

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024  
Number 3638, 43 pp., 10 figures, 1 table March 31, 2009

## New Early Eocene Mammalian Fauna from Western Patagonia, Argentina

MARCELO F. TEJEDOR,<sup>1,2,8</sup> FRANCISCO J. GOIN,<sup>3,8</sup> JAVIER N. GELFO,<sup>3,8</sup>  
GUILLERMO LÓPEZ,<sup>3</sup> MARIANO BOND,<sup>3,8</sup> ALFREDO A. CARLINI,<sup>3,8,9</sup>  
GUSTAVO J. SCILLATO-YANÉ,<sup>3,8</sup> MICHAEL O. WOODBURNE,<sup>4</sup> LAURA  
CHORNOGUBSKY,<sup>5,8</sup> EUGENIO ARAGÓN,<sup>6,8</sup> MARCELO A. REGUERO,<sup>3,8</sup>  
NICHOLAS J. CZAPLEWSKI,<sup>7</sup> SERGIO VINCON,<sup>2</sup> GABRIEL M. MARTIN,<sup>2,8</sup>  
AND MARTÍN R. CIANCIO<sup>3,8</sup>

### ABSTRACT

Two new fossil mammal localities from the Paleogene of central-western Patagonia are preliminarily described as the basis for a new possible biochronological unit for the early Eocene of Patagonia, correlated as being between two conventional SALMAs, the Riochican (older) and the Vacan subage of the Casamayoran SALMA. The mammal-bearing strata belong to the Middle Chubut River Volcanic-Pyroclastic Complex (northwestern Chubut Province, Argentina), of

<sup>1</sup> Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, U.S.A. (mtejedor@unpata.edu.ar).

<sup>2</sup>Current address: LIEB (Laboratorio de Investigaciones en Evolución y Biodiversidad), Facultad de Ciencias Naturales, Sede Esquel, Universidad Nacional de la Patagonia "San Juan Bosco", Sarmiento 849, 9200 Esquel, Provincia del Chubut, Argentina.

<sup>3</sup> División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina (fgoin@fcnym.unlp.edu.ar).

<sup>4</sup> Department of Geology, Museum of Northern Arizona, Flagstaff, AZ 86001. Research Associate, Department of Vertebrate Paleontology, American Museum of Natural History, (mikew@npgcable.com).

<sup>5</sup> Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo n° 470, 1405 Buenos Aires, Argentina (lchorno@macn.gov.ar).

<sup>6</sup> Centro de Investigaciones Geológicas, Universidad Nacional de La Plata, Calle 1 n° 644, B1900FWA La Plata, Argentina (earagon@cig.museo.unlp.edu.ar).

<sup>7</sup> University of Oklahoma, Oklahoma Museum of Natural History, 2401 Chautauqua Ave, Norman, OK 73072-7029, U.S.A. (nczaplewski@ou.edu).

<sup>8</sup> CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina).

<sup>9</sup> Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Straße 4, CH-8006 Zürich, Switzerland.

Paleocene-Eocene age. This complex includes a variety of volcanoclastic, intrusive, pyroclastic, and extrusive rocks deposited after the K-T boundary. Geochronological data taken from nearby volcanic deposits that underlie and overlie the mammal-bearing levels indicate that both faunas are of late early Eocene age (Ypresian-Lutetian boundary). In addition to more than 50 species of mammals, including marsupials, ungulates, and xenarthrans, two lower molars are the oldest evidence of bats in South America. Paleobotanical and palynological evidence from inferred contemporary localities nearby indicate subtropical environments characterized by warm and probably moderately humid climate. Remarkably, this new fauna is tentatively correlated with Eocene mammals from the La Meseta Formation in the Antarctic Peninsula. We conclude that the two localities mentioned above are part of a possible new biochronological unit, but the formal proposal of a new SALMA awaits completion of taxonomic analysis of the materials reported upon here. If the La Meseta fauna is correlated biochronologically to western Patagonia, this also suggests a continental extension of the biogeographic Weddellian Province as far north as central-western Patagonia.

## INTRODUCTION

The past two decades have seen an increase in the number of studies on the evolution of Paleogene South American mammals. Consequently, knowledge of their taxonomy, biostratigraphy, biogeography, and geochronology has been substantially improved. As an example, the biochronological sequence for the South American Paleogene showed no relevant changes from 1948 through the middle 1980s (Simpson, 1948; Marshall et al., 1983; Pascual et al., 1965, Patterson and Pascual, 1972). Subsequent taxonomic, geochronological, and biostratigraphic studies have contributed greatly in improving our understanding of the faunal evolution and succession of South American mammals (Flynn and Swisher, 1995, and references therein; Pascual et al., 1996). This has resulted in the identification of nearly 20 South American Land Mammal Ages (SALMAs). Land Mammal Ages have been recognized as biochronological units (Pascual et al., 1965; Woodburne, 1977; Archibald et al., 1987; Pascual and Ortiz Jaureguizar, 1990).

One of the most recent renovations in South American biostratigraphy was the revision and isotopic calibration of the Casamayoran SALMA. The Casamayoran was previously considered an early Eocene mammal record in South America (55–50 Ma; Marshall et al., 1983). Cifelli (1985) divided the Casamayoran into two subages: Vacan, the older, and Barrancan, the younger. Recently, the geochronology of the Casamayoran SALMA has been revised at the locality of Gran Barranca (Barrancan subage), south-central Chubut Province. Several  $^{40}\text{Ar}/^{39}\text{Ar}$  dates as well as

magnetic polarity stratigraphy from Gran Barranca indicated a much younger age than previously recognized for the Barrancan subage levels, with an age ranging from 37.60–35.69 Ma (Kay et al., 1999). This indicates that the Barrancan is of late Eocene age. More recent calibrations indicated an age of about 38.5 Ma for the upper boundary of the Barrancan levels, and 41.5 Ma for the base (Madden et al., 2005). There are no published dates for sediments deposited during the older, “Vacan” subage of the Casamayoran, although Carlini et al. (2005: fig. 1) suggested a time interval of ca. 44–45 Ma for it.

These new findings represent a major change regarding South American biochronology. During most of the second half of the 20th century, the Casamayoran (Barrancan plus Vacan) SALMA was regarded as early Eocene (e.g., Simpson, 1935b). Thus, the above-mentioned revisions have left a faunal gap in the early Eocene record of South American mammals. This gap is partially filled by the new faunas from the Chubut River region, discussed below.

Lower in the Paleogene sequence, the uppermost Salamanca Formation and the whole Río Chico Group (Legarreta and Uliana, 1994) are present in several localities of Chubut and Santa Cruz provinces, where they underlie the Sarmiento Group. They have long been considered Paleocene in age (Simpson, 1948, 1967a, b). Marshall et al. (1981) correlated the Hansen Member (“Banco Negro Inferior”) of the Salamanca Formation (Andreis et al., 1975), and the overlying sediments of the Río Chico Group with Chron 26r, which corresponds to a temporal range between  $61.70 \pm 0.2$  and

58.70  $\pm$  0.2 Ma (Gradstein et al., 2004). However, two localities of the Banco Negro Inferior have been correlated with Chron 27r (Somoza et al., 1995), i.e., between 63.20 and 62.0 Ma (Gradstein et al., 2004). Because of the original correlation with the Paleocene faunas of the Bolivian locality of Tiupampa (Muizón, 1991), the Banco Negro Inferior was originally assigned to the Tiupampian SALMA (Pascual and Ortiz Jaureguizar, 1990). However, Bonaparte et al. (1993) named the new Peligran SALMA on the basis of the distinct mammal assemblage present there. Relative ages of the Peligran and Tiupampian SALMAs have been under intense debate (see Pascual and Ortiz Jaureguizar, 1990; Bonaparte et al., 1993; Gelfo, 2006).

Above the Salamanca Fm. various levels of the Río Chico Group crop out, mostly in southeastern Chubut and in northeastern Santa Cruz provinces. Simpson (1935b) recognized “faunal zones” in the region of San Jorge Basin, southeastern Chubut Province, representing distinct faunal episodes in the early Tertiary: from oldest to youngest these were the “*Carodnia* faunal zone”, the “*Kibenikhorh* faunal zone”, and the “*Ernestokokenia* faunal zone”. Legarreta and Uliana (1994; see also Bond et al., 1995) presented a new lithostratigraphy naming the formations Peñas Coloradas, Las Flores, and Koluel Kaike, respectively, corresponding to the already mentioned faunal zones. Following Bond et al. (1995), these episodes represent at least three discrete SALMAs, from oldest to youngest, a post-Tiupampian or post-Peligran SALMA, Itaboraian (*Kibenikhorh* faunal zone, Las Flores Formation and locality), and Riochican (*Ernestokokenia* faunal zone), leaving the *Carodnia* faunal zone as a fourth episode between the Peligran and Itaboraian, poorly understood and not sufficiently known to justify naming a new SALMA. The suggested age for the Riochican SALMA was between 58.5 and 55 Ma (Pascual and Ortiz Jaureguizar, 1991). An important limitation—as noted by Bond et al. (1995)—is the difficulty of recognizing these SALMAs outside the region, even elsewhere in Patagonia.

In brief, taking into account the inferred numerical ages for the Riochican SALMA and the Vacan subage of the Casamayoran

SALMA, there seems to be an impressive 10 million year time gap between them—i.e., 55 Ma for the top of the Riochican, and 45 Ma for the base of the Vacan. Ongoing work addresses this “black hole” in our knowledge of the South American Paleogene faunal successions in two ways: first, we review the previously inferred ages for the whole Río Chico succession (Raigemborn et al., in preparation); second, we are prospecting Paleogene levels outside the San Jorge Gulf region (which contains no fossiliferous levels representing this time gap as currently known).

The present work represents the first of a series of contributions that propose a new approach to the problem. Here we describe two fossil mammal localities of late early Eocene age from western Patagonia, filling part of the current early to middle Eocene gap in the South American fossil record. On the basis of these localities, we suggest they may represent a new biochronological unit, one of the most diverse mammalian faunas known up to now from South America.

## ABBREVIATIONS AND TERMINOLOGY

LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad—Vertebrate Paleontology Collection, Facultad de Ciencias Naturales, Sede Esquel, Universidad Nacional de la Patagonia “San Juan Bosco”; MLP, Museo de La Plata; AMNH, American Museum of Natural History. The dentition is referred with the letters i/I, c/C, p/P, and m/M for lower and upper incisors, canines, premolars, and molars, respectively, followed by the corresponding number, while an “x” refer to a tooth of uncertain position.

## GEOGRAPHIC SETTING

The new fossiliferous localities, named Laguna Fria and La Barda, are the westernmost Paleogene mammal-bearing sites in Patagonia. They are located in northwestern Chubut Province, Argentina, near the town of Paso del Sapo, along the south side of the middle Chubut River (fig. 1). The area is surrounded by the Sierras de Huancache (northeast), Sierras de Cutancunú (south), and Sierras de Taquetrén (east).

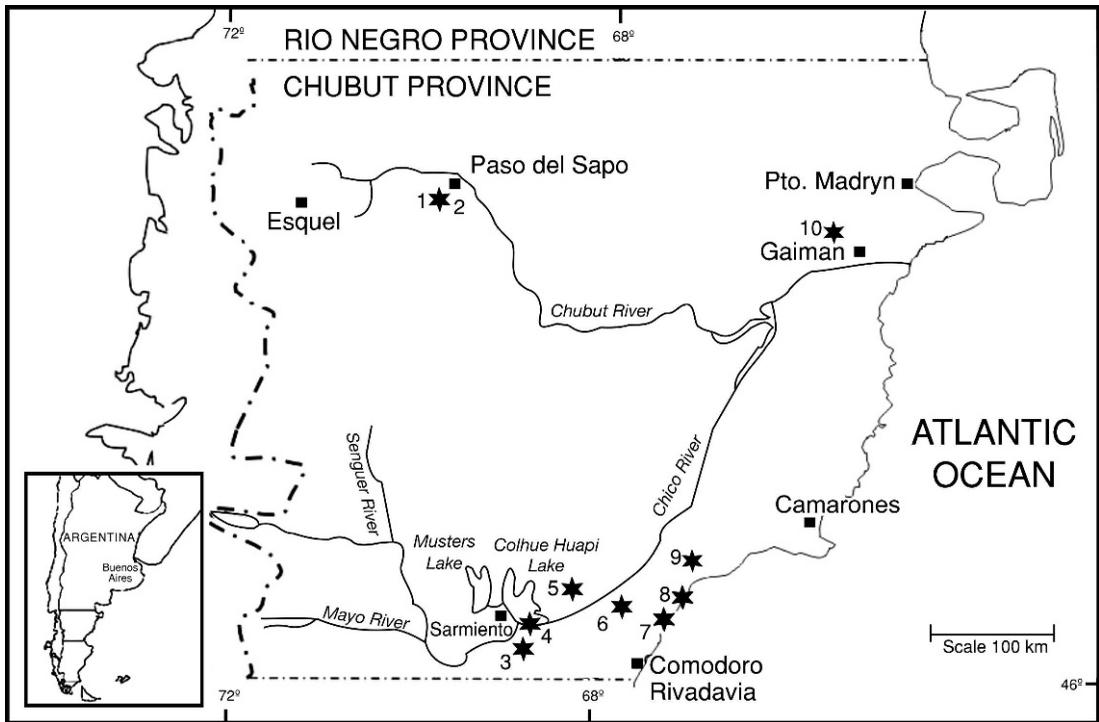


Fig. 1. Location map showing both fossiliferous localities of Paso del Sapo and the remaining known Paleogene localities of central Patagonia discussed in the text. 1. Laguna Fría; 2. La Barda; 3. Las Flores; 4. Gran Barranca; 5. Cañadón Vaca; 6. Cañadón Hondo; 7. Bajo Palangana; 8. Punta Peligro; 9. Cerro Redondo; 10. Cerro Pan de Azúcar.

#### Laguna Fría

(42°43'31.5"S, 69°51'36.1"W, 844 masl)

Laguna Fría is located within Estancia San Ramón, a farm owned by Mr. Rafael Nicoletti, about 170 km northeast of the city of Esquel and 28 km west of Paso del Sapo (fig. 1, #1). The fossil site was discovered in the 1950s by Rosendo Pascual, who collected a small sample of specimens currently housed in the Museo de La Plata. Some of the sparnotheriodontid liptopterns described below were collected by him. In September, 1999, during a visit to Estancia San Ramón, several specimens of mammals collected in Laguna Fría were donated by Mrs. Coca San Martín, a local resident and former owner of the farm. In addition, successive field trips to Laguna Fría and La Barda (see below) have provided

hundreds of vertebrate specimens, especially mammals. Some material was collected on the surface, but most was obtained by screen-washing of about 3 tons of sediments and subsequent sorting in the laboratory.

#### La Barda

(42°46'48.5"S, 69°51'43.3"W; 1056 masl)

This new locality is in Estancia 26 de Mayo, property of the family of the late Mr. Juan Pedro Grenier, 195 km northeast of Esquel and 28 km southwest of Paso del Sapo (fig. 1, #2). It was discovered in December 2001 and fieldwork was carried out during the following austral summers until February 2005. Hundreds of mammals were also collected there, mostly fragmentary, both by hand picking and dry screening of sediments.

## STRATIGRAPHY AND GEOCHRONOLOGY

### STRATIGRAPHIC CONTEXT

Aragón and Mazzoni (1997) reviewed the geology and stratigraphy of the Middle Chubut River Volcanic-Pyroclastic Complex. The regional geology, stratigraphy, geochemistry, petrogenesis, and paleobotany of this complex have been studied by Petersen (1946), Archangelsky (1974), Volkheimer and Lage (1981), Lage (1982), Rapela et al. (1984), Aragón and Romero (1984), Aragón et al. (1987), Mazzoni and Aragón (1985), and Mazzoni et al. (1989). These studies indicate that the complex is of Paleocene-Eocene age, and includes a variety of volcanoclastic, intrusive, pyroclastic, and extrusive rocks deposited over several million years. A great variety of volcanogenic bodies such as ignimbrites, domes, lava flows, necks, intrusives, tuffs, and volcanoclastic deposits (of predominantly lacustrine origin), all of them frequently interbedded, has been described in the region. These deposits were previously grouped in the Huitrera and El Mirador formations by Volkheimer and Lage (1981) and Lage (1982). Later, Aragón and Mazzoni (1997) defined 12 formal stratigraphic units within the whole complex. Three of them are relevant for this study: Ignimbrita Barda Colorada Formation (IBC), Tufolitas Laguna del Hunco Formation (TLH), and Andesitas Huancache Formation (AH). The TLH bears an extraordinary fossil flora exposed at a few localities; this flora was recently revised by Wilf et al. (2003).

The Ignimbrita Barda Colorada Formation overlies the latest Cretaceous/earliest Paleocene Lefipán Formation (fig. 2). It represents a major volcanic event (in volume more than 100 km<sup>3</sup>) that deposited a large 80 m thick ignimbritic plateau related to the formation of a 25 km wide caldera. The Tufolitas Laguna del Hunco Formation (TLH) conformably overlies the IBC Formation (fig. 2) and corresponds to the lacustrine deposits within the caldera. The IBC is interstratified with several other postcaldera volcanic units (Andesitas Estrechura, Ignimbritas Rulos, Riolitas Gualjaina, and Vitrófiros Huitrera;

see Aragón and Mazzoni, 1997). In this work, we propose that one of the fossiliferous localities, Laguna Fría, may correspond to the TLH deposits. Finally, the Andesitas Huancache are predominantly lavas alternating with intercalated tuffs, volcanic agglomerates, and sandstones. Together with the IBC, the AH are the thickest deposits of the complex. The second fossiliferous locality described here, the La Barda locality, occurs within the AH interbedded tuffs.

The levels of Laguna Fría overlie unconformably the IBC (Aragón and Mazzoni, 1997) at the ignimbritic plateau outside the caldera and are unconformably overlain by lava flows of the AH (upper member; fig. 2). The AH at this locality includes a sequence of alkaline basalts with a few interbedded tuffs. The extrusive centers of these flows are to the NW (Cerro Negro, in Piedra Parada). The distribution and geometry of the Laguna Fría Tuffs are filiform, and were controlled by the paleogeography of the fluvial valleys. Running to the southeast, this large paleovalley system developed first over the IBC and then directly over the Lefipán Formation, in the vicinity of La Barda, and, finally, it cut into the Paso del Sapo Formation near Cerro Gorro Frigio, in its southernmost extreme.

Figure 2 is a stratigraphic column of Laguna Fría, where the Laguna Fría Tuffs fill a paleovalley cut in the IBC and are later cut by another paleovalley filled with basalts of the AH. Further up in the basaltic AH fill occur a few interbedded tuffs such as La Barda.

### GEOCHRONOLOGY

<sup>40</sup>K/<sup>40</sup>Ar dates indicate an age of 58.6 Ma for the IBC (see Archangelsky, 1974, corrected with 1978 decay constants). The intracaldera lake beds (TLH) at the locality with the leaf flora have several <sup>40</sup>Ar/<sup>39</sup>Ar dates of the tuffs that indicated ages near 52 Ma (Wilf et al., 2003). Since the TLH overlies the IBC, these <sup>40</sup>Ar/<sup>39</sup>Ar ages suggest that the IBC must be older than 52 Ma.

