters in Cenozoic land mammal age faunas, South America. **Palaeovertebrata**, **19**:169-210.

MARSHALL, L.G. & MUIZON, C.D., 1988. The dawn of the Age of Mammals in South America. **National Geographic Research**, **4**:23-55.

MARSHALL, L.G.; HOFFSTETTER, R. & PASCUAL, R., 1983. Mammals and stratigraphy: geochronology of the mammal-bearing Tertiary of South America. **Palaeovertebrata**, Mémoire Extraordinaire, **1983**:1-93.

MARSHALL, L.G.; CIFELLI, R.L.; DRAKE, R.E. & CURTIS, G.H., 1986. Vertebrate paleontology, geology, and geochronology of the Tapera de López and Scarritt Pocket, Chubut Province, Argentina. **Journal of Paleontology**, **60**:920-951.

MARSHALL, L.G.; WEBB, S.D.; SEPKOSKI, J.J., JR. & RAUP, D.M., 1982. Mammalian evolution and the Great American Interchange. **Science**, **215**:1351-1357.

MCKENNA, M.C. & BELL, S.K., 1997. **Classification of mammals above the species level**. New York: Columbia University Press. 631p.

PASCUAL, R. & ORTIZ JAUREGUIZAR, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. **Journal of Human Evolution**, **19**:23-60.

PASCUAL, R.; VUCETICH, M.G.; SCILLATO YANÉ, G.J. & BOND, M., 1985. Main pathways of mammal diversification in South America. In: STEHLI, F.G. & WEBB, S.D. (Eds.) **The Great American Biotic Interchange**. New York: Plenum Press. p.219-247.

PATTERSON, B., 1934. *Trachytherus*, a typotherid from the Deseado beds of Patagonia. **Field Museum of Natural History**, **6**:119-139.

PATTERSON, B. & PASCUAL, R., 1968. The fossil mammal fauna of South America. **Quarterly Review of Biology**, **43**:409-451.

PAULA COUTO, C., 1983. Geochronology and paleontology of the basin of Tremembé-Taubaté, State of São Paulo. **Iheringia**, **8**:5-31.

POWELL, J. & DERACO, M., 2003. Un nuevo leontinido (Mammalia, Notoungulata) del miembro superior de la Formación Lumbrera (Subgrupo Santa Bárbara) del noroeste Argentino. **Ameghiniana**, **37**: 68-69R.

PROTHERO, D.R. & BERGGREN, W.A., 1992. **Eocene-Oligocene Climatic and Biotic Evolution**. Princeton: Princeton University Press. 568p.

REGUERO, M.A., 1993. Los Typotheria y Hegetotheria (Mammalia, Notoungulata) Eocenos de la localidad Cañadón Blanco, Chubut. **Ameghiniana**, **30**:336.

REGUERO, M.A. & CASTRO, P.V., 2004. Un nuevo Trachytheriinae (Mammalia, †Notoungulata) del Deseadense (Oligoceno tardío) de Patagonia, Argentina: implicancias en la filogenia, biogeografía y bioestratigrafía de los Mesotheriidae. **Revista Geológica de Chile**, **31**:45-64.

REGUERO, M. & CERDEÑO, E., 2001. New Hegetotheriidae (Notoungulata) from the Deseadan (Late Oligocene) of Salla (Bolivia). **Ameghiniana**, **38**:17R.

REGUERO, M. & CERDEÑO, E., 2005. New late Oligocene Hegetotheriidae (Mammalia, Notoungulata) from Salla, Bolivia. **Journal of Vertebrate Paleontology**, **25**:674-684.

REGUERO, M. & ESCRIBANO, V., 1996. *Trachytherus spegazzinianus* Ameghino, 1889 (Notoungulata: Mesotheriidae) de la edad Deseadense (Oligoceno superior - Mioceno inferior) de Argentina y Bolivia. **Naturalia Patagónica**, Ciencias de la Tierra, **4**:43-71.

REGUERO, M. & LÓPEZ, G., 1999. Un nuevo Archaeohyracidae (Notoungulata, Hegetotheria) del Paleógeno de Antofagasta de la Sierra, provincia de Catamarca, Argentina. **Ameghiniana**, **36**:107.

REGUERO, M.A.; UBILLA, M. & PEREA, D., 1995. A new species of Archaeohyracidae (Mammalia: Notoungulata) from Fray Bentos Formation (Deseadan) of Uruguay. In: JORNADAS ARGENTINAS DE PALEONTOLOGÍA DE VERTEBRADOS, 11., 1995, Tucumán. **Resúmenes...** Tucumán: Asociación Paleontológica Argentina. p.16.