At Laguna Fría a 52.05 ± 0.23 Ma <sup>40</sup>Ar/<sup>39</sup>Ar age was obtained from an ignimbrite that conformably overlies the IBC

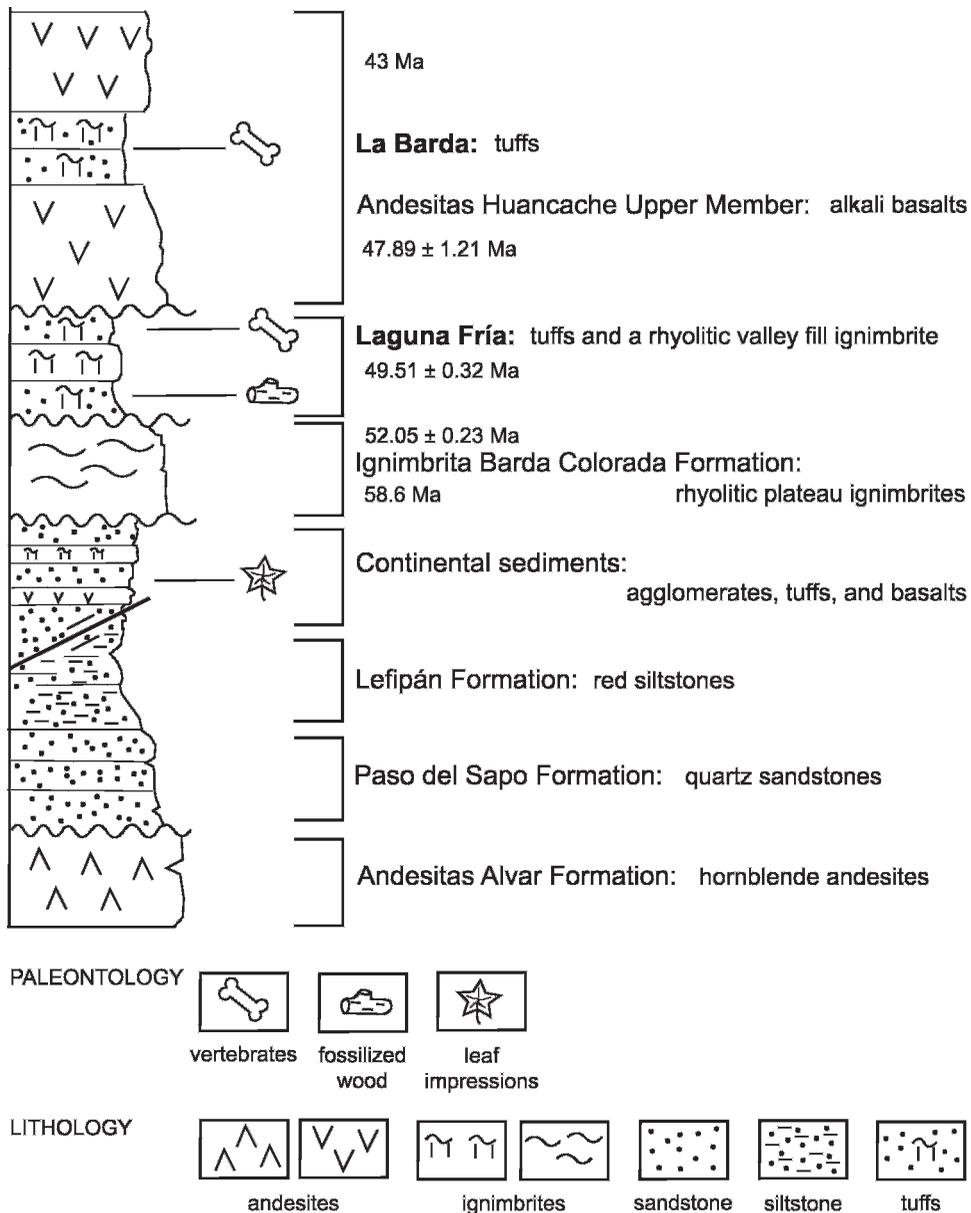


Fig. 2. Stratigraphic column including the localities of Laguna Fría and La Barda.

(Gosses et al., 2006, sample 1). In turn, a basal ignimbrite in the fossil-bearing tuffs of the extracaldera valley-fill deposits is dated at  $49.51 \pm 0.32$  Ma (Gosses et al., 2006). Finally, the overlying AH basalt dated at  $47.89 \pm 1.21$  Ma using the  $^{40}\text{Ar}/^{39}\text{Ar}$  method (Gosses et al., 2006, samples 2 and 3, taken about

100 meters above the ignimbrite sampled and dated at  $49.51 \pm 0.32$  Ma) are found within this member between the valley-fill ignimbrite and the AH basalt. Thus, the Laguna Fría mammal-bearing tuffs overlie unconformably the IBC and are covered unconformably by the AH alkaline basalt, meaning their age is

close to the  $49.51 \pm 0.32$  Ma ignimbrite, younger than the  $52.05 \pm 0.23$  Ma ignimbrite and older than the  $47.89 \pm 1.21$  Ma AH basalt.

The La Barda Tuffs interbedded with the AH lava flows are somewhat younger as they occur above the  $47.89 \pm 1.21$  Ma basalt. The Andesitas Huancache to the west have yielded three  $^{40}\text{K}/^{40}\text{Ar}$  dates near 43 Ma (Mazzoni et al., 1991). The La Barda Tuffs underlie the 43 Ma lava flows of the AH; as discussed below, and judging from the faunal similarities between the Laguna Fría and La Barda assemblages, it is reasonable to assume a 45–47 Ma age for the deposition of the La Barda mammal-bearing tuffs.

#### PRELIMINARY TAXONOMY

The taxonomy presented below is preliminary because many of the taxa will require detailed analysis, naming, description, and comparisons. The preliminary taxonomy given below is useful to understand the uniqueness of these new early Eocene mammalian assemblages. Most of the new taxa will be described in depth and named elsewhere. However, the description of the new species *Polydolops unicus*, sp. nov., is necessary because its first occurrence will be used to define this unit.

Order “Didelphimorphia” Gill, 1872

Family Peradectidae Crochet, 1979

**Gen. et sp. nov. 1**

Figure 3A

One upper and three lower molars from Laguna Fría are referred to this new taxon (LIEB-PV 1031, a left M<sup>?</sup>3). The upper molar has a reduced styler shelf, shallow ectoflexus, vestigial StC and StD, moderately developed StB, centrocrista linear and paraconule, and metaconule vestigial or absent. The lower molars match the upper, and they also present peradectoid traits. They show a vestigial postcingulum and less twinned entoconid and hypoconulid, compared to other peradectids. Trigonids and talonids are subequal in length but talonids are wider.

Family Caroloameghiniidae Ameghino, 1901

**Gen. et sp. nov. 2**

Figure 3B

Three lower molars collected at Laguna Fría and one upper molar from La Barda (LIEB-PV 1098, a left MX) are referred to this new taxon. It closely anticipates the molar structure of *Caroloameghinia* in the following traits: trigonid approximately one third the size of the talonid; protoconid and metaconid of similar height and development; reduced paraconid; well-developed, high and labiolingually compressed entoconid; very reduced hypoconulid that is not twinned with the entoconid; and reduced anterobasal cingulum. It differs from *Procaroloameghinia* and *Caroloameghinia* in the more reduced paraconid, more anteroposteriorly compressed trigonid, better-developed entoconid and talonid basin, and absence of crenulations in the molar surface. LIEB-PV 1098 is an upper molar tentatively referred to this new taxon; it shows characters that also anticipate the morphology of *Caroloameghinia*. The molar is badly worn but it presents a linear centrocrista, short preparacrista, paracone, and StB close to each other, and postmetacrista transverse to the dental axis. Because of wear, it is not possible to confirm the presence of a paraconule and metaconule, but at least a metaconule was likely present due to the “angulate” wear pattern on the protoconal area. StB is the largest cusp of the styler series and apparently the StC was absent.

This new taxon shares all the diagnostic characters of the Caroloameghiniidae, i.e., brachydont crowns and bunodont cusps, poorly developed crests, reduced anterobasal cingulum, postcingulum absent, anteroposterior compression of the trigonid, and well-developed talonid and entoconid. In addition, the lower molars are similar in size to *Caroloameghinia mater*. In general, this taxon shows an intermediate pattern between *Procaroloameghinia* and *Caroloameghinia*.

Family ?Caroloameghiniidae

This taxon is represented by a single specimen, an isolated, left mx talonid (LIEB-PV 1099) from La Barda. The bunoid aspect

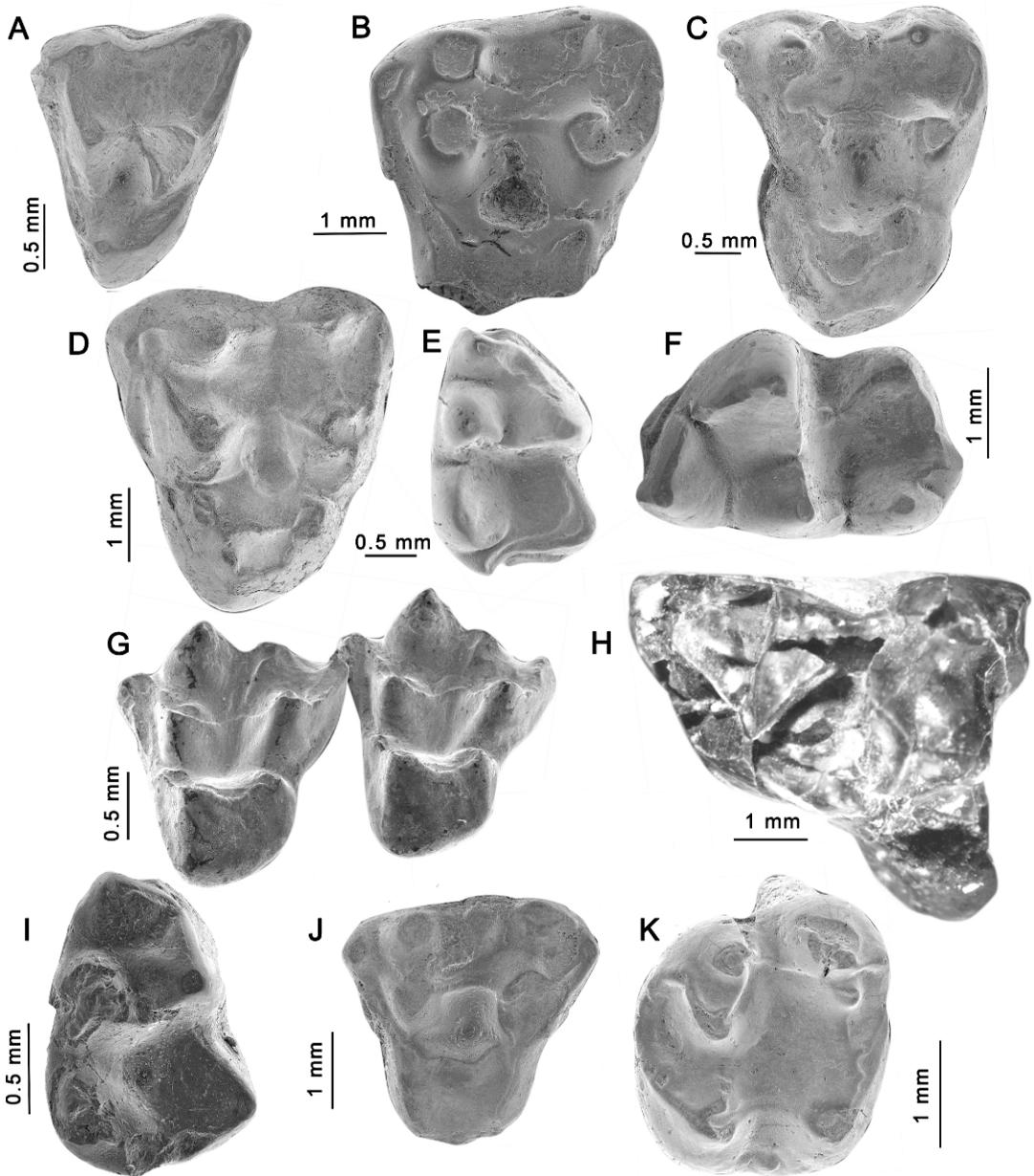


Fig. 3. Marsupials from Laguna Fria (LF) and La Barda (LB). **A**, Peradectidae gen. et sp. nov., LIEB-PV 1031 (LF); **B**, Caroloameghiniidae gen. et sp. nov., LIEB-PV 1098 (LF); **C**, Peradectoidea gen. et sp. nov., LIEB-PV 1097, left M3 (LB); **D**, *Protodidelphis* sp. nov., LIEB-PV 1091, left M?3 (LB); **E**, *Pauladelphys* sp. nov., LIEB-PV 1123, m2 in a fragment of right dentary (LF); **F**, cf. *Itaboraidelphys* sp., LIEB-PV 1064, an isolated right m2 or m3 (LF); **G**, *Paucituberculata* gen. et sp. nov. 1, LIEB-PV 1135, a left maxillary fragment with M2-3 and part of M4 (LF); **H**, Sparassodonta, Hathliacynidae, gen. et sp. nov. LIEB-PV 1036, M?3 in a maxillary fragment (LF); **I**, *Eomicrobiotherium* sp., LIEB-PV 1040, a right m?3 (LF); **J**, *Palangania* sp., LIEB-PV 1106, left M?3 (LB); **K**, *Gashternia ctalehor*, LIEB-PV 1132, a right M4 (LB).

of the cusps is noted, as well as the large entoconid and the presence of supernumerary cusps anterior to the entoconid and hypoconid. These traits are characteristic of the Caroloameghiniidae, but the conical shape of the entoconid and the presence of a vestigial postcingulum are not seen in other caroloameghiniids. Its size does not match with the above-described molars.

Family *Incertae sedis*

**Gen. et sp. nov. 3**

Figure 3C

Several upper and lower molars of this new taxon were collected at both localities of Paso del Sapo. The molars are brachydont and bunodont. Upper molars (e.g., LIEB-PV 1097, a left M3; fig. 3C) have a robust protocone, StB and StD relatively conical, vestigial “StC”, poorly developed ectoflexus, and conules not winged. The centrocrista is linear and low. As in peradectians, there is no difference between the relative height of the stylar shelf and the trigon basin. The lower molars have a reduced anterobasal cingulum and a reduced hypoconulid, and they lack a postcingulum. Trigonid and talonid are subequal in length. The talonid basin is wide and entoconid and hypoconid are subequal in height and development; the hypoconulid is small. The wide trigon and talonid basins and the robust protocone suggest a strong adaptation toward grinding. Judging from this morphology, this new taxon exhibits an omnivorous, or omnivorous-frugivorous adaptation.

Family Protodidelphidae Marshall 1987

*Protodidelphis*, **sp. nov.**

Figure 3D

This new species of *Protodidelphis* is well represented by several lower and upper isolated teeth from La Barda. It differs from other species of the genus mostly in its smaller size and less bunoid aspect. The upper molars (e.g., LIEB-PV 1097, a left M3; fig. 3D) have a well-developed metaconule and the crest joining the StB and StD is straight, unlike the Itaboraian species of the genus. The lower molars have a hypoconulid slightly more de-

veloped in m3–4 than in other *Protodidelphis* species. The overall crown surface is simple and devoid of cluttering crests; the stylar region is not specialized for “crowding” against the paracone and metacone; the centrocrista is linear and there is no special elevation of the stylar shelf relative to the talon surface. The lower molars have normal trigonid vs. talonid proportions; the paraconid is not reduced or otherwise specialized as to size or location; the metaconid and entoconid do not develop strong opposing crests; the entoconid is basically conical and isolated; the hypoconulid is located near, but isolated from the entoconid, and connected to the hypoconid.

*Protodidelphis* cf. *Protodidelphis*, **sp. nov.**

About a dozen isolated upper and lower teeth are here tentatively referred to the above-described new species of *Protodidelphis*, but this material comes from Laguna Fria whereas the *Protodidelphis* sp. nov. is characteristic of La Barda. Because only some of this material is well preserved, a precise attribution is difficult. Some minor differences are observed: the LF material is slightly larger in size, with more inflated molars, more developed metaconule, StB and StD closer to each other, and the preparacrista ends labially in a position closer to the anterolingual side of the StB in M2–3.

*Protodidelphis*, sp.

Two isolated lower molars (LIEB-PV 1092, isolated left m?1; LIEB-PV 1142, isolated left m?3) clearly differ from the other *Protodidelphis* specimens recorded in Paso del Sapo. These came from La Barda and are about twice the size of *Protodidelphis*, sp. nov. One of them, LIEB-PV 1092, is strongly worn, but the talonid appears to be shorter than in other species of *Protodidelphis*, and the hypoconid is less projecting labially. The other molar, LIEB-PV 1142, differs in a few details (i.e., more projecting hypoconid, paraconid more robust), but it is certainly from a different locus in the molar series. However, both molars are assigned to *Protodidelphis* on the

basis of their bunoid pattern, well-developed entoconid, relatively low paraconid, reduced hypoconid, and anterobasal cingulum. Because of the size and morphology of the talonid, they cannot be referred to any *Protodidelphis* species known up to now, including those listed above.

Family Derorhynchidae Marshall, 1987

Genus *Pauladelphys* Goin et al., 1999

*Pauladelphys*, sp. nov.

Figure 3E

This new species of *Pauladelphys* is well represented by dentition, maxillae, and mandibles mostly from Laguna Fria and a few specimens from La Barda. It differs from *Pauladelphys juanjoi*, from the Antarctic Peninsula, in several features of the molar series. The lower molars have a cristid obliqua more parallel to the dental axis; paraconid less reduced and anteroposteriorly compressed; anterobasal cingulum narrower; labial slope of the entoconid almost flat (LIEB-PV 1123, fragment of right dentary with complete m2; fig. 3E). Upper molars show a larger metaconule; StB less posteriorly placed; paracone farther from the StB. This is a fully tribosphenic taxon in which the molars are sharply crested. All stylar cusps are present; StB is sometimes very large; the centrocrista is V-shaped. The stylar shelf is elevated above the talon basin. The paraconule is present, but small and variably winged; the metaconule is larger and also variably winged. The lower molars also are fully tribosphenic and crested, with the cusps subpyramidal. This new species of *Pauladelphys* is almost equal in size to the type species of the genus. However, several traits (e.g., StB less displaced posteriorly, less reduced and compressed anteroposteriorly paraconid) suggest that *Pauladelphys* sp. nov. is more generalized than *P. juanjoi*.

Genus *Derorhynchus* Paula Couto, 1952

*Derorhynchus* cf. *D. minutus* Goin et al., 1999

This taxon is represented by eight specimens from Laguna Fria. The lower molars closely resemble, in size and structure, those of

*Derorhynchus minutus*, from the late early Eocene of the La Meseta Formation in Antarctica. Lower molars have all characteristic features of the *Derorhynchus* species: small paraconid, short talonid, and high, spirelike entoconids. The Laguna Fria specimens are almost identical in size to those of the La Meseta Fm.

*Derorhynchus* sp.

Though scarce, two specimens (LIEB-PV 1102, right m4; LIEB-PV 1140, isolated left talonid) from Laguna Fria can be confidently referred to the genus *Derorhynchus*, as they share most of the lower molar pattern (see above) with species of this genus.

Family Sternbergiidae McKenna and Bell

1997

Genus *Marmosopsis* Paula Couto 1962

*Marmosopsis* sp.

The referred specimens are two right mx (LIEB-PV 1286, and LIEB-PV 1287), both from La Barda. We tentatively assign them to *Marmosopsis* sp. for the following reasons: laterally compressed lower molars, proportionally long talonids, and slender, though sharp, trigonid cusps.

cf. *Itaboraidelphys* Marshall and Muizon, 1984

cf. *Itaboraidelphys* sp.

Figure 3F

All materials referred to this species are from Laguna Fria: illustrated is an isolated right m2 or m3 (LIEB-PV 1064), and additional referred materials include an isolated left metastylar area (M1 or M2; LIEB-PV 1066); isolated lower left premolar (LIEB-PV 1067); fragment of left upper molar (Mx; LIEB-PV 1110); and right metastylar fragment (LIEB-PV 1075).

In size and overall morphology, these specimens resemble the pattern seen in the Itaboraian-aged *Itaboraidelphys*, previously known from Itaboraí (Brazil) and Las Flores (Argentina). In the upper molars, the post-metacrista is well developed and trenchant;

premolars are laterally compressed, and molars have unreduced talonids and well-developed paracristids.

“Didelphimorphia” indet.

Gen. et sp. indet. A

Three upper molars from Laguna Fría are difficult to assign. LIEB-PV 1042, possibly an M1, is completely preserved. This is a subtriangular tooth, canted anterolingually. The protocone is pointed anterolingually; paraconule and metaconule, respectively, are about half-way along the pre- and postprotocristae, and do not closely abut the lingual bases of the paracone and metacone; they do not appear to have been strongly winged. The preparacrista extends past the anterior base of the paracone to reach a small cusplule at the lingual base of StA. Paracone and metacone are well separated, about equally tall, but the metacone is somewhat more massive than the paracone. The centrocrista is linear, but weakly expressed. The talon basin is deep and separated by the centrocrista from the elevated styler shelf. The styler shelf is narrow and bears a complete complement of styler cusps, all relatively small and much lower than the paracone or metacone. The ectoflexus is virtually absent. The postmetacrista is strongly crested and performed a shearing function. The elevation of the styler shelf shows the derived nature of this tooth relative to a peradectian. Apparently the connection of the preparacrista to StB rather than to StA is a non-microbiotherian character.

Order Paucituberculata Ameghino, 1894

Family indet.

**Gen. et sp. nov. 4**

Figure 3G

A left maxillary fragment with M2–3 and part of M4 (LIEB-PV 1135; fig. 3G) was collected in La Barda. The protocone is the lowest and widest cusp of the trigon; the paracone is small and lower than the metacone, the latter is pointed and has a metacrista posteriorly, longer than the paracrista in both

molars. Paraconule and metaconule are developed.

Two additional specimens from La Barda are here referred tentatively to the same taxon. LIEB-PV 1137 is a well-preserved mandibular fragment with one lower molar and roots of an additional molar. The molar probably corresponds to an m2 or m3. Trigonid and talonid length is subequal; the paracristid is well developed and the metacristid has a deep fovea; paraconid and metaconid are close to each other, more than is expected for didelphimorphians. The anterobasal cingulum is narrow. LIEB-PV 1138 is almost identical to the former, but the metaconid is more separated from the paraconid, as occurs in m1s of Paucituberculata.

**Gen. et sp. nov. 5**

This taxon is represented by one upper and three lower molars from La Barda. The upper molar LIEB-PV 1151 shows a morphology similar to the above-described Paucituberculata, but larger in size and with cusps more inflated. The protocone and StB are the largest cusps and even more inflated; the metacone is subequal in size but taller than the paracone; the centrocrista is deep and its distal part is oriented labial and posteriorly. The metaconule and paraconule are more developed than in Gen. et sp. nov. 4, both winged, but the metaconule lacks the postmetaconular crest. The specimen LIEB-PV 1101 is a left lower molar that shows the paraconid and metaconid close to each other; talonid wider than trigonid; hypoconid is labially expanded. The specimen LIEB-PV 1136 is most probably a left m4. As in the lower molars of the Gen. et sp. nov. 4, the entoconid is compressed laterally.

Order ?Paucituberculata

Gen. et sp. indet. B

LIEB-PV 1108 is a left mandible from La Barda, with four alveoli and the root of a hypertrophied and procumbent i1. The mandibular ramus is low in comparison with Gen. et sp. indet. A, about half its height.

Order Sparassodonta Ameghino, 1894  
Family Hathliacynidae Ameghino, 1894

**Gen. et sp. nov. 6**

Figure 3H

This new taxon is based on LIEB-PV 1036, a maxillary fragment with M<sup>3</sup> (fig. 3H), and LIEB-PV 1037, isolated metastylar portion of a right M<sup>2</sup>, both from Laguna Fría. Although an additional specimen, LIEB-PV 1141, a fragment of a left M<sup>2</sup>, was collected at La Barda, it is here assigned to the same taxon. LIEB-PV 1036 has a slightly reduced stylar shelf, with an StB still present, conical, and similar in size to the paracone; paracone and metacone are twinned, with the metacone much larger, resulting in a nearly absent centrocrista. The postmetacrasta, although broken, appears to have been well developed. There is a small paraconule, but apparently the metaconule was absent or extremely reduced.

LIEB-PV 1036 is much larger than the oldest known hathliacynids (*Allkoquirus australis*, from the early Paleocene of Bolivia, and the species of *Patene*, widely distributed between the late Paleocene and late Eocene of Patagonia and Brazil; Muizon, 1991; Marshall, 1978). The difference in height between paracone and metacone, and the reduction of the protocone are surprising in comparison with primitive hathliacynids. Also differing, the StB is not reduced and is subequal in size to the paracone.

A second aspect of major biostratigraphic significance is the fact that the upper molar LIEB-PV 1036 is very similar to a fragmentary upper molar assigned to Borhyaenidae indet. (MLP 79-I-17-5), held in the Museo de La Plata collection. Although it lacks the protocone, most of the tooth is well preserved and is comparable to the Laguna Fría molar in the StB dimensions, reduction of the other stylar cusps, width of the stylar shelf, and length of the postmetacrasta. The major difference between the specimens is that, apparently, the Laguna Fría molar has a larger metacone. This difference, however, does not "invalidate" the potential attribution of both specimens to the same genus, and, probably, to the same species. Specimen MLP 79-I-17-5 was collected in 1979 at Bajo Palangana, Chubut

Province, by M. McKenna and R. Turnbull, who tentatively correlated those levels with the "?Casamayoran" (McKenna and Turnbull, unpublished data). The stratigraphy of Bajo Palangana correlates almost completely with the Río Chico Group or Formation.

Family Borhyaenidae Ameghino, 1894  
Subfamily Borhyaeninae Ameghino, 1894  
cf. *Nemolestes*

LIEB-PV 1038 is an isolated left m<sup>4</sup> from Laguna Fría. The talonid is unicuspid and reduced, approximately 20% of the total length; the trigonid is formed exclusively by the paraconid and protoconid. Although partially broken, the paracristid seems to have been well developed. The anterobasal cingulum is present but weak.

The early representatives of the Sparassodonta are still poorly known. As an example, there is a citation of "cf. *Nemolestes* sp." from the Itaboraian of Brazil and Riochican of Argentina (see Marshall, 1978; Marshall et al., 1983). Also, indeterminate specimens are mentioned for Itaboraian levels of Itaboraí (Brazil) and Las Flores (Patagonia) (Goin, personal obs.), as well as indeterminate borhyaenids from the Riochican of Cerro Redondo (see Simpson, 1935b).

Gen. et sp. indet. C

LIEB-PV 1093 is a right m<sup>1</sup> from La Barda. The trigonid is formed exclusively by the protoconid and the much lower paraconid; there is no keel basal to the paraconid. The anterobasal cingulum is vestigial and the preparacristid is short. The talonid is wider than the trigonid with only one central cusp and two labial and lingual slopes. The talonid ends in a small distal cusplule (hypoconulid?), with a lingual edge ending in a tiny crenulation (entoconid?). The presence of a central cusp in the talonid is a trait also seen in several borhyaenines, such as *Plesiofelis* and *Pharsophorus*, as well as in the proborhyaenids. The absence of a metaconid characterizes not only the m<sup>1</sup> of proborhyaenids, but also all the lower molars of prothylacynines and m<sup>1</sup> of borhyaenines.

Order Microbiotheria Ameghino 1887  
 Family Microbiotheriidae Ameghino 1887  
 Genus *Eomicrobiotherium* Marshall 1982  
*Eomicrobiotherium* sp.

Figure 3I

A single specimen of this taxon was found at Laguna Fría (LIEB-PV 1040, right m<sup>3</sup>). It is robust, bunoid, with a short talonid which is relatively narrow, though slightly wider than the trigonid; large terminal but labially placed paraconid; protoconid and metaconid also large. The talonid is shorter than the trigonid; the cristid obliqua extends anterolingually to the rear of the trigonid posterior to the protoconid. The lingual half of the talonid is raised relative to the talonid basin, strongly blocking the lingual exit of that basin. The apically broken entoconid is a massive cusp. A broken wear surface suggests the former presence of a hypoconulid posterolingual to the entoconid, but another broken surface may show that this cuspid was present near the posterior midline of the tooth. A short anterior and posterior cingulum is present.

The massive nature of the cusps, the anterior projection of the low paraconid relative to the higher and more unified protoconid and metaconid, and the tall lingual margin of the talonid are all very distinctive features.

Gen. et sp. indet. D

This taxon is known from two specimens from Laguna Fría: LIEB-PV 1039, a fragment of right dentary with the alveoli for i1-m2, and LIEB-PV 1041, a right Mx. The alveoli for the incisors in LIEB-PV 1039 are not staggered as occurs in i2 of didelphimorphians. The four incisors appear to have been subequal in size, but i4 was probably smaller. The canine also was relatively small. LIEB-PV 1041 does not preserve the styler shelf. The paracone and metacone are similar in size and height, and the centrocrista is linear, as in all other microbiotheriids. The protocone is robust and the trigon basin is wide; small paraconule and metaconule are present. Precise affinities of this taxon are difficult to assess, but the robustness of the molars suggests a possible relation with *Pachybiotherium acclinum*.

Family ?Microbiotheriidae  
 Gen. et sp. indet. E

LIEB-PV 1094 is an upper right molar lacking the protocone, probably an M4 because of the reduced metastylar area and absence of StD, that was collected at La Barda. Paracone and metacone are similar in size, but the paracone is slightly taller. The centrocrista is linear; the precingulum is short and narrow. StB and StA are subequal and a tiny StC is placed behind the posterior crest of the StB.

Order ?Microbiotheria Ameghino, 1887  
 Gen. et sp. indet. F

Two lower molars from Laguna Fría and two uppers from La Barda are included in this taxon. The uppers show a linear centrocrista and short postmetacrista. The metaconule is much larger than the paraconule; neither is winged. The protocone is not wide, as seen in Caroloameghiniidae. These upper molars differ from microbiotheriids in having a well-developed metaconule and short postmetacrista. On the contrary, the short postmetacrista and relative size of the metaconule suggest affinities with Caroloameghiniidae. The lower molars are twice the size of Gen. et sp. indet. E. In the specimen LIEB-PV 1043, probably an m1, the metaconid is small and placed posterior to the protoconid; the trigonid/talonid width is similar; the entoconid is laterally compressed and close to the metaconid; and the hypoconid is robust and does not project labially; and the hypoconulid is very small and nearly centrally placed.

Order Polydolopimorphia Ameghino, 1897  
 Suborder Hatcheriformes Case et al., 2004  
 Family Glasbiidae Clemens, 1966  
*Palangania* cf. *P. brandmayri* Goin et al., 1998

Two lower molars from La Barda (LIEB-PV 1089 and 1090) and one from Laguna Fría (LIEB-PV 1051) are here assigned to this taxon. Trigonid and talonid lengths are similar, but the talonid is wider. The labial side is clearly twice the height of the lingual side. The trigonid shows a distinctively low

protoconid and a small crest joining lingually the paraconid and metaconid; thus the trigonid basin is closed. The hypoconid is broad and the hypoconulid is relatively central; the anterobasal cingulum is absent, as is the postcingulum.

These molars resemble *Palangania brandmayri* in having low trigonid cusps, similar in height; metacristid is not vertical but forms an inclined surface toward the talonid; hypoconulid reduced and separated from the entocoid; entoconid large and bulbous. These molars are nearly the same size as those of the type species of *Palangania*.

*Palangania* sp.

Figure 3J

A single specimen (LIEB-PV 1106, left M<sup>3</sup>; fig. 3J), an upper molar from La Barda, is complete but worn. The protocone is a prominent cusp and the trigon basin is deep and wide. The stylar shelf is reduced and StB and StD are placed close to the paracone and metacone, respectively; a lower StC is present. The centrocrista is almost linear, somewhat curved labially; the preparacrista ends on the anterolingual side of the StB and the post-metacrista is short. Due to the wear, it is not possible to confirm the presence of a metaconule, but a paraconule was already present. Also, the StC is relatively larger and the stylar shelf is more developed labiolingually. Although smaller and more generalized, this molar resembles the M<sub>3</sub> of *Palangania brandmayri*.

Suborder Bonapartheriiformes Goin and Candela, 2004

Family Gashterniidae Marshall, 1987

*Gashternia ctalehor* Simpson, 1935

Figure 3K

The holotype of this species, AMNH 28533, a right mandibular fragment with m<sub>1</sub>-2 partially preserved is from the upper Paleocene of Patagonia. Several upper and lower molars attributed to this taxon were found at La Barda. *Gashternia* differs from other Polydolopimorphia in having lower molars with trigonid and talonid divided by

a deep flexus anterior to the cristid obliqua. The metaconid is higher than the protoconid in m<sub>2</sub>-4 and becomes fused to the metaconid from m<sub>1</sub> to m<sub>4</sub>. The anterobasal cingulum and hypoconulid are vestigial. Upper molars (e.g., LIEB-PV 1132, right M<sub>4</sub>; fig. 3K) have a deep lingual flexus separating the protocone from the hypertrophied and lingually displaced metaconule. StB and StD are the most developed stylar cusps while StC is lacking in all molars. The postmetaconular crest reaches the labial edge forming a wide sulcus.

The selenodont condition of *Gashternia* makes it one of the most singular South American marsupials. In the original description, Simpson (1948: 69) wrote:

this peculiar little jaw is quite unlike anything else known to me. ... There is some suggestion that it may be a marsupial, chiefly the fact that the probabilities somewhat favor the presence of only three premolars, but this is not certain.

The material from Paso del Sapo led us to understand the morphology of all molars, including the uppers, and strongly supports the inclusion of *Gashternia* in the Metatheria.

Suborder Polydolopiformes Kinman, 1994

Family Polydolopidae Ameghino, 1897

Subfamily Polydolopinae Ameghino, 1897

Genus *Polydolops* Ameghino, 1897

*Polydolops unicus*, sp. nov.

HOLOTYPE: LIEB-PV 1252, right maxillary fragment with P<sub>3</sub>-M<sub>3</sub> (fig. 4a). P<sub>3</sub> width = 2.96; P<sub>3</sub> length = 2.46; M<sub>1</sub> width = 3.60; M<sub>1</sub> length = 2.89; M<sub>2</sub> width = 4.41; M<sub>2</sub> length = 2.6; M<sub>3</sub> width = 2.41; M<sub>3</sub> length = 2.24.

ETYMOLOGY: From the Latin *unicus*, "unique", recognizing the exceptionally derived morphology of its second upper molars.

REFERRED SPECIMENS: The holotype and LIEB-PV 1240\*, left maxillary fragment with M<sub>2</sub>-3; LIEB-PV 1241\*, left M<sub>1</sub>, LIEB-PV 1242\*, right M<sub>1</sub>, LIEB-PV 1243\*, right M<sub>1</sub>, LIEB-PV 1244\*, right, broken M<sub>1</sub>; LIEB-PV 1245, left maxillary fragment with M<sub>1</sub>-2; LIEB-PV 1246, left M<sub>1</sub>; LIEB-PV 1247, left M<sub>2</sub>; LIEB-PV 1248, left M<sub>2</sub>; LIEB-PV 1249,

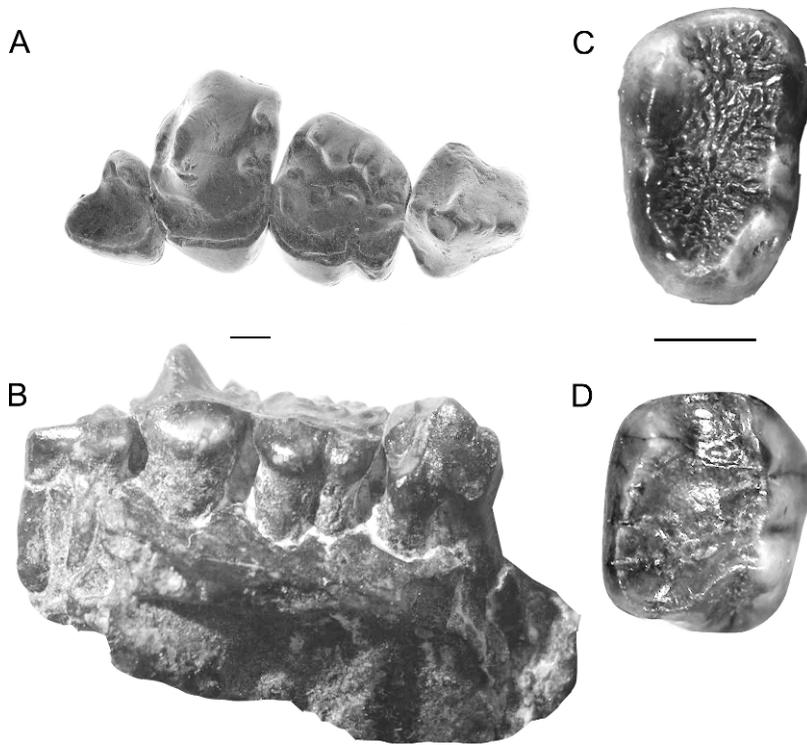


Fig. 4. *Polydolops unicus* sp. nov., the most unusual and representative mammal of Paso del Sapo. Holotype, LIEB-PV 1252, right maxillary fragment with P3–M3 (LF) in **A**, occlusal, and **B**, lingual views; **C**, LIEB-PV 1277, right m3 (LB). Scale bar = 1 mm; **D**, LIEB-PV 1271, right m2 (LB).

left M2; LIEB-PV 1250, left M2; LIEB-PV 1251, right maxillary fragment with P3–M3; LIEB-PV 1253, right M1; LIEB-PV 1254, right M1; LIEB-PV 1255, right M1; LIEB-PV 1256, right, broken M2; LIEB-PV 1257, right M3; LIEB-PV 1258, right M3; LIEB-PV 1212\*, left dentary with broken m1, complete m2, and roots of m3; LIEB-PV 1217\*, right dentary with m1–3; LIEB-PV 1259\*, left mandible with m1–2 and roots of p3; LIEB-PV 1260\*, left mandible with m2–3; LIEB-PV 1261\*, left m2; LIEB-PV 1262\*, right mandible with m1–2; LIEB-PV 1263, left mandible with m1–2; LIEB-PV 1265, left m2; LIEB-PV 1266, left, broken m2; LIEB-PV 1267, right mandible with broken p3, complete m1–2, and roots of m3; LIEB-PV 1268, right mandible with m2; LIEB-PV 1269, right mandible with m2; LIEB-PV 1270, right mandible with m2; LIEB-PV 1271, right mandible with broken m1, complete m2, and roots of m3; LIEB-PV 1272, left m1; LIEB-PV

1273, right m1; LIEB-PV 1274, right m1; LIEB-PV 1275, right m2; LIEB-PV 1276, broken right m2; LIEB-PV 1277, right m3; LIEB-PV 1278, right m3.

**GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE:** Specimens marked above with an asterisk (\*) come from Laguna Fría, while the remainder are from La Barda; Tufolitas Laguna del Hunco Formation, early middle Eocene, western Patagonia.

**DIAGNOSIS:** *Polydolops unicus* (fig. 4) differs from other species of *Polydolops* in the following characters: large size, although smaller than *P. mayoi* and *P. abanicoi*; shorter face, and higher and more robust maxillae and mandibles; M1 comparatively shorter; M2 broader than M1; the metacone and StB of M2 are fused and hypertrophied, thus forming a single cusp strongly projecting over the occlusal plane of the upper molars; m1–2 (and probably m3) relatively small and short in relation to the size of the mandibular corpus;

m1–2 hypoconid placed more anteriorly than in *P. rothi*.

DESCRIPTION: Abundant upper and lower teeth, mandibles, and maxillae of this new taxon are preserved, coming from both localities at Paso del Sapo. This new species is the most specialized polydolopine known to date; the functional significance of these adaptations are under study.

The holotype preserves most of the maxilla and cheek teeth. The maxilla is high in relation to other polydolopines, and it has a moderately developed infraorbital foramen located above the root of P3. The suture line between the maxilla and the anterior part of the jugal is preserved, showing that the jugal was vertically high. P3 is mesiodistally short and buccolingually wide, nearly as wide as the M1. The crown shows a large principal cusp and a smaller one anteriorly placed. The major cusp has two crests, anterior and posterior, and two “ridges”, labial and lingual. The crests are not sharp compared to the ridges. The posterior root is broad, probably twice the size of the anterior root. A little-developed talon is present posterolingually. M1 is proportionally shorter and wider than P3, much wider in the posterior half. There are two cusp rows labially, not aligned but with an irregular pattern, especially in the more labial row; both rows join in a relatively large StB. A reduced paracone is seen on the lingual side of the StB. In the styler shelf, the internal row is formed by the StC and StD aligned and subequal in size and height, and the StE somewhat lower than the StB. A metacone is observed between StD and StE, with the base fused to these styler cusps, and the metacone is almost the height of StE. The labial row is formed by four accessory cuspules. M1 exhibits two lingual lobes, with a paraconule in the anterior one. Three subequal cusps are observed in the anterior half of the posterior lobe: the first is probably the protocone, followed by an accessory cusp, and the third is probably the metaconule, but the homologies are difficult to assess.

M2 is an odd tooth, very derived and unique among the Metatheria. Its degree of specialization is even more surprising considering that M1 and M3 do not show the same specialization. The unusual buccolingual width is clearly greater than in M1, and more

than twice that of M3. The lingual edge of M2 is aligned with the lingual edges of M1 and M3, thus leaving the labial edge projecting beyond the labial edge of M1. Another surprising character is the possible presence of four roots, with a large lingual and three labial roots. It is possible that the anterolabial and centrolabial roots are parts of the same root with two lobes. But the most remarkable trait is the enormous cusp placed centrolabially; this hypertrophied tooth has modified the total volume of the tooth as well as the supporting root; as a result, the labial roots have developed an additional lobe. This huge cusp appears to be formed by the fusion of the metacone and StD. The lingual margin of M2 is relatively linear with poorly developed paraconule and metaconule that have metaconular crests. The trigon basin is rugged. The M3 is reduced and simplified compared to M1–2, being generally subtriangular in shape, longer lingually than labially.

There is remarkable variability in the size and robustness of the mandibles, probably suggesting sexual dimorphism. The anterior part of the mandibles is not preserved in any specimen of *P. unicus*, thus there is no information on the incisors and anterior premolars. The p3 is only known in two specimens but only the base was preserved; it was apparently short and robust. The lower molars are compact, robust, and slightly hypsodont labially (labial side clearly higher than the lingual side). The m1–2 are subequal in length and width, while m3 is longer and narrower. The occlusal surface was crenulated. The m1 shows a very reduced and short trigonid, with two low cusps. Behind the trigonid, there are three lingual and three labial cusps. The labial cusps are shallow and robust, the posterior (hypoconid) being the most robust. The m2 is shorter and shallower than the m1, with just four lingual and four labial cusps, among which the metaconid (as in other polydolopines) is the highest and more robust. The most striking trait in m2 is the anterior position of the hypoconid; this trait was incipient in *Polydolops rothi*, but has a high degree of specialization in *P. unicus*. This trait clearly distinguishes *P. unicus* from any other polydolopine species. In polydolopines, the posthypocristid is almost parallel to

the posterior margin of the tooth, slightly curving forward to meet the hypoconid. To the contrary, in *P. unicus* (and in a much lesser degree in *P. rothi*), the posthypocristid is oblique to the dental axis, slightly concave. This odd morphology is certainly related to the occlusion with the huge cusp of M2, and due to the hypertrophy of this cusp the interdental space between m2–3 leave a place for the occlusal closure.

REMARKS: *Polydolops unicus* is the most specialized polydolopine known. This is especially noteworthy in light of the specialization of the entire Polydolopinae, whose morphology has diverged considerably from the tribosphenic pattern. On the other hand, *P. unicus* was previously unknown from other stratigraphic levels in Patagonia, and its relative abundance in the Paso del Sapo mammal assemblages is surprising, thus characterizing the faunal associations. Therefore, *P. unicus* may be considered as a fossil guide (see below). The only known polydolopine that may be treated as a potential ancestor of the morphology of *P. unicus* is *P. rothi*, which shows a derived pattern in the molar morphology having: (1) M2 with enlarged StD, lingually inclined and coalescent with the metacone forming a transversal axis to the dentary; (2) m2 with the hypoconid anteriorly displaced with consequent development of the slightly concave hypocristid. These characters may allow *P. unicus* and *P. rothi* to be considered different genera, but this hypothesis should be tested in an integrated analysis of the whole family.

*Polydolops rothi* Simpson, 1936

The holotype of this species is MLP 11–122, a left dentary with p3–m2 from Cerro Pan de Azúcar, near Gaiman, Chubut Province, but several upper and lower specimens were found in La Barda and Laguna Fría. *Polydolops rothi* differs from other species of the genus for its poorly to moderately developed p3; size intermediate between the larger *P. mayoi* and the smaller *P. clavulus*; m1 with the sharp crest of the trigonid short; hypoconulid clearly more anterior than the entoconid; M2 slightly reduced in width with respect to M1; metacone and StB well developed and partially fused at the base of M2.

*Polydolops*, sp. nov. 1

LIEB-PV 1153, a maxillary fragment with M1–2, as well as four lower molars are included in this new species recovered in La Barda and Laguna Fría. It differs from *Polydolops serra*, the morphologically closest taxon, in its smaller size; double StC in M1; accessory labial cusps that form a crenulate crest; metacone and StD almost fused in M2; the large lingual cusp of m1 the talonid is the second posterior to the trigonid (instead of the first, as in *P. serra*). Also, m1 is proportionally larger and narrower than in *P. clavulus*, having three labial cusps instead of four, as in *P. clavulus*. Compared with *Polydolops* sp. nov. 3 (see below), this taxon is smaller; M1 has three cusps in the posterior lobe; there is no ectoflexus; the metacone is well distinct in M2; and m1 has the second lingual cusp undivided and comparatively much larger.

*Polydolops*, sp. nov. 2

LIEB-PV 1173, a right maxillary fragment with M1–2, as well as several maxillary and mandibular remains and isolated teeth have been assigned to this new taxon collected in both localities of Paso del Sapo. In general, it is morphologically closer to the above-described *Polydolops* sp. nov. 1 than to any other known polydolopine, except for its larger size and several other traits including: M1 with two lingual cusps instead of three in the posterior lobe; m1 with the second labial cusp divided and comparatively much smaller; labial accessory cusp larger than in sp nov. 2; and hypoconid of m2 more posteriorly placed and with the second lingual cusp proportionally smaller. The morphology of M1—with three cusp rows from which the two labial ones are merged—is clearly distinguishable from all other known polydolopines.

*Polydolops*, sp. nov. 3

LIEB-PV 1178 is a right mandibular fragment with p3–m1 from La Barda. This is the only specimen assigned to this new taxon and differs from *P. thomasi* by having a p2 comparatively larger; more significant size difference between p3 (larger) and m1 (small-

er); anterior lingual cusp of m1 divided into two adjacent cusps. It differs from *P. mayoi* in its smaller size; p2 with two roots and smaller m1 relative to p3. In general, this new taxon shows a combination of generalized and derived traits.

Genus *Amphidolops* Ameghino, 1902  
*Amphidolops*, **sp. nov. 1**

Only three teeth from Laguna Fría are referred to this new species: LIEB-PV 1172, a right m2, and two M1s. This is the smallest species of the genus *Amphidolops* and differs from *A. serrula* for a more elongated metacone in M2 and very distinct talonid cusps; M1 is proportionally shorter, with wider styler shelf; the most posterior labial cusp is the tallest; the metacone in M1 is placed more anteriorly. It differs from *Amphidolops* sp. nov. 2 (below) in the presence of only one line of labial cusps in M1, and fewer lingual cusps in m2.

*Amphidolops*, **sp. nov. 2**

LIEB-PV 1187, a right m2, and several isolated lower and upper molars from both localities of Paso del Sapo are referred to this new species. With respect to other species of *Amphidolops*, it is intermediate in size between *A. sp. nov. 1* and *A. yapa*. It differs from *A. serrula* in its more linear labial side on m2; cusps of lower molars are more distinct; hypoconid of m1–2 is more developed and placed more anteriorly; and M1 has two cusp rows. This new taxon differs from *A. sp. nov. 1* by having two lines of labial cusps in M1 and more lingual cusps in m2.

Superorder Xenarthra Cope, 1889  
Order Cingulata Illiger, 1811  
Family Dasypodidae Gray, 1821  
Subfamily Dasypodinae Gray, 1821  
Tribe Astegotheriini Ameghino, 1906  
Genus *Riostegotherium* Oliveira and Bergqvist, 1998  
*Riostegotherium*, **sp. nov.**  
Figure 5A, B

Several isolated plates of the dorsal carapace of this new taxon were recovered at La Barda

and Laguna Fría. These are small dasypodids similar in size to the living *Dasypus hybridus* or *D. septencinctus*, with very thin osteoderms having fine punctations on their surface, and central figure in the semimovable plates, as seen in *R. yanei*, from the Itaboraian of Brazil (Oliveira and Bergqvist, 1998). The foramina surrounding the central figure are placed in an arch, but are fewer than in *R. yanei*. The central keel in the central figure on the exposed surface is not well defined. There are few relatively large foramina on the posterior margin.

Genus *Prostegotherium* Ameghino, 1902  
*Prostegotherium* cf. *astrifer*  
Figure 5 C, D

This species has been collected at Laguna Fría and La Barda. This dasypodid is also of small size, although larger than *Astegotherium*. Its osteoderms show several punctations surrounding the central figure, not placed as an arch as in *Riostegotherium*, but as an anteriorly pointed “V”. The plates have a wrinkled surface, but less so than *Stegosimpsonia*, with the central figure subtriangular.

Genus *Astegotherium* Ameghino, 1902  
*Astegotherium*, **sp. nov.**  
Figure 5E

Several isolated plates from Laguna Fría are assigned to this new taxon. This small dasypodid is of similar size to the living *Dasypus hybridus* or *D. septencinctus*, with very thin and smooth osteoderms, and a lageniform central figure in the movable scutes, as in *A. dichotomus*, from the Casamayoran (Vacan, Carlini et al. 2002c); very few (or no) foramina surrounding the central figure; poorly defined sulcus separating the central figure from the peripheral ones. The central keel of the exposed surface is even less elevated than in the Casamayoran species, and has one or rarely two large foramina on the posterior margin.

Genus *Stegosimpsonia* Vizcaíno, 1994  
*Stegosimpsonia*, **sp. nov.**  
Figure 5F

Also from La Barda and Laguna Fría are several isolated plates of the dorsal

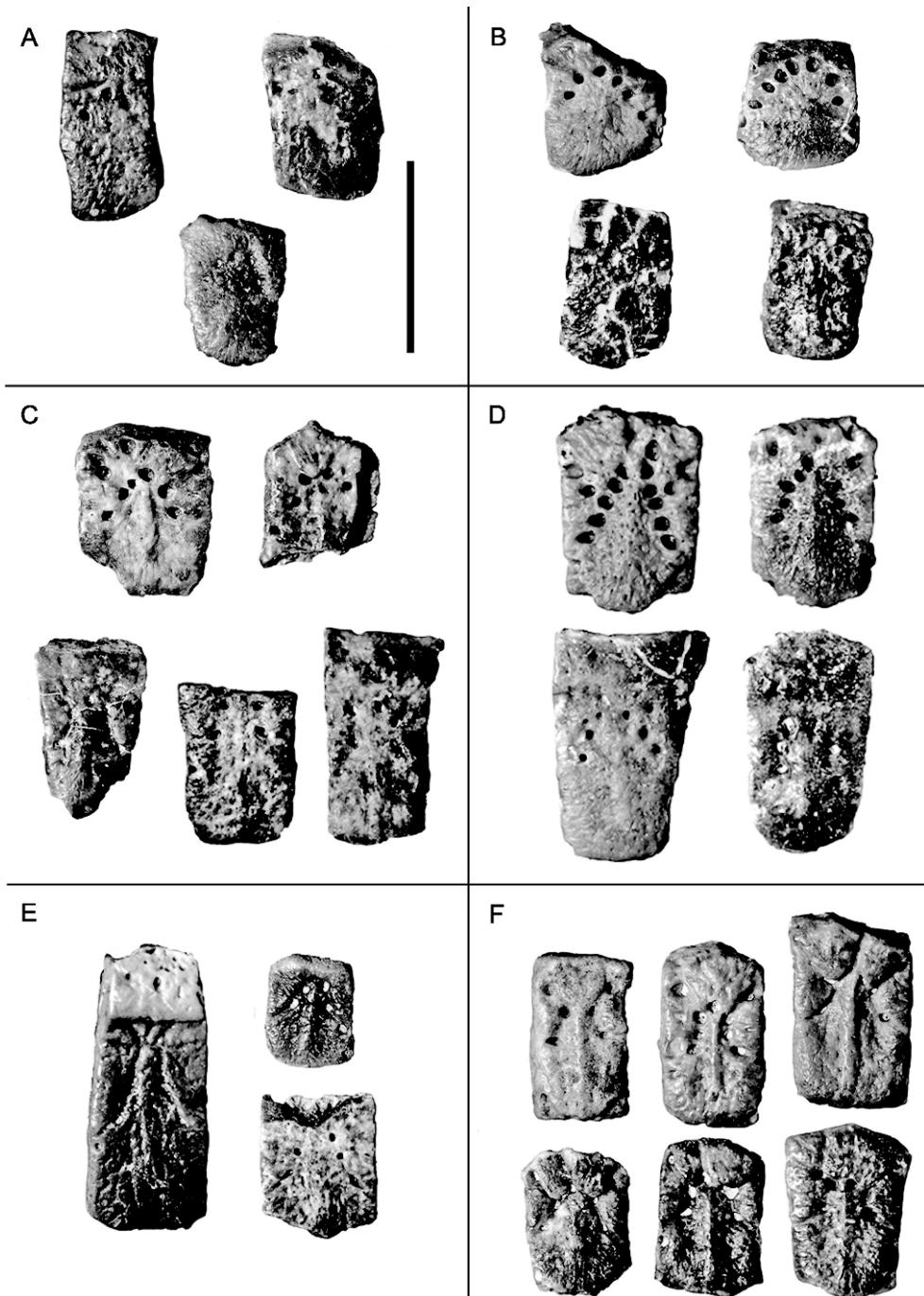


Fig. 5. Dasyopodidae from Laguna Fría (LF) and La Barda (LB) assemblages. A, scutes of *Riostegotherium* sp. nov. from LF; B, scutes of *Riostegotherium* sp. nov. from LB; C, scutes of *Prostegotherium* cf. *astrifer* from LF; D, scutes of *Prostegotherium* cf. *astrifer* from LB; E, scutes of *Astegotherium* sp. nov. from LF; F, scutes of *Stegosimpsonia* sp. nov. from LF (also in LB, but not shown). Scale bar = 10 mm.

carapace of this small dasypodid of similar size to the living *Dasyus hybridus* or *D. septencinctus*. The osteoderms are thicker than in other astegotheriins from the same locality, with a more wrinkled surface; lageniform central figure in the movable plates, as in *S. chubutana* from the Casamayoran (Barrancan subage, Carlini et al. 2002b), but differs from the latter by having fewer and more symmetrically placed foramina on their surface. The central keel of the exposed surface is better defined, with scarce but relatively large foramina on the posterior margin, having a relatively large one at the junction of a proximal sulcus with the external edge of the plate.

Order Chiroptera  
Family indet.  
**Gen. et sp. nov. 9**  
Figure 6

Remarkably, two lower bat molars were discovered in Laguna Fría, a well-preserved left m<sup>2</sup> (fig. 6) and a right talonid, both apparently of the same species (Tejedor et al., 2005). The first appearance of bats in the fossil record is in the early Eocene of North America (Jepsen, 1966; Novacek, 1985; 1987; Habersetzer and Storch, 1989), Europe (Russell et al., 1973), and Australia (Hand et al., 1994). Up to now, the oldest South American record was of middle or late Eocene age at Santa Rosa locality (Yahuarango Formation) in Perú (Czaplewski and Campbell, 2004; Czaplewski, 2005).