REGUERO, M.A.; UBILLA, M. & PEREA, D., 2003b. A new species of *Eopachyrucos* (Mammalia, Notoungulata, Interatheriidae) from the late Oligocene of Uruguay. **Journal of Vertebrate Paleontology**, **23**:445-457.

REGUERO, M.A.; CROFT, D.A.; FLYNN, J.J. & WYSS, A.R., 2003a. Small archaeohyracids from Chubut Province, Argentina and central Chile: implications for trans-Andean temporal correlation. **Fieldiana, 48**:1-17.

REGUERO, M.A.; CROFT, D.A.; LÓPEZ, G.J. & ALONSO, R.N., in press. Eocene archaeohyracids (Mammalia: Notoungulata: Hegetotheria) from the Puna, northwest Argentina. **Journal of South American Earth Sciences**.

RIGGS, E.S. & PATTERSON, B., 1935. Description of some notoungulates from the Casamayor (*Notostylops*) beds of Patagonia. **Proceedings of the American Philosophical Society**, 75:163-215.

RINGUELET, A.B.D., 1957. Estudio del género *Chasicotherium* Cabrera y Kraglievich 1931 (Notoungulata-Homalodotheriidae). **Ameghiniana, 1**:7-14.

ROTH, S., 1901. Notas sobre algunos nuevos mamíferos fósiles. **Revista del Museo de La Plata, 10**:251-258.

ROTH, S., 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. **Revista del Museo de La Plata, 11**:133-158.

SHOCKEY, B.J., 1997a. **Toxodontia of Salla, Bolivia (late Oligocene): taxonomy, systematics, and functional morphology**. Dissertation (Ph.D.), University of Florida. Unpublished.

SHOCKEY, B.J., 1997b. Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: late Oligocene): systematics and functional morphology. **Journal of Vertebrate Paleontology, 17**:584-599.

SHOCKEY, B.J., 2005. New leontiniids (Class Mammalia, Order Notoungulata, Family Leontiniidae) from the Salla Beds of Bolivia (Deseadan, late Oligocene). **Bulletin of the Florida Museum of Natural History, 45**:249-260.

SHOCKEY, B.J.; CROFT, D.A. & ANAYA, F., 2007. Analysis of function in the absence of extant functional analogs: a case study of mesotheriid notoungulates. **Paleobiology, 33**:228-248.

SHOCKEY, B.J.; HITZ, R. & BOND, M., 2004. Paleogene notoungulates from the Amazon Basin of Peru. **Natural History Museum of Los Angeles County, Science Series, 40**:61-69.

SHOCKEY, B.J.; SALAS, R.; QUISPE, R.; FLORES, A.; SARGIS, E.J.; ACOSTA, J.; PINO, A.; JARICA, N.J. & URBINA, M., 2006. Discovery of Deseadan fossils in the upper Moquegua Formation (late Oligocene - ?early Miocene) of southern Peru. **Journal of Vertebrate Paleontology, 26**:205-208.

SIMPSON, G.G., 1932a. Skulls and brains of some mammals from the *Notostylops* beds of Patagonia.

American Museum Novitates, 578:1-11.

SIMPSON, G.G., 1932b. New or little-known ungulates from the *Pyrotherium* and *Colpodon* beds of Patagonia. **American Museum Novitates, 576**:1-13.

SIMPSON, G.G., 1934. A new notoungulate from the early Tertiary of Patagonia. **American Museum Novitates, 735**:1-3.

SIMPSON, G.G., 1935a. Descriptions of the oldest known South American mammals, from Rio Chico Formation. **American Museum Novitates, 793**:1-25.

SIMPSON, G.G., 1935b. Occurrence and relationships of the Rio Chico fauna of Patagonia. **American Museum Novitates, 818**:1-21.

SIMPSON, G.G., 1945a. The principles of classification and a classification of mammals. **Bulletin of the American Museum of Natural History**, 85:1-350.

SIMPSON, G.G., 1945b. A Deseado hegetothere from Patagonia. **American Journal of Science**, 243:550-564.

SIMPSON, G.G., 1948. The beginning of the age of mammals in South America. Part I. **Bulletin of the American Museum of Natural History, 91**:1-232.

SIMPSON, G.G., 1967. The beginning of the age of mammals in South America. Part II. **Bulletin of the American Museum of Natural History, 137**:1-260.

SIMPSON, G.G., 1980. **Splendid Isolation, the Curious History of South American Mammals**. New Haven: Yale University Press. 266p.