The Laguna Fría specimens are identified as bats because of their complete labial cingulum running continuously from the anterior base of the paraconid to the hypoconulid, a probable synapomorphy in the early stages of bat evolution (Hand et al., 1994). The molar cusps are strongly merged into the molar crests rather than being individualized. The trigonid is anteroposteriorly compressed. The paraconid is small and low, much smaller and slightly less lingually situated than the metaconid. The talonid is not strikingly lower than the trigonid. The entoconid is moderate in height; it bears a straight entocristid (in occlusal view). The cristid obliqua extends from the hypoconid to a point low on the

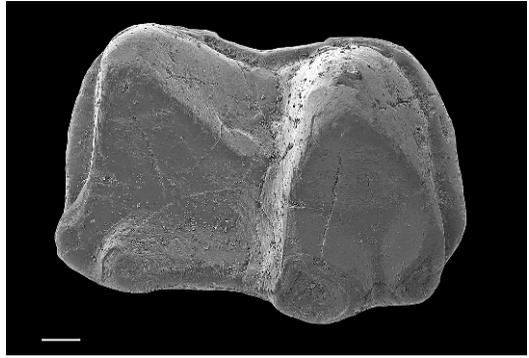


Fig. 6. Occlusal view of the Laguna Fría bat. Scale bar = 200  $\mu$ m.

posterior wall of the trigonid slightly labial to the midline of the tooth. The postcristid extends from the hypoconid to a small hypoconulid (the “nyctalodont” condition) and is separated from the entoconid by a small groove. The hypoconulid is fully merged into the postcristid and is not distinguishable as a separate cusp; it merely forms the posteriorly curving lingual terminus of the postcristid and is positioned directly posterior rather than posterolabial to the entoconid. This is a derived condition relative to the primitive tribosphenic arrangement involving distinct talonid cusps (entoconid, hypoconid, and medial or submedial hypoconulid). The primitive tribosphenic condition is present in the archaic bats *Ageina*, *Archaeonycteris*, *Eppsinycteris*, *Hassianycteris*, *Honrovits*, *Icaronycteris*, and *Necromantis* (Simmons and Geisler, 1998; Czaplewski, personal obs.). However, the same configuration of the postcristid-hypoconulid as in the Laguna Fría bats is found in other Eocene bats such as *Dizzya* (Phlisidae), *Lapichiropteryx*, and *Stehlinia* (Palaeochiropterygidae), and certain extinct or extant representatives of the Emballonuridae, Furipteridae, Minopteridae, Molossidae, Mormoopidae, Natalidae, Phyllostominae, some Rhinolophidae, Rhinopomatidae, and some Vespertilionidae. Although the Laguna Fría bats probably represent a new species, given the few specimens and characters available and their similarity to numerous extinct and extant bats from several lineages, we are unable to assign the Laguna Fría specimens to a taxon more circumscribed than Chiroptera.

South American Native Ungulates  
Order "Condylarthra"  
Family Didolodontidae (Scott, 1913)

The Family Didolodontidae (Scott, 1913) includes the most primitive South American ungulates, characterized by a low and bunodont dentition. They are recorded at several Patagonian localities in Argentina (Ameghino, 1906; Simpson, 1948, 1967a) from the Peligran through the Mustersan (Paleocene–?middle Eocene), and from the Itaboraian (late Paleocene) of Saõ José de Itaboraí (Río de Janeiro, Brazil) (Paula Couto, 1952).

**Gen. et. sp. nov. 7**

Represented by a left mandibular fragment with a well-preserved m3 (LIEB-PV 1611) collected in Laguna Fría. It is about the size of the Protolipternidae, especially *Protolipterna ellipsodontoides*, from the Itaboraian of Brazil (Paula Couto, 1952). The m3 shows a strongly arcuate paracristid, as in Didolodontidae and primitive Litopterna (Bonaparte et al., 1993), but its more medial and anterior point seems to descend to the trigonid basin. The paraconid is a conspicuous cusp, anterolabially placed with the base connate to the metaconid. Among the Didolodontidae, the paraconid is also a distinct cusp, as in the Peligran *Escribania chubutensis* (Gelfo, 1999, 2004) and the Itaboraian taxa *Paulacoutoia proto-cenica* and *Lamegoia conodonta*. In contrast, the paraconid of younger didolodontids shows a trend toward merging to the metaconid, as in the Barrancan subage (late Casamayoran) *Didolodus multicuspis* or *Ernestokenia*, where the paraconid is no longer distinct. The paraconid is variably present in Protolipternidae, but tends to be almost or completely merged to the metaconid. Other distinctive characters are the short mesiodistal extension of the talonid; a small cusp located at the base and anterior to the entoconid; a short, cusped cristid obliqua that connects the hypoconid with the labial side of the metaconid; and a transverse, sharp cristid running from the entoconid to the posterior side of the hypoconulid. This peculiar cristid divides the talonid basin into an anterior, larger portion that opens posterolingually to

the metaconid, and a posterior portion forming the basal contact between entoconid and hypoconulid.

**Gen. et. sp. nov. 8**

Figure 7A

This second taxon is represented by a right partial mandible with part of the talonid of m2 and complete m3 (LIEB-PV 1612; fig. 7A) also recovered in Laguna Fría. Even when heavily worn, the m2 hypoconulid seems central and distally placed. This condition is similar to that of Didolodontidae, where the entoconid and hypoconulid are separated, distinct, and never fused as in some Mioclaenidae Kollpaniinae, or close to each other as seen in some Protolipternidae, such as *Asmithwoodwardia*. This new taxon clearly differs in having the entoconid even larger than the hypoconid, closing the talonid basin. To a lesser degree, *Didolodus* and *Paulacoutoia* also show an increase of the entoconid size and reduction of the hypoconulid. The anterior cingulum is short without labial or lingual expansions. The trigonid basin of the m3 is shallow and the base of the protoconid contacts the base of the lingual cusps. The paraconid is very close and slightly labial to the metaconid, and connects the protoconid by a short paracristid more transversely oriented than in the Gen. et. sp. nov. 7. The metaconid is more distal than the protoconid. The talonid basin is almost completely filled by a huge entoconid, even larger than that of m2. There is no distal cingulum. The cristid obliqua is short, low, and rounded, and parallels the toothrow.

Order Litopterna (Ameghino, 1989)

Family Protolipternidae (Cifelli, 1983)

This family was recognized by Cifelli (1983a) to contain three small, dentally primitive ungulates, basically from the Itaboraian of Brazil. Two of them, *Asmithwoodwardia* and *Miguelsoria*, were previously considered didolodontids. However, based on reassessed postcranial elements (Cifelli, 1983b), *Miguelsoria* was reallocated in the Protolipternidae as a primitive member of the Litopterna, together with *Protolipterna*. *Asmithwoodwardia*

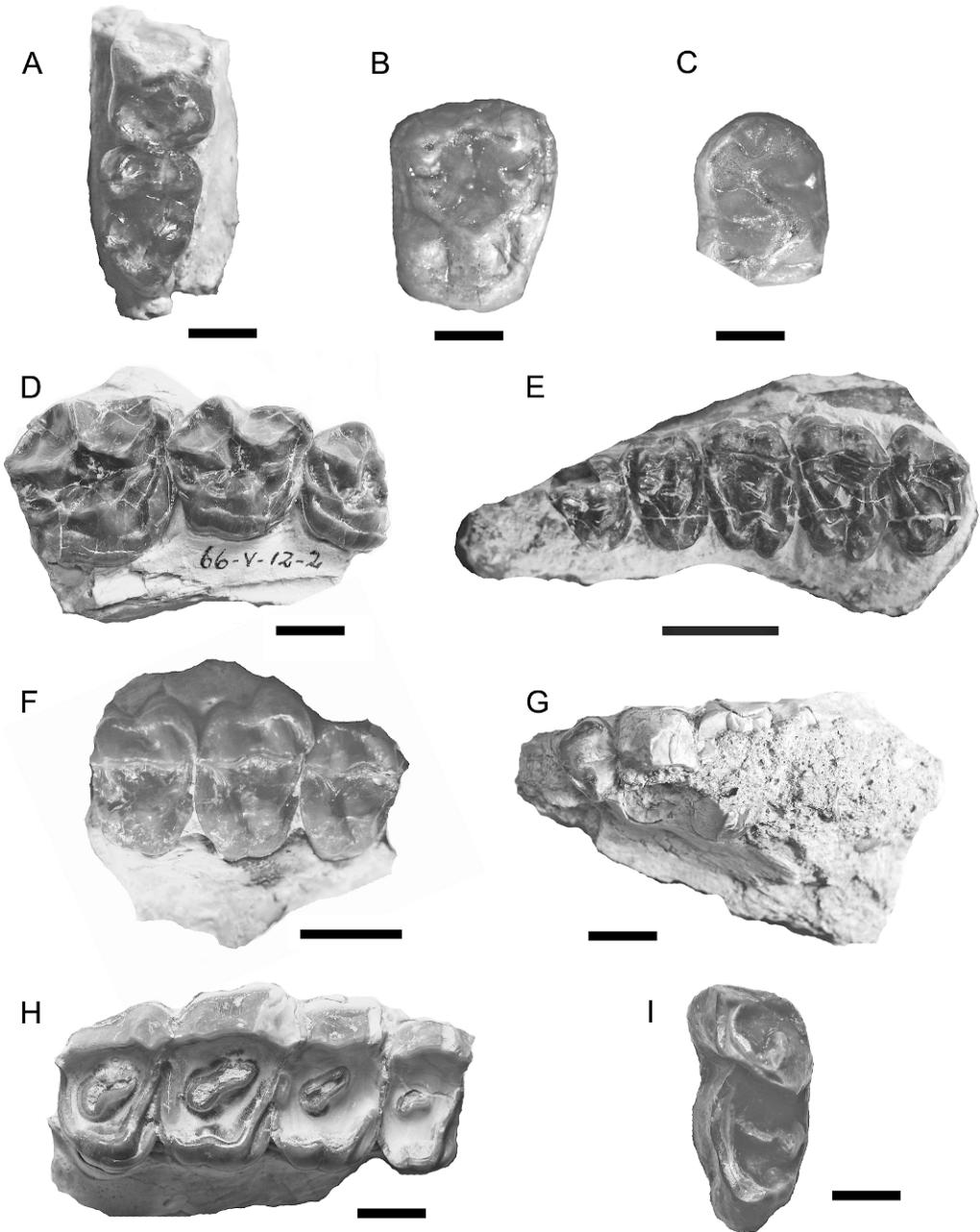


Fig. 7. South American native ungulates from Laguna Fría (LF) and La Barda (LB). **A**, LIEB-PV 1612, *Didolodontidae*, gen. et sp. nov., right m2-3; **B**, *Asmithwoodwardia subtrigona*, LIEB-PV 1636, left M2; **C**, *Asmithwoodwardia subtrigona*, LIEB-PV 1617, right m2; **D**, Spartootheriodontidae, Gen. et sp. indet. G, MLP-66-V-12-2, right maxillary fragment with three molariforms (P4-M2?) (LF); **E**, *Henricosbornia lophofonta*, LIEB-PV 1633, right maxilla with P4-M2 (LB); **F**, *Othnielmarshia lacunifera*, LIEB-PV 1618, right maxilla with M1-3 (LF); **G**, *Edvardotrouessartia sola*, LIEB-PV 1619; right maxilla with P2-4 (LF); **H**, *Isotemnus* sp., LIEB-PV 1646, right maxilla with P4-M3 (LF); **I**, *Isotemnus* sp., LIEB-PV 1659, left m2 (LF). Scale bar = 1 mm.

*dia* was also included in the Protolipternidae by Cifelli (1983a) without full explanations (Gelfo and Tejedor, 2004). For the present paper, we use Protolipternidae sensu McKenna and Bell (1997).

*Asmithwoodwardia*, **sp. nov.**

Figure 7B, C

This taxon is represented by an m1 or m2 (LIEB-PV 1613) from La Barda. It differs from *Asmithwoodwardia scotti* and *A. subtrigona* in labiolingual width and in the arrangement of the talonid cusps. The hypoconulid is central and posteriorly placed, while the hypoconulid of *A. scotti* and *A. subtrigona* are closer to the entoconid in m1–2. In the trigonid, a small paraconid is appressed against the mesiolabial side of the metaconid.

*Asmithwoodwardia subtrigona* Ameghino (1901) is represented by several isolated teeth from Laguna Fría and a larger sample from La Barda (fig. 7B, C). It is a small South American ungulate with a bunodont dentition and controversial systematic position. *Asmithwoodwardia* is represented by two species: *A. scotti*, from the Itaboraian of Brazil (Paula Couto, 1952), and *A. subtrigona*, from the Vacan subage (Lower Casamayoran SALMA, ?middle Eocene; Cifelli, 1983b) from Patagonia (Ameghino, 1901; Simpson, 1948). However, McKenna and Bell (1997) suggested that *Ernestokokenia*, a larger Patagonian ungulate, is a junior synonym of *Asmithwoodwardia* (contra Simpson, 1948; Muizon and Cifelli, 2000). *A. scotti* is well represented by isolated teeth and an almost complete skull associated with the lower jaw. Instead, the type of *A. subtrigona* (MACN 10723) consists of two isolated teeth, an upper and a lower molar. Simpson (1948) regarded the upper molar of *A. subtrigona* as an M2 or possibly M3, while Paula Couto (1952) suggested that it was an M1 or M2. The specimens from La Barda are comparable to *A. subtrigona* and lead us to confirm that the type specimen is an M3 (Gelfo and Tejedor, 2004). This taxon differs from *A. scotti* in its larger size, and in exhibiting conspicuous postparaconular and premetaconular cristae; the M3 is less transversally elongate, and it has a hypocone in

M3. Despite the mentioned differences, the development of the hypocone of M3s in primitive bunodont ungulates seems highly variable.

Family Sparnotheriodontidae (Soria, 1980b)

The Sparnotheriodontidae are considered basal forms of the Order Litopterna (Soria, 1980b, 1989, 2001; Hoffstetter and Soria 1986; López, 1999). However, the systematic position of this family is also controversial. It has been referred to the Order Notoungulata (Soria, 1980a; Marshall et al., 1983), Order Condylarthra (Cifelli, 1983b; Mones, 1986), or placed as a subfamily of the Macraucheniiidae (McKenna and Bell, 1997).

Gen. et sp. indet. G

Figure 7D

Several specimens clearly referable to the Sparnotheriodontidae were collected in Laguna Fría, including a right maxillary fragment (MLP 66-V-12-2; fig. 7D) with three molariforms (P4–M2?), right M3 (MLP 66-V-12-1), and a broken left M1 or M2 (LIEB-PV 1615). These remains are comparable in size to *Victorlemoinea labyrinthica* Ameghino (1901) with some morphological differences (e.g., more reduced hypocone in the first molars and shorter lingual crest of the metaconid) indicating a possible attribution to a different taxon, probably related to *Notolophus arquinoiensis* Bond et al. (2006).

?*Victorlemoinea longidens* Ameghino (1901)

An incomplete right lower molariform (p4 or m1 LIEB-PV 1614) was collected in Laguna Fría. This bicrescentic tooth is similar in size and morphology to *Victorlemoinea longidens*. *Victorlemoinea labyrinthica* and *V. longidens* were collected in Vacan levels of Patagonia (Simpson, 1967a). The oldest record of the Family Sparnotheriodontidae is *Victorlemoinea prototypica* Paula Couto (1952), from the Itaboraian of Brazil, and its youngest record is *Phoradiadius divortiensis* Simpson et al. (1962) from the Divisaderan of Mendoza, Argentina.

## Order Notopterna (Soria, 1984b)

## Family ?Amilnedwardsiidae (Soria, 1984a)

This family includes small bunodont ungulates with poorly developed ectoloph and paraloph, and a lophoid metaconule. The Casamayoran genera *Amilnedwardsia*, *Rutimeyeria*, and *Ernestohaekelia*, named by Ameghino (1901), were referred by the author to this family as taxa of generalized morphology. These genera are almost exclusively represented by upper molars, with the exception of a lower molariform from the Casamayoran of Cañadón Hondo (Chubut Province), mentioned by Soria (1984b) as referable to Amilnedwardsiidae.

## Gen. et sp. indet. H

There are two left mandibular fragments from Laguna Fría, one with p2 and p3 partially broken, and p4–m2 (LIEB-PV 1616), and a second specimen with p3–4 (LIEB-PV 1617). They are selenodont and bicrescentic with the entoconid contacting the hypoconulid. Comparison to other lower molariforms mentioned by Soria (1989) indicates that these specimens should be regarded as Gen. et sp. indet. members of the Family Amilnedwardsiidae. However, given their fragmentary nature and the similarities between the Amilnedwardsiidae and the Notopterna Indaleciidae, they could also be referred to the latter family.

## Order Notoungulata (Roth, 1903)

## Family Henricosborniidae (Ameghino, 1901)

This family has several generalized dental characters placing them in a basal position with respect to other notoungulates. As G.G. Simpson (1948: 147) said:

The henricosborniids are clearly the most primitive known notoungulates, and they nearly fulfill all the theoretical requirements for a generalized type ancestral to all others known.

Traditionally, species referred to this family characterize both the Riochican and Vacan faunal associations.

*Henricosbornia lophodonta* Ameghino (1901)

## Figure 7E

Maxillary and mandibular fragments referred to the Family Henricosborniidae are abundant in both localities of Paso del Sapo, with complete series of premolars and molars, as well as isolated teeth. The presence of a strong metacone, a convex mesostyle area in the upper molars, and a distinct hypoconulid in m1–2 relate these specimens to *Henricosbornia lophodonta*, a typical taxon in several Vacan levels, but also recorded in the upper levels of the Riochican of Bajo Palangana, Chubut Province. In Paso del Sapo, additional mandibular fragments are doubtfully assigned to the genus *Henricosbornia*, morphologically more related to *H. lophodonta* Ameghino (1901) but closer to the size of *H. waitehor* Simpson (1935a).

Other fragmentary materials with simpler ectolophs, a different configuration of the metaloph, and smaller size are here referred as cf. *Henricosbornia*.

*Othnielmarshia lacunifera* Ameghino (1901)

## Figure 7F

A right maxillary fragment with complete M1–3 (LIEB-PV 1618, fig. 7F) was collected in Laguna Fría. These molars have a strong labial cingulum and a shortened crochet in M1, vestigial in M2, and absent in M3. It is referred to *Othnielmarshia lacunifera*. On the other hand, there are several isolated lower molars with the entoconids clearly separated from the hypoconulids that may be also attributable to this species. The type of *O. lacunifera* comes from “west of Río Chico”, and thus is Vacan in age (Simpson, 1967a) and Simpson himself collected materials in Cañadón Vaca.

## Family Notostylopidae (Ameghino, 1897)

Notostylopids acquired a specialized, styli-form incisors and diastema during their early stages of their evolution, giving them a rodentlike appearance. In Patagonia, this family is known from the Riochican through the Mustersan, but the latest representatives were collected in the Tinguirirican of central

Chile (referred to the late Eocene–early Oligocene by Flynn et al., 2003). They were never diverse but were the most abundant ungulates during the Vacan and Barrancan subages. Three genera are described for the Paso del Sapo localities below.

*Edvardotrouessartia sola* Ameghino (1901)  
Figure 7G

Two maxillary fragments were collected at Laguna Fría, one with broken P2–4 (LIEB-PV 1619; fig. 7G), and the other with incomplete P4 (LIEB-PV 1620). The premolars show a flat paracone and, in labial view, the characteristic pyramidal shape of *Edvardotrouessartia sola*. Specimens of *E. sola* came from “west of Río Chico” (Simpson, 1967a, b), and there are excellent collections also from Cañadón Vaca in the Museo de La Plata and Museo de Mar del Plata. Thus until now, *E. sola* was exclusive to the Vacan.

*Homalostylops parvus* Ameghino (1897)

A mandibular fragment with m1–2 of a small notostylopid was collected in La Barda (LIEB-PV 1621). By its size and the presence of an accessory cusp in the middle of the metalophid, it is certainly referred to *Homalostylops parvus*, one of the few species recorded for both the Vacan and Barrancan subages. A left mandibular fragment with m2 (LIEB-PV 1622), also collected in La Barda, is referable to this species.

*Notostylops* sp.

Mandibular fragments and isolated upper teeth that can be referred to the genus *Notostylops* are abundant in both localities of Paso del Sapo. However, their specific attribution is difficult. *Notostylops* has been found in the upper levels of the Riochican (i.e., in the *Ernestokokenia chaishoer* faunal zone), and in the Casamayoran sensu lato (Vacan and Barrancan subages).

It is important to note that, although the lower molars of *Notostylops* and *Homalostylops* are very similar morphologically, there is a significant difference in size.

Family Oldfieldthomasiidae (Simpson, 1945)

This family includes small- to moderate-sized ungulates with a generalized crown morphology, thus being basal with respect to the Typotheria-Hegetotheria radicle. The oldest oldfieldthomasiids are from the Itaboraian of Brazil and Patagonia (Pascual and Ortiz Jaureguizar, 1992), and one of its taxa, *Kibenikhorina* Simpson (1935a), characterizes the middle levels of the Riochican (“*Kibenikhorina* faunal zone”; see Simpson, 1935b). The youngest record of this family is from the Fray Bentos Formation in Uruguay (Ubilla et al., 1999).

Gen. et. sp. indet. I

Some mandibular fragments collected in Laguna Fría show simple molars with open trigonids, transversely crestlike entoconid, not fully fused to the hypolophid and separated from the metaconid by a deep sulcus. This morphology is certainly related to the Oldfieldthomasiidae. The diagnostic characters for the oldfieldthomasiid species are generally for the upper molariforms; therefore, these lower materials are here described as Gen. et. sp. indet. However, the general morphology, crown height, and size closely approximate the genus *Kibenikhorina* (e.g., LIEB-PV 1658).

Family Archaeopithecidae (Ameghino, 1897)

This family includes small, generalized notoungulates with relatively high-crowned molars, recorded from the “*Ernestokokenia chaishoer* faunal zone”, (Upper Riochican; see Simpson, 1935b) and they were relatively abundant up to Mustersan levels (Cladera et al., 2004).

*Archaeopithecus* cf. *A. rogeri* Ameghino (1897)

Several maxillary and mandibular fragments (e.g., LIEB-PV 1625 to 1628), as well as isolated teeth (e.g., LIEB-PV 1629) referred to this family have been found in La Barda and Laguna Fría. The Archaeopithecidae is based on *Archaeopithecus rogeri* Ameghino (1897), of unclear stratigraphic provenance, probably Barrancan, and *Acropithecus rigidus* Ameghino (1901), from Cañadón Vaca (Vacan). Based on

the morphology of the ectoloph and for the presence of a strong anterolingual cingulum in the premolars, the materials collected at the Paso del Sapo localities are closely related to *Archaeopithecus rogeri*, but the species assignment is still uncertain.

Family Interatheridae (Ameghino, 1897)

Subfamily Notopithecinae (Simpson, 1945)

This subfamily includes the oldest and more generalized members of the Interatheriidae but since this grouping is mainly recognized on the basis of plesiomorphic characters, its taxonomic status is debated. The notopithecines are tyotheres of small size, probably browsers and, in part, ecologically equivalent to the members of the families Oldfieldthomasiidae and Archaeopithecidae. Some Notopithecinae (e.g., *Notopithecus*) show craniodental and postcranial characters convergent with those found in lemuriform primates from the early Tertiary of the Northern Hemisphere, thus explaining why Ameghino characterized this group as “southern monkeys”.

The Notopithecinae appeared in the fossil record in the uppermost levels of the Riochican from Bajo Palangana, eastern Chubut province (Simpson, 1967b), and its youngest record came from the Tinguirirican of central Chile (Flynn et al., 2003). Among the Eocene faunal associations of Patagonia, the notopithecines are abundant with five genera recognized: *Notopithecus* Ameghino (1897), for the Riochican and Casamayoran of Patagonia, and with some doubts for the Eocene of Bolivia; *Antepithecus* Ameghino (1901) and *Transpithecus* Ameghino (1901) from the Casamayoran (s.l.) of Patagonia; *Guilhermoscottia* Ameghino (1901) from the Mustersan of Patagonia; and *Punapithecus* López and Bond (1995) from levels referred to the Mustersan in Catamarca, northwestern Argentina.

Gen. et sp. indet. J

A few isolated teeth that may be attributable to the Notopithecinae were collected at Laguna Fría. Some of these are probably related to the genus *Notopithecus* (e.g., LIEB-PV 1655, an isolated lower p3) but a broader systematic revision is needed.

Family Isotemnidae (Ameghino, 1897)

The Isotemnidae are moderate to large ungulates characterized by having large canines and a generalized molar pattern for the Toxodontia. This family is represented by numerous maxillary and mandibular fragments and isolated teeth in both localities of Paso del Sapo.

*Isotemmus* sp. Ameghino (1897)

Figure 7H, I

There are two specimens, a left maxilla with P4–M3, slightly worn (LIEB-PV 1647) and a right maxilla also with P4–M3 (LIEB-PV 1646; fig. 7h, i), with transverse molars, well-developed, columnar metacone and lingual cingulum absent. These traits characterize *Isotemmus* and clearly differ from *Pleurostylodon* Ameghino (1897). Also, there are several mandibular fragments (LIEB-PV 1650 to 1653) referred to the genus *Isotemmus*, based on the structure of the metaconid, which is not oriented posteriorly and thus the talonid basin is open. The lower molars have better developed lophids than *Isotemmus ctalego* from Cañadon Hondo (Itaboraian) and *Isotemmus* sp. from the *Ernestokokenia chaishoer* zone of Bajo Palangana. This is indicative of a post-Riochican evolutionary stage. In Patagonia, the genus *Isotemmus* is also recorded in Riochican and Vacan levels.

Order Astrapotheria (Lydekker, 1894)

Family indet.

Gen. et sp. indet. K

A left m1 or m2 (LIEB-PV 1623) recovered at Laguna Fría is attributed to the Astrapotheria. However, the family attribution is difficult because the morphology resembles that in the genus *Trigonostylops* Ameghino (1901) (Astrapotheria, Trigonostylopidae) as well as that in *Tetragonostylops* Price and Paula Couto (1950) (Astrapotheria, Astrapotheriidae). Both genera can be recognized by their upper molariforms, but the lowers lack diagnostic characteristics. The species of *Trigonostylops* are known from the Riochican through the Mustersan of Patagonia, while

*Tetragonostylops* comes from the Itaboraian of Brazil and Vacan of Argentina.

Order ? Astrapotheria  
Gen. et sp. indet. L

Among the materials from Laguna Fría, there is a right maxillary fragment with part of the hypertrophied and compressed canine that may be attributable to the Astrapotheria (LIEB-PV 1624), but its more precise attribution is doubtful. We are unable to refer this specimen to any other South American order of ungulates.

## DISCUSSION

### MARSUPIALS

The mammalian fauna of Paso del Sapo includes nearly 30 species from several marsupial orders, of which about 19 species are new or probably new. These marsupials are closely related to those from older SALMAs, such as the Itaboraian and Riochican (12 species); none of these species are present in sediments younger than those from Paso del Sapo.

Marsupials are the most abundant mammals from Paso del Sapo, and are represented by almost all the South American marsupial orders. Among them, the diversity and richness of the Polydolopinae is remarkable, comprising not only the richest polydolopine fauna from Patagonia but the richest in South America to date. It is noteworthy that several marsupials had frugivorous adaptations (i.e., polydolopines and caroloameghiniids), and this may be related to the diversification of plants, as indicated for the record of 102 leaf species in the nearby early Eocene caldera lake deposits of Laguna del Hunco (Wilf et al., 2003, 2005), as well as the Eocene paleoflora from Río Pichileufú (Berry, 1938; Petersen, 1946; see also Wilf et al., 2003), located about 160 km NNW of Laguna del Hunco, that contains several of the same species as Laguna del Hunco.

### XENARTHANS

Due to the manner of collecting (mostly screening and washing), all specimens are

isolated, but it appears that a large number of specimens are represented. All of the osteoderms are from members of the Tribe Astegotheriini, the most primitive among dasypodids (Carlini et al., 2002a). Consequently, the absence of Euphractinae is remarkable by comparison with their abundance in the Barrancan subage (upper Casamayoran) from Gran Barranca, Chubut (*Meteutatus* and especially *Utaetus*). The faunal differences are also remarkable with respect to the Vacan subage, where the first Euphractinae are recorded, together with a lower diversity of Astegotheriini with more advanced taxa. These differences with respect to the Casamayoran faunas (Carlini et al., 2002b, 2002c), as well as the presence of a new species of *Riostegotherium* (a genus until now only present in the Itaboraian of Brazil) and, with the youngest record in Paso del Sapo, a new species of *Stegosimpsonia* and another new species of *Astegotherium*, all of which are more primitive than the Casamayoran species, certainly suggests an older age for the sediments of Laguna Fría and La Barda (Carlini et al., 2002a). In addition, the diversity of Astegotheriini indicates a warmer and more humid paleoenvironment than that inferred for the Casamayoran. At this time, the species from Laguna Fría and those from the Vacan (Carlini et al., 2002c) include the greatest diversity of Astegotheriini.

### BATS

As mentioned above, we are unable to assign the Laguna Fría bat specimens to any rank other than Chiroptera. However, judging from the observable morphology, its size and lower molar features indicate insectivorous feeding habits. In this respect, it is noteworthy that the Laguna Fría mammal assemblage is probably contemporary with the very rich early Eocene Laguna del Hunco flora (Wilf et al., 2003), which suggests the early radiation of modern angiosperm lineages in Patagonia as well as their insect pollinators, which could have served as food for the bats.

### UNGULATES

There are no significant differences in taxonomic composition and ecological roles

among the ungulates from Laguna Fría and La Barda. In general, they are characterized by the dominance of small to moderate size animals, with brachydont, bunodont to lophodont dentitions. Despite the above-mentioned differences regarding minor morphological details, the Didolodontidae and Protolipternidae include the smallest ungulates from Paso del Sapo. The most conspicuous taxon is *Asmithwoodwardia subtrigona*, recovered in both localities but more abundant at La Barda. The latter locality has a low taxon diversity of Didolodontidae and Protolipternidae but a high minimum number of individuals.

Along with *Asmithwoodwardia*, the Didolodontidae from Laguna Fría are represented by larger taxa, probably two new genera and species (here named Gen. et sp. nov. 1 and Gen. et sp. nov. 2). These are larger when compared particularly with *Asmithwoodwardia*; in contrast, they are smaller than any other known Didolodontidae (e.g., *Escribania chubutensis*, from the Peligran, or *Didolodus multicuspis*, from the Barrancan subage). This increase in size, along with particular characters, such as the transverse and sharp cristid running from the entoconid to the posterior side of the hypoconulid in Gen. et sp. nov. 7 or the larger entoconid closing the talonid basin in Gen. et sp. nov. 8, could be related to a wide spectrum of adaptive strategies. However, it is necessary to test the possible intra- or interspecific variability within these samples.

Small bunodont ungulates are well represented in both faunas from Paso del Sapo. In contrast, the absence of some taxa common in the South American Paleogene is remarkable, such as the larger Didolodontidae and Protolipternidae. One is the poorly known *Ernestokokenia*, morphologically similar to *Asmithwoodwardia* but larger in size, found in different Patagonian localities from the Riochican through the Casamayoran. Simpson (1935b) divided the Río Chico Formation into three faunal zones, from older to younger: *Carodnia*, *Kibenikhorja*, and *Ernestokokenia chaishoer*, the latter characterized by *E. chaishoer* but also *E. yirunhor*, recovered in the *Kibenikhorja* zone as well. The absence of *Ernestokokenia* in the Paso del Sapo assemblage deserves more attention. There is no record of either

*Escribania chubutensis*, from the Peligran SALMA, or any species of *Didolodus*, well represented in the Casamayoran. This is interesting because the presence of primitive bunodont ungulates is usually characterized by a broad size range, as for example in the Itaboraian. To summarize, the size range in the Riochican and Casamayoran Didolodontidae, not seen in Paso del Sapo, may be due to local taphonomic and/or paleoecological conditions instead of temporal differences.

The most significant and best represented bunodont ungulate from Paso del Sapo is *Asmithwoodwardia subtrigona*, also recorded in the Vacan subage. As mentioned above, the more primitive *Asmithwoodwardia scotti* is known from the Itaboraian of Brazil. Therefore, judging from the Didolodontidae and Protolipternidae, an age ranging from the post-Itaborian through Vacan can be inferred for the Paso del Sapo fauna.

The two members of the Sparnotheriodontidae reported herein were recovered only from Laguna Fría and are comparable to *Victorlemoinea labyrinthica* and *?Victorlemoinea longidens*. Both species came from “west of Río Chico”, which most probably belongs to a Cañadón Vaca locality (Vacan). *Victorlemoinea* is also represented in the Itaboraian by *V. prototypica*, and in the *Ernestokokenia* faunal zone of the Riochican by an m3 from the Feruglio collection (n° 13) (Simpson, 1935a, 1948). The sparnotheriodontids here considered Gen. et sp. indet. appear more advanced than the primitive *Victorlemoinea prototypica*, and more similar in size to *V. labyrinthica*. In contrast, the new specimens show intermediate character states compared with *Notolophus arquinotiensis* from the Antarctic Peninsula (Bond et al., 2006). For example, *Victorlemoinea labyrinthica* has a strong crest between the metaconule and the protocone, shorter in MLP 66-v-12-2 from Paso del Sapo, and absent in the Antarctic form. Even though sparnotheriodontids show a broad temporal and latitudinal range (from the Itaboraian of Brazil through the Divisaderan of Mendoza, Argentina), the similarities to the *Victorlemoinea* species from Patagonia relate the Paso del Sapo taxa to the Vacan forms.

Among the Notoungulata, the Henri-cosborniidae and Notostylopidae are common

in both localities described in this paper. The first family includes two genera, *Henricosbornia* and *Othnielmarshia*, that are probably present in the “*Ernestokokenia chaishoer* faunal zone”, the youngest levels of the Riochican SALMA (Simpson, 1935a, 1935b; Bond et al., 1995), and certainly in the Vacan (Simpson, 1948). The Scarritt Collection (Simpson, 1948, 1967a, b) includes several specimens of *Othnielmarshia lacunifera*, from Cañadón Vaca. However, the precise stratigraphic provenance for the type is unknown. It came from “west of Río Chico” (Ameghino, 1901), probably from the Upper Río Chico or from the coarser tuffs of the Vacan (Simpson, 1948). *Henricosbornia waitehor*, similar to *H. lophodonta* based on the lower dentition, with narrower molars, was described for the *Kibenikhor* zone (middle Riochican) (Simpson, 1935a, 1935b).

One of the most conspicuous members of the mammalian fauna from the late Riochican (*Ernestokokenia chaishoer* faunal zone) to the late Casamayoran (Barrancan) was the notostylopid *Notostylops* sp. Both localities of Paso del Sapo have produced several specimens of *Notostylops* with no specific attribution for the reasons mentioned above. Besides the common *Notostylops* sp., the presence of *Homalostylops parvus* in La Barda, and *Edvardotrouessartia sola* in Laguna Fría, previously known for all of the Casamayoran and from the Vacan, respectively (Simpson, 1948), are most important in estimating the age of this fauna. *Edvardotrouessartia* seems to be even more valuable, not only for its restricted Vacan distribution, but also because the characters that distinguish *Homalostylops* from *Notostylops* seem to be ambiguous. Following Simpson (1948), almost all characters shown by *Homalostylops parvus* closely resemble those of *Notostylops*, except for its smaller size; thus, Simpson retained the genera with doubts based on the holotype differences.

The isotemnids recorded in Paso del Sapo exhibit a high degree of lophodonty, reminiscent of species such as *Isotemnus primitivus* or *Anisotemnus distentus*, both from the Vacan subage (Simpson, 1967b).

The Archaeopithecidae, also well represented in both localities of Paso del Sapo, are here referred as *Archaeopithecus* cf. *rogeri*. This

taxon does not provide much information and the taxonomy of the whole family needs a thorough revision. Moreover, the type of *A. rogeri* (MACN 10816) has no precise locality information although it probably came from the south of Colhue-Huapi, as well as other synonymous species, thus being of Casamayoran age (Simpson, 1967b).

#### NEW SALMA FOR THE PALEOGENE OF SOUTH AMERICA?

Based on both the Laguna Fría Local Fauna and the La Barda Local Fauna, composed of a remarkable diversity and abundance of mammals, many of them previously unknown or with morphological novelties, we suggest that these assemblages may represent a new Paleogene SALMA. Also, the apparent correlation with the La Meseta Fauna of the Antarctic Peninsula is discussed. We estimate the age of the Paso del Sapo units as between 49.5 Ma and 45 Ma. They therefore fill a faunal gap between the Casamayoran and Riochican SALMAS.

A data matrix of 118 genera and eight faunas/SALMAS, was built for a quantitative analyses (table 1, fig. 8). Data were obtained from the literature (Bond et al., 1995; Pascual et al., 1996) and personal observations. Mammal assemblages include the Paso del Sapo fauna, the *Carodnia* zone, and the Tiupampan, Peligran, Itaboraian, Riochican, and Casamayoran SALMAS. As mentioned above, the Casamayoran SALMA was divided into Vacan and Barrancan subages. The temporal distribution of taxa in each fauna/SALMA was scored as presence (1) or absence (0) in the data matrix. Pseudo-extinctions were not coded in the matrix. The cluster analysis was performed with NTSYS 2.0 software (Rohlf, 1997) using the Jaccard coefficient, and the unweighted pair-group method using arithmetic averages (UPGM). Because of that, only the presence of taxa between faunas was considered to establish similarity between them, avoiding the shared absences, as a similarity criterion (Cheetman and Hazel, 1969). The Cophenetic Correlation Coefficient (CCC, Sneath and Sokal, 1973) was computed for the resulting phenogram.

The results of the cluster analysis (CCC: 0.93638) shows a principal group formed by

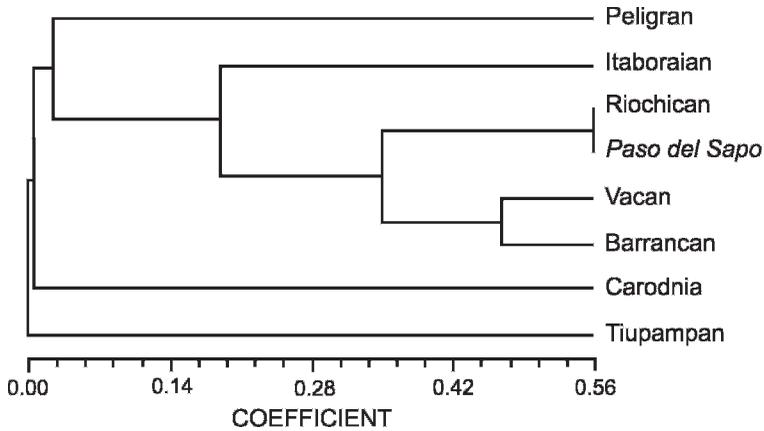


Fig. 8. Results of the cluster analysis using data matrix of 118 genera and eight faunas/SALMAs described in table 1.

the (Peligran (Itaborian (Riochican – Paso del Sapo) (Vacan – Barrancan) )), leaving the *Carodnia* Zone with a low similarity value to this group, external to it, and the Tiupampan with no relation with the rest of the cluster (coefficient 0.00) (fig. 8). The *Carodnia* zone value could be biased due to the low diversity of taxa found in this association, and the common presence of the genus *Carodnia* (but different species) with the Itaboraian. The lack of similarity of the Tiupampan with respect to other SALMAs reflects the immigrant nature of the taxa therein, which are more related to those of the North American Puercan Land Mammal Age, than to those of the Paleogene of South America. The Casamayoran subages—Vacan and Barrancan—show the highest similarity in the analysis. The Paso del Sapo fauna is more closely related to the Riochican than to any other SALMA.