SIMPSON, G.G., 1984. **Discoverers of the Lost World**. New Haven: Yale University Press. 222p.

SIMPSON, G.G. & MINOPRIO, J.L., 1949. A new adiathine litoptern and associated mammals from a Deseadan faunule in Mendoza, Argentina. **American Museum Novitates, 1434**:1-27.

SIMPSON, G.G.; MINOPRIO, J.L. & PATTERSON, B., 1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. **Bulletin of the Museum of Comparative Zoology, 127**:239-293.

SOKAL, R.R. & ROHLF, F.J., 1995. **Biometry**. San Francisco: W.H. Freeman & Company. 887p.

SORIA, M.F. & ALVARENGA, H.M.F., 1989. Nuevos restos de mamíferos de la Cuenca de Taubaté, estado de São Paulo, Brasil. **Anais da Academia Brasileira de Ciências, 61**:157-175.

SYDOW, H., 1988. **Postcranial skeleton of *Trachytherus* (Mammalia, Notoungulata) with an evaluation of dentition**. Master's thesis, University of Florida. Unpublished.

TOWNSEND, K.E., 2004. **Stratigraphy, paleoecology, and habitat change in the middle Eocene of North America**. Dissertation (Ph.D.), Washington University. Unpublished.

VILLARROEL, C. & COLWELL DANIS, J., 1997. A new leontiniid notoungulate. In: KAY, R.F.; MADDEN, R.H.; CIFELLI, R.L. & FLYNN, J.J. (Eds.) **Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia**. Washington, D.C.: Smithsonian Institution Press. p.355-381.

VUCETICH, M.G., 1980. Un nuevo Notostylopidae (Mammalia: Notoungulata) proveniente de la Formación Lumbrera (Grupo Salta) del noroeste Argentino. **Ameghiniana, 17**:363-372.

VUCETICH, M.G. & RIBEIRO, A.M., 2003. A new and primitive rodent from the Tremembé Formation (Late Oligocene) of Brazil, with comments on the morphology of the lower premolars of caviomorph rodents. **Revista Brasileira de Paleontologia, 5**:73-82.

WEBB, S.D., 1976. Mammalian faunal dynamics of the great American interchange. **Paleobiology, 2**:220-234.

WERTHEIM, J.A.; CROFT, D.A.; FLYNN, J.J. & WYSS, A.R., 2005. New rodent faunas spanning several SALMAs from the Laguna del Laja region, Andean Main Range, central Chile. **Journal of Vertebrate Paleontology, 25**:129A.

WERTHEIM, J.A.; FLYNN, J.J.; GANS, P. & WYSS, A.R., 2004. New chronologic information for the Laguna del Laja mammal fauna(s): implications for the SALMA sequence. **Journal of Vertebrate Paleontology, 24**:128A.

WOLFE, J.A., 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. **Palaeogeography, Palaeoclimatology, Palaeoecology, 9**:27-57.

WYSS, A.R.; CHARRIER, R. & FLYNN, J.J., 1996. Fossil mammals as a tool in Andean stratigraphy: Dwindling evidence of late Cretaceous volcanism in the South central Main Range. **Paleobios, 17**:13-27.

WYSS, A.R.; FLYNN, J.J. & CROFT, D.A., 2005. New notohippids (Notoungulata, Eutheria) from the central Chilean Andes. **Journal of Vertebrate Paleontology, 25**:132A.

WYSS, A.R.; CHARRIER, R.; CROFT, D.A.; FLYNN, J.J. & WERTHEIM, J.A., 2003. New middle Cenozoic mammals from the Laguna del Laja region (Cura-Mallín Formation, south central Chile). **Journal of Vertebrate Paleontology, 23**:113A.

WYSS, A.R.; FLYNN, J.J.; NORELL, M.A.; SWISHER, C.C., III; CHARRIER, R.; NOVACEK, M.J. & MCKENNA, M.C., 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. **Nature, 365**:434-437.

WYSS, A.R.; FLYNN, J.J.; NORELL, M.A.; SWISHER, C.C., III; NOVACEK, M.J.; MCKENNA, M.C. & CHARRIER, R., 1994. Paleogene mammals from the Andes of central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. **American Museum Novitates, 3098**:1-31.

WYSS, A.R.; NORELL, M.A.; FLYNN, J.J.; NOVACEK, M.J.; CHARRIER, R.; MCKENNA, M.C.; SWISHER, C.C.; FRASINETTI, D. & JIN, M., 1990. A new early Tertiary mammal fauna from central Chile: implications for Andean stratigraphy and tectonics. **Journal of Vertebrate Paleontology, 10**:518-522.