The Paso del Sapo mammalian fauna will be defined by the first occurrence of *Polydolops unicus*, sp. nov. This species is extremely abundant both at Laguna Fría and La Barda, showing an unusual, very distinct dental morphology.

Also, this fauna is characterized (table 1) by the presence of *Astegotherium*, *Riostegotherium*, *Stegosimpsonia*, *Eomicrobiotherium*, *Pauladelphys*, *Edvardtrouessartia*, *Homalostylops*, *Othnielmarshia*, Peradectidae new genus 1, *Caroloameghiniidae* new genus 2, Peradectoidea new genus 3, *Paucituberculata* new genus 4,

Hathliacynidae new genus 5, Didolodontidae new genus 7, Didolodontidae new genus 8, Chiroptera new genus 9.

Taxa that last occur in Paso del Sapo are all marsupials and include: *Gashternia*, *Itaboraidelphys*, *Marmosopsis*, *Nemolestes*, *Palangania*, *Protodidelphis*. Taxa that also occur in earlier and later SALMAs are *Amphidolops*, *Derorhynchus*, *Polydolops*, *Archaeopithecus*, *Asmithwoodwardia*, *Henricosbornia*, *Isotemus*, *Notostylops*. Additionally, taxa unknown in Paso del Sapo but that occur in earlier and later SALMAs are *Eohyrax*, *Ernestokokenia*, *Maxschlosseria*, *Notopithecus*, *Oldfieldthomasia*, *Tetragonstylops*, *Trigonostylops*, *Victorlemoinea*.

#### MEASURED SECTION

The outcrops of the Laguna Fría Local Fauna are located in the Estancia San Ramón farm, property of Mr. Rafael Nicoletti, about 170 km northeast of the city of Esquel, and 28 km west of Paso del Sapo (figs. 1, 9, 10). Figure 9 presents a measured section of Laguna Fría. The fossiliferous interval of the Laguna Fría tuffaceous sediments (likely correlative of the Tufolitas Laguna del Hunc Formation exposed within the Sierra Huncache Caldera) is about 60 meters thick. The top of the stratigraphic unit is obscured by alluvium. The Laguna Fría sediments rest unconformably on a ?rhyolitic tuff, about 2 m

TABLE 1  
 Data matrix of 118 taxa included in 8 faunas/SALMAs represented in the Paleogene of South America that allowed the quantitative analysis shown in Figure 7

	PELIGRAN	TIUPAMPIAN	"CARODNIA"	ITABORAIA	RIOCHICAN	PASO DEL SAPO	VACAN	BARRANCAN
<i>Monotrematum</i>	1	0	0	0	0	0	0	0
<i>Peligrotherium</i>	1	0	0	0	0	0	0	0
<i>Sudamerica</i>	1	0	0	0	0	0	0	0
<i>Astegotherium</i>	0	0	0	0	0	1	1	0
<i>Machlydotherium</i>	0	0	0	0	0	0	1	1
<i>Meteutatus</i>	0	0	0	0	0	0	1	1
<i>Prostegotherium</i>	0	0	0	0	1	1	1	1
<i>Riostegotherium</i>	0	0	0	1	0	1	0	0
<i>Stegosimpsonia</i>	0	0	0	0	0	1	1	1
<i>Utaetus</i>	0	0	0	0	0	0	0	1
<i>Allqokirus</i>	0	1	0	0	0	0	0	0
<i>Amphidolops</i>	0	0	0	0	0	1	0	1
<i>Andinodelphys</i>	0	1	0	0	0	0	0	0
<i>Arminiheringia</i>	0	0	0	0	0	0	0	1
<i>Bobbschaefferia</i>	0	0	0	1	0	0	0	0
<i>Caroloameghinia</i>	0	0	0	0	0	0	0	1
<i>Coona</i>	0	0	0	0	0	0	1	1
<i>Derorhynchus</i>	1	0	0	1	0	1	1	0
<i>Didelphopsis</i>	1	0	0	1	0	0	0	0
<i>Eomicrobiotherium</i>	0	0	0	0	0	1	0	1
<i>Epidolops</i>	0	0	0	1	0	0	0	0
<i>Eudolops</i>	0	0	0	0	0	0	0	1
<i>Gashternia</i>	0	0	0	1	0	1	0	0
<i>Guggenheimia</i>	0	0	0	1	0	0	0	0
<i>Incadelphis</i>	0	1	0	0	0	0	0	0
<i>Itaboraidelphys</i>	0	0	0	1	0	1	0	0
<i>Jaskhadelphys</i>	0	1	0	0	0	0	0	0
<i>Khasia</i>	0	1	0	0	0	0	0	0
<i>Marmosopsis</i>	0	0	0	1	0	1	0	0
<i>Mayulestes</i>	0	1	0	0	0	0	0	0
<i>Minusculodelphis</i>	0	0	0	1	0	0	0	0
<i>Mirandatherium</i>	0	0	0	1	0	0	0	0
<i>Mizquedelphys</i>	0	1	0	0	0	0	0	0
<i>Monodelphopsis</i>	0	0	0	1	0	0	0	0

TABLE 1  
(Continued)

	PELIGRAN	TIUPAMPIAN	"CARODNIA"	ITABORAIAN	RIOCHICAN	PASO DEL SAPO	VACAN	BARRANCAN
<i>Nemolestes</i>	0	0	0	1	1	1	0	0
<i>Palangania</i>	0	0	0	0	1	1	0	0
<i>Patene</i>	0	0	0	1	0	0	0	1
<i>Pauladelphys</i>	0	0	0	0	0	1	1	0
<i>Peradectes</i>	0	1	0	0	0	0	0	0
<i>Polydolops</i>	0	0	0	1	1	1	1	1
<i>Procaroloameghinia</i>	0	0	0	1	0	0	0	0
<i>Protodidelphis</i>	0	0	0	1	1	1	0	0
<i>Pucadelphys</i>	0	1	0	0	0	0	0	0
<i>Roberthoffstetteria</i>	0	1	0	0	0	0	0	0
<i>Szalimia</i>	0	1	0	0	0	0	0	0
<i>Tiulordia</i>	0	1	0	0	0	0	0	0
<i>Acolodus</i>	0	0	0	0	0	0	0	1
<i>Acoelohyrax</i>	0	0	0	0	0	0	0	1
<i>Adiantoides</i>	0	0	0	0	0	0	1	0
<i>Albertogaudrya</i>	0	0	0	0	0	0	0	1
<i>Alcidedorbignya</i>	0	1	0	0	0	0	0	0
<i>Anadinodus</i>	0	1	0	0	0	0	0	0
<i>Anisolambda</i>	0	0	0	1	1	0	1	1
<i>Anisotemnus</i>	0	0	0	0	0	0	1	1
<i>Antepithecus</i>	0	0	0	0	0	0	0	1
<i>Archeopithecus</i>	0	0	0	0	1	1	1	1
<i>Asmithwoodwardia</i>	0	0	0	1	0	1	1	0
<i>Bramaniya</i>	0	0	0	0	1	0	0	0
<i>Camargomendesia</i>	0	0	0	1	0	0	0	0
<i>Carodnia</i>	0	0	1	1	0	0	0	0
<i>Carolozittelia</i>	0	0	0	0	0	0	1	1
<i>Cimolestes</i>	0	1	0	0	0	0	0	0
<i>Colbertia</i>	0	0	0	1	0	0	0	0
<i>Didolodus</i>	0	0	0	0	0	0	0	1
<i>Edvardotrouessartia</i>	0	0	0	0	0	1	1	0
<i>Enneocoelus</i>	0	0	0	0	0	0	1	0
<i>Eohyrax</i>	0	0	0	0	1	0	1	1
<i>Ernestohaekelia</i>	0	0	0	0	0	0	1	0
<i>Ernestokokemia</i>	0	0	0	1	1	0	1	1

TABLE 1  
(Continued)

	PELIGRAN	TIUPAMPIAN	"CARODNIA"	ITABORAIAN	RIOCHICAN	PASO DEL SAPO	VACAN	BARRANCAN
<i>Escribania</i>	1	0	0	0	0	0	0	0
<i>Florentinoaneghinia</i>	0	0	0	0	0	0	1	0
<i>Guiljelmosfloweria</i>	0	0	0	0	0	0	0	1
<i>Guiljelmoscottia</i>	0	0	0	0	0	1	0	0
<i>Henricosbornia</i>	0	0	0	1	1	1	1	1
<i>Homalostylops</i>	0	0	0	0	0	1	1	1
<i>Isotemnus</i>	0	0	0	1	1	1	1	1
<i>Itaboratherium</i>	0	0	0	1	0	0	0	0
<i>Kibenikhorja</i>	0	0	0	1	0	0	0	0
<i>Lamagoia</i>	0	0	0	1	0	0	0	0
<i>Maxschlosseria</i>	0	0	0	0	1	0	1	0
<i>Miguelsoria</i>	0	0	0	1	0	0	0	0
<i>Molmodus</i>	0	1	0	0	0	0	0	0
<i>Notophitecus</i>	0	0	0	0	1	0	1	1
<i>Notostylops</i>	0	0	0	0	1	1	1	1
<i>Oldfieldthomasia</i>	0	0	0	0	1	0	1	1
<i>Othnielmarshia</i>	0	0	0	0	0	1	1	0
<i>Pagimula</i>	0	0	0	0	0	0	0	1
<i>Paulocoutoia</i>	0	0	0	1	0	0	0	0
<i>Paulogervasia</i>	0	0	0	0	0	0	0	1
<i>Peripantostylops</i>	0	0	0	0	0	0	1	0
<i>Pleurostylodon</i>	0	0	0	0	0	0	1	1
<i>Proectocion</i>	0	0	0	0	0	0	0	1
<i>Protolipterna</i>	0	0	0	1	0	0	0	0
<i>Pucanodus</i>	0	1	0	0	0	0	0	0
<i>Raulvaccia</i>	1	0	0	0	0	0	0	0
<i>Ricardohydekkeria</i>	0	0	0	0	1	0	0	0
<i>Riostegotherium</i>	0	0	0	1	0	0	0	0
<i>Scaglia</i>	0	0	0	0	0	0	1	0
<i>Sheccenia</i>	0	0	0	1	0	0	0	0
<i>Silmoclaenus</i>	0	1	0	0	0	0	0	0
<i>Sparnotheriodon</i>	0	0	0	0	0	0	1	0
<i>Tetragonsotylops</i>	0	0	0	1	0	0	1	0
<i>Thomashuxleya</i>	0	0	0	0	0	0	1	1
<i>Tuclaenus</i>	0	1	0	0	0	0	0	0

TABLE 1  
(Continued)

	PELIGRAN	TIUPAMPIAN	"CARODNIA"	ITABORAIAN	RIOCHICAN	PASO DEL SAPO	VACAN	BARRANCAN
<i>Transpithectus</i>	0	0	0	0	0	0	0	1
<i>Trigonostylops</i>	0	0	0	0	1	0	1	1
<i>Ultrapithectus</i>	0	0	0	0	0	0	0	1
<i>Victor-lemoinea</i>	0	0	0	1	1	0	1	0
<i>Wainka</i>	0	0	1	0	0	0	0	0
Gen. nov. 1 (Peradectidae)	0	0	0	0	0	1	0	0
Gen. nov. 2 (Caroloameghiniidae)	0	0	0	0	0	1	0	0
Gen. nov. 3 (Peradectoidea)	0	0	0	0	0	1	0	0
Gen. nov. 4 (Paucituberculata)	0	0	0	0	0	1	0	0
Gen. nov. 5 (Hathiacynidae)	0	0	0	0	0	1	0	0
Gen. nov. 7 (Didolodontidae)	0	0	0	0	0	1	0	0
Gen. nov. 8 (Didolodontidae)	0	0	0	0	0	1	0	0
Gen. nov. 9 (Chiroptera)	0	0	0	0	0	1	0	0
<b>Total coincident with Paso del Sapo</b>	<b>7</b>	<b>19</b>	<b>2</b>	<b>10</b>	<b>10</b>	<b>32</b>	<b>14</b>	<b>10</b>
<b>Total of taxa</b>				<b>34</b>	<b>20</b>	<b>38</b>	<b>38</b>	<b>39</b>

thick, that in turn lies conformably on an ignimbrite dated at  $49.51 \pm 0.32$  Ma as described above. Regional correlation indicates that the Laguna Fría Tuffs are unconformably overlain by the upper member of the Andesitas Huancache (fig. 2). The unconformity shown at the base of the Laguna Fría Tuffs is likely of only short duration in that the tuffaceous basal sediments there likely represent a continuation of the volcanic event from which the ignimbrite was erupted.

#### ESTIMATED AGE

As indicated above a  $49.51 \pm 0.32$  Ma ignimbrite immediately underlies the mammal-bearing tuffs of the Laguna Fría locality (figs. 2, 9). This gives a maximum age for the base of the Paso del Sapo fauna. Overlying the mammal-bearing levels at Laguna Fría is a basalt dated at  $47.89 \text{ Ma} \pm 1.21 \text{ Ma}$  (Gosses et al., 2006, samples 2 and 3). In turn, the mammal-bearing tuffs at La Barda are deposited above the  $47.89 \pm 1.21$  Ma basalt, and are interbedded with the Andesitas Huancache lava flows. To the west, the Andesitas Huancache deposits have yielded three K/Ar dates near 43 Ma (Mazzoni et al., 1991). The La Barda Tuffs underlie the 43 Ma lava flows of the AH (fig. 2). This gives a maximum time span for the Paso del Sapo fauna of 49.5–43 Ma. Several lines of reasonings suggest that the actual range is even narrower time: (1) As mentioned below, the Paso del Sapo mammals suggest an older age than those of the Vacan subage; the Vacan was tentatively considered (Carlini et al., 2005: fig. 1) as representing a time interval of ca. 44–45 Ma. (2) The faunal similarities between the Laguna Fría and La Barda assemblages suggest that deposition of the mammal-bearing tuffs at both localities represented a relatively short time span. (3) As discussed below, the Laguna Fría and the La Barda mammals share several significant taxa with the mammalian association collected at TELM 5 (or *Cucullaea* 1 Allomember) of the La Meseta Formation in the Antarctic Peninsula. Numerical ages for TELM 5 levels based on Strontium isotopic determinations are between 49 and 51 Ma (Ivany, 2007). Summarizing, we preliminarily conclude that the best estimate for the time span of the Paso

del Sapo fauna as a possible new biochronological unit including the La Meseta fauna is between 49.5 Ma and 45 Ma.

**RELATION TO OTHER SALMAS:** Kay et al. (1999) recently revised the age of the Barrancan subage (late Casamayoran SALMA) to about 39 Ma (Carlini et al., 2005; Madden et al., 2005). This also resulted in an upward revision of the correlation of the Mustersan SALMA to latest Eocene (ca. 36 Ma). Prior to the work of Kay et al. (1999), the Casamayoran SALMA had been conventionally considered as early Eocene, and the Mustersan as late Eocene. Considering the revisions stemming from Kay et al. (1999) and those presented by Carlini et al. (2005) that give an estimation of 44–45 Ma for the Vacan, mainly based on the faunas, and the preceding Riochican SALMA with an estimated age of no younger than 55 Ma (Pascual and Ortíz Jaureguizar, 1991) thus left a gap in the early to medial Eocene record in the South American mammal age sequence. Recognition of the Paso del Sapo mammalian fauna now fills part of that gap.

#### RELATIONS WITHIN THE PASO DEL SAPO MAMMALIAN FAUNA

The La Barda Local Fauna contains taxa that pertain to the same genera as found in the Laguna Fría Local Fauna, but are represented by different species, compatible with the above-discussed differences in radioisotopic age of the two local faunas. The only recognized correlative of these two Paso del Sapo assemblages is the fauna from the La Meseta Formation of the Antarctic Peninsula (Vizcaíno et al., 1998). This correlation is based on the La Meseta Fauna sharing taxa exclusively with the Laguna Fría, including the didelphimorphian *Pauladelphys* and a litoptern related to *Notolophus*, among other taxa such as *Polydolops* and *Derorhynchus*, the latter also found elsewhere in Patagonia. Taxa present in La Meseta but not in Laguna Fría include the gondwanathere *Sudamerica* sp. At the moment this is considered a likely paleogeographic restriction of a possible gondwanan inhabitant from more western localities in Argentina, or a currently unfilled sampling bias in the Argentine Paso del Sapo sites. The



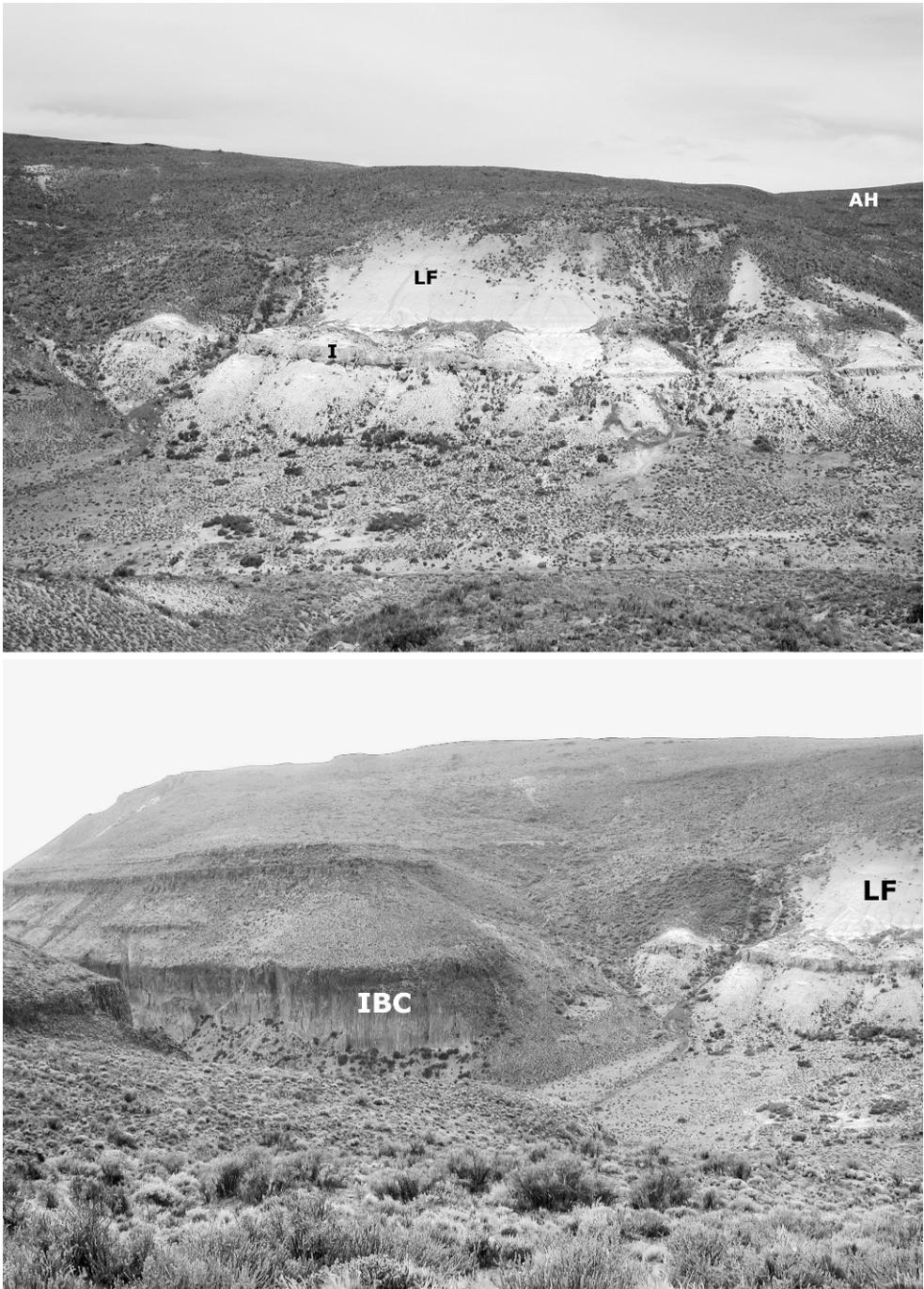


Fig. 10. **Top:** General view of the measured area shown in figure 9. LF: fossiliferous levels; I: underlying ignimbrite dated in  $49.51 \pm 6.032$  Ma; AH: Andesitas Huancache, overlying basalts dated in  $47.89 \pm 6.121$  Ma. **Bottom:** Partial exposures of the Laguna Fría (LF) section and the Barda Colorada ignimbrite (IBC); between both levels is the ignimbrite mentioned above (I), underlying Laguna Fría.

A third possible area where the Paso del Sapo levels may be represented is the Gaiman region (fig. 1, #10), where Simpson (1935a) described a pink sandstone level at the base of the Cerro Pan de Azúcar profile, which has yielded so far only three mammalian taxa: *Polydolops rothi*, *Protodidelphis* sp., and *Isotemnus ctalego*. (1) It is noteworthy that *P. rothi* occurs only at this locality and at Paso del Sapo local faunas. (2) Though represented by very scarce remains, both the La Barda larger specimen of *Protodidelphis* and that from Gaiman are very similar, probably conspecific (they are the largest known species of *Protodidelphis*); (3) *Isotemnus ctalego* comes from Cerro Pan de Azúcar and also the Itaboraian of Cañadón Hondo (i.e., *Kibenikhoria* faunal zone), Chubut.

#### CLIMATIC SETTING

Wilf et al. (2003, 2005) indicate that Laguna del Hunco flora, recovered from the Sierra Huancache Caldera located 20 km northwest of Laguna Fría, lived in a subtropical climate with moderate seasonality. The Laguna del Hunco flora was recovered from the Tufolitas Laguna Hunco Formation, dated at 52–54 Ma. The Pichileufú Flora, from the vicinity of Bariloche, Patagonia, is of about 47 Ma in age and reflects a similar climatic setting, even though located about 300 km northwest of Laguna Fría. On this basis it appears that the Paso del Sapo mammals lived under the conditions indicated by these floras.

We also note that the radioisotopic age of the Laguna del Hunco flora is close to that estimated for the faunas from Laguna Fría and La Barda (Wilf et al., 2003), at the time of the early Eocene climatic optimum. As a response to this short period of warm and equable climate in middle latitudes on both hemispheres, the diversification of plants and animals in central-western Patagonia, is reflected in the rich fauna and flora from Paso del Sapo. Thus, the Laguna del Hunco flora is an outstanding complement to the data provided by the abundant and diverse mammals from Laguna Fría and La Barda.

This paleoflora includes taxa that are extinct today in South America, but some relatives are still present in Australasia, thus

reinforcing the persistence and potential importance of the Weddellian Biogeographic Province (sensu Zinsmeister, 1979, 1982) as a biogeographic connection for western Patagonia's biotas. It is possible that some of the Paso del Sapo mammals reflect geographic, temporal, and phylogenetic relationships with those from the Eocene of the Antarctic Peninsula, such as the derorhynchid marsupials and sparnotheriodontid litopterns from Laguna Fría, with strong affinities with the Antarctic forms. In sum, the taxonomic and potential biogeographic relations between Paso del Sapo and Eocene fauna from Antarctica lead us to support affinities also as a biochronological unit.

The mammals from Laguna Fría may reflect a relatively short period of volcanic quiescence after the ignimbritic event of Barda Colorada, followed by a basaltic event of the Huancache andesites. It is possible that a gradual change occurred in the environment, but not a rapid local extinction triggered by the Huancache event. These later andesites were lava flows instead of ignimbritic explosions, thus having a less catastrophic effect at a regional scale compared with the Barda Colorada ignimbrite.

#### ACKNOWLEDGMENTS

A special thanks to Mrs. "Coca" San Martín and Mr. Rafael Nicolletti for allowing us to work in Estancia San Ramón (Laguna Fría), as well as to the Grenier family who allowed us to work in their land, Estancia 26 de Mayo (La Barda). We are also grateful to our collaborators in the field and the laboratory: Ariel Humai, Claudia Tambussi, Constanza Koefoed, Viviana Albarracín, María Luisa Pemberton, Leonardo Avilla, and Érika Abrantes. Marcela Tomeo improved Figure 1, 3, and 4.

#### REFERENCES

- Ameghino, F. 1897. Mammifères crétacés de l'Argentine. (Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). Boletín del Instituto Geográfico Argentino 18: 405–521.
- Ameghino, F. 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de

- Patagonie. *Boletín de la Academia Nacional de Ciencias (Córdoba)* 16: 349–426.
- Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Historia Natural (Buenos Aires)* (Ser. 3) 8: 1568.
- Andreis, R.R., M.M. Mazzoni, and L.A. Spalletti. 1975. Estudio estratigráfico y paleoambiental de las sedimentitas terciarias entre Pico Salamanca y Bahía Bustamante, Provincia de Chubut, República Argentina. *Revista de la Asociación Geológica Argentina* 30(1): 85–103.
- Aragón, E., and M.M. Mazzoni. 1997. Geología y estratigrafía del complejo volcánico piroclástico del río Chubut medio (Eoceno), Chubut, Argentina. *Revista de la Asociación Geológica Argentina* 52(3): 243–256.
- Aragón, E., M.M. Mazzoni, and J. Merodio. 1987. Caracterización geoquímica de la Ignimbrita Barda Colorada en el Río Chubut medio. *Actas 10° Congreso Geológico Argentino* 4: 171–173.
- Aragón, E., and E. Romero. 1984. Geología, paleoambientes y paleobotánica de yacimientos terciarios del occidente de Río Negro, Neuquén y Chubut. *Actas 9° Congreso Geológico Argentino* 4: 475–507.
- Archangelsky, S. 1974. Sobre una edad de la flora del Hunco, Provincia de Chubut. *Ameghiniana* 11(4): 413–417.
- Archibald, J.D., W.A. Clemens, P.D. Gingerich, D.W. Krause, E.H. Lindsay, and K.D. Rose. 1987. First North American land mammal ages of the Cenozoic Era. In M.O. Woodburne (editor), *Cenozoic mammals of North America: geochronology and biostratigraphy*: 24–76. Berkeley: University of California Press.
- Berry, E. 1938. Tertiary flora from the rio Pichileufu, Argentina. *Geological Society of America Special Papers* 12: 1–149.
- Bonaparte, J.F., L. Van Valen, and A.G. Kramarz. 1993. La Fauna local de Punta Peligro: Paleoceno inferior de la provincia de Chubut, Patagonia, Argentina. *Evolutionary Monographs* 14: 1–61.
- Bond, M., A.A. Carlini, F.J. Goin, L. Legarreta, E. Ortiz-Jaureguizar, R. Pascual, and M.A. Uliana. 1995. Episodes in South American land mammal evolution and sedimentation: testing their apparent concurrence in a Paleocene succession from central Patagonia. *Actas 6° Congreso Argentino de Paleontología y Bioestratigrafía*: 47–58. Trelew: Argentina.
- Bond, M., M.A. Reguero, S.F. Vizcaíno, and S.A. Marensi. 2006. A new 'South American ungulate' (Mammalia: Litopterna) from the Eocene of the Antarctic Peninsula. In J.E. Francis, E. Pirrie and J.A. Crame (editors), *Cretaceous-Tertiary high-latitude paleoenvironments, James Ross Basin, Antarctica*. Geological Society of London Special Publications 258: 163–176.
- Carlini, A.A., M. Ciancio, and G.J. Scillato-Yané. 2005. Los Xenarthros de Gran Barranca: más de 20 Ma de Historia. *Actas 16. Congreso Geológico Argentino, La Plata* 1: 315–322.
- Carlini, A.A., G.J. Scillato-Yané, F.J. Goin, and F. Pradeiro. 2002a. Los Dasypodidae (Mammalia, Xenarthra) del Eoceno. 1) El registro en Paso del Sapo. NO de Chubut (Argentina): exclusivamente Astegotheriini. Resúmenes 1er Congreso Latinoamericano de Paleontología de Vertebrados: 23. Santiago, Chile.
- Carlini, A.A., G.J. Scillato-Yané, R.H. Madden, M. Ciancio, and E. Soibelzon. 2002b. Los Dasypodidae (Mammalia, Xenarthra) del Eoceno. 3) Las especies del Casamayorensis de la Barranca Sur del lago Colhué Huapi, S. de Chubut (Argentina): el establecimiento de los Euphractinae. Resúmenes 1er Congreso Latinoamericano de Paleontología de Vertebrados: 24–25. Santiago, Chile.
- Carlini, A.A., G.J. Scillato-Yané, R.H. Madden, E. Soibelzon, and M. Ciancio. 2002c. Los Dasypodidae (Mammalia, Xenarthra) del Eoceno. 2) El conjunto de especies del Casamayorensis de Cañadón Vaca, SE de Chubut (Argentina) y su relación con las que le suceden. Resúmenes 1er Congreso Latinoamericano de Paleontología de Vertebrados: 24. Santiago, Chile.
- Cladera, G., E. Ruigomez, E. Ortiz Jaureguizar, M. Bond, and G. López. 2004. Tafonomía de la Gran Hondonada (Formación Sarmiento, Edad-mamífero Mustersense, Eoceno Medio), Chubut, Argentina. *Ameghiniana* 41: 315–330.
- Cifelli, R.L. 1983a. Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates* 2761: 1–31.
- Cifelli, R.L. 1983b. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). *American Museum Novitates* 2772: 1–49.
- Cifelli, R.L. 1985. Biostratigraphy of the Casamayoran, Early Eocene of Patagonia. *American Museum Novitates* 2820: 1–26.
- Cheetham, A.H., and J.E. Hazel. 1969. Binary (Presence-Absence) similarity indices. *Journal of Paleontology* 43: 1130–1136.
- Czaplewski, N.J. 2005. A review of the pre-Pleistocene fossil record of bats (Chiroptera) in South America. In A.W.A. Kellner, D.D.R. Henriques and T. Rodrigues (editors), *Boletim de Resumos 2° Congresso Latino-Americano de Paleontologia de Vertebrados*. Museu Nacional Serie Livros 12: 87–89. Rio de Janeiro.

- Czaplewski, N.J., and K.E. Campbell Jr.. 2004. A possible bat (Mammalia: Chiroptera) from the ?Eocene of Amazonian Peru. *In* K. E. Campbell, Jr. (editor), *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru*. Natural History Museum of Los Angeles County Science Series 40: 141–144.
- Feruglio, E. 1949. Descripción Geológica de la Patagonia. Buenos Aires: Yacimientos Petrolíferos Fiscales (Y.P.F.), 349 pp.
- Flynn, J.J., and C.C. Swisher III.. 1995. Chronology of the Cenozoic South American land mammal ages. *In* W.A. Berggren, D.V. Kent, M.P. Aubry and J. Hardenbol (editors), *Geochronology, time-scales, and global stratigraphic correlation*. SEPM (Society For Sedimentary Geology) Special Publication 54: 317–333.
- Flynn, J.J., A.R. Wyss, D.A. Croft, and R. Charrier. 2003. The Tinguiririca fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal 'Age'. *Palaeogeography Palaeoclimatology Palaeoecology* 195: 229–259.
- Gelfo, J.N. 1999. New aspects of the paleocene genus *Escribania* (Mammalia: Condylarthra). *Ameghiniana* 36(4), Supl.: 12R.
- Gelfo, J.N. 2004. A new South American mioclaenid (Mammalia: Ungulatomorpha) from the Tertiary of Patagonia, Argentina. *Ameghiniana* 41: 475–484.
- Gelfo, J.N. 2006. Los Didolodontidae (Mammalia: Ungulatomorpha) del Terciario Sudamericano: sistemática, origen y evolución. Ph. D. thesis, Universidad Nacional de La Plata, Argentina.
- Gelfo, J.N., and M.F. Tejedor. 2004. Implicancias sistemáticas de nuevos restos de *Asmithwoodwardia subtrigonia* (Mammalia: Litopterna ?) del Paleógeno de Patagonia. Resúmenes 20 Jornadas Argentinas de Paleontología de Vertebrados: 30.
- Gosses, J., A. Carroll, E. Aragón, and B. Singer. 2006. The Laguna del Hunco Formation: Lacustrine and Sub-Aerial Caldera Fill Chubut Province, Argentina. Geological Society of America Annual Meeting Abstracts 38(7): 502.
- Gradstein, F., J. Ogg, and A. Smith. 2004. *A geologic time scale*. Cambridge: Cambridge University Press.
- Habersetzer, J., and G. Storch. 1989. Ecology and echolocation of the Eocene Messel bats. *In* V. Hanak, T. Horacek and J. Gaisler (editors), *European bat research: 213–233*. Prague: Charles University Press.
- Hand, S.J., M. Novacek, H. Godthelp, and M. Archer. 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology* 14: 375–381.
- Hofftetter, R., and M. Soria. 1986. *Neodolodus colombianus* gen et sp. nov., un nouveau Condylarthre (Mammalia) dans le Miocene de Colombie. *Comptes Rendus de l'Academie des Sciences Serie II* 303(17): 1619–1622.
- Ivany, L.C. 2007. Contributions to the Eocene climatic record of the Antarctic Peninsula. U.S. Geological Survey and the National Academies Extended Abstracts: 68.
- Jepsen, G.L. 1966. Early Eocene bats from Wyoming. *Science* 154: 1333–1339.
- Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G. Re, M. Heizler, and H. Sandeman. 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* 95: 13235–13240.
- Lage, J. 1982. Descripción geológica de la Hoja 43c, Gualjaina. Provincia del Chubut. Servicio Geológico Nacional Boletín 189: 1–72.
- Legarreta, L., and M.A. Uliana. 1994. Asociaciones de fósiles y hiatus en el Supracretácico-Neógeno de Patagonia: una perspectiva estratigráfico-secuencial. *Ameghiniana* 31(3): 257–281.
- López, G.M. 1999. *Phoradiadius divortiensis*, un conflictivo Litopterna de la Formación Divisadero Largo de la provincia de Mendoza, Argentina. *Ameghiniana* 36(4) Supl.: 14R.
- López, G.M., and M. Bond. 1995. Un nuevo Notopithecinae (Notoungulata, Tytotheria) del Terciario inferior de la Puna Argentina. *Studia Geologica Salmanticensis* 31: 87–99.
- Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrate of Argentina. 3. A study of extinct Argentine ungulates. *Anales del Museo de La Plata Paleontología* 2: 1–91.
- Madden, R.H., E. Bellosi, A.A. Carlini, M. Heizler, J.J. Vilas, G. Re, R.F. Kay, and M.G. Vucetich. 2005. Geochronology of the Sarmiento Formation at Gran Barranca and elsewhere in Patagonia: calibrating middle Cenozoic mammal evolution in South America. *Actas 16° Congreso Geológico Argentino, La Plata. Tomo 4*: 411–412.
- Marshall, L.G. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences* 117: 1–89.
- Marshall, L.G., R.F. Butler, R.E. Drake, and G.H. Curtis. 1981. Calibration of the beginning of the Age of Mammals in Patagonia. *Science* 212: 43–45.

- Marshall, L.G., R. Hoffstetter, and R. Pascual. 1983. Geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata*, mémoir extraordinaire: 1–93.
- Mazzoni, M.M., and E. Aragón. 1985. El complejo volcánico piroclástico de la Formación Huitrera (Paleoceno-Eoceno), en el área del Río Chubut medio, República Argentina. *Actas 4° Congreso Geológico Chileno* 3: 275–300.
- Mazzoni, M.M., E. Aragón, and J. Merodio. 1989. La Ignimbrita Barda Colorada del Complejo Volcánico Piroclástico del Río Chubut medio. *Revista de la Asociación Geológica Argentina* 44(1/4): 246–258.
- Mazzoni, M., K. Kawashita, S. Harrison, and E. Aragón. 1991. Edades radimétricas eocenas en el borde occidental del Macizo Norpatagónico. *Revista de la Asociación Geológica Argentina* 46(1–2): 150–158.
- McKenna, M.C., and S.K. Bell. 1997. The classification of mammals above species level. New York: Columbia University Press.
- Mones, A. 1986. *Paleovertebrata Sudamericana*. Catálogo sistemático de los vertebrados fósiles de América del Sur. Parte 1. Lista preliminar y bibliografía. Courier Forschungs Institut Senckenberg 82.
- Muizon, C.D.e. 1991. La fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucía), Bolivia. In R. Suárez Soruco (editor), *Fósiles y facies de Bolivia*. Vol. 1. Vertebrados. *Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos* 12(3–4): 575–624.
- Muizon, C.De., and R. Cifelli. 2000. The “condylarths” (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. *Geodiversitas* 22(1): 47–150.
- Novacek, M. 1985. Evidence for echolocation in the oldest known bats. *Nature* 315: 140–141.
- Novacek, M. 1987. Auditory features and affinities of the Eocene bats *Icaronycteris* and *Palaeochiropteryx* (Microchiroptera, incertae sedis). *American Museum Novitates* 2877: 1–18.
- Oliveira, E.V., and L.P. Bergqvist. 1998. A new Paleocene armadillo (Mammalia, Dasypodoidea) from Itaboraí Basin, Brazil. *Paleógeno de América del Sur y de la Península Antártica (Santa Rosa)* 5: 35–40.
- Pascual, R., and E. Ortiz-Jaureguizar. 1990. Evolving climates and mammal faunas in Cenozoic South America. *Journal of Human Evolution* 19: 23–60.
- Pascual, R., and E. Ortiz-Jaureguizar. 1991. El ciclo faunístico Cochabambiano (Paleoceno temprano): su incidencia en la historia biogeográfica de los mamíferos sudamericanos. In R. Suárez Soruco (editor), *Fósiles y facies de Bolivia*. Vol. 1. Vertebrados. *Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos* 12(3–4): 559–574.
- Pascual, R., and E. Ortiz-Jaureguizar. 1992. Evolutionary pattern of land mammal faunas during the Late Cretaceous and Paleocene in South America: A comparison with the North American pattern. *Annales Zoologici Fennici* 28: 245–252.
- Pascual, R., E. Ortiz Jaureguizar, and J.L. Prado. 1996. Land-mammals: paradigm for Cenozoic South American geobiotic evolution. In G. Arratia (editor), *Contributions of southern South America to vertebrate paleontology*. *Münchener Geowissenschaftliche Abhandlungen* 30(A): 265–319.
- Pascual, R., E.J. Ortega Hinojosa, D. Gondar, and E. Tonni. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas (Buenos Aires)* 6: 165–193.
- Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. In A. Keast, F.C. Erk and B. Glass (editors), *Evolution, mammals, and southern continents*: 247–309. Albany: State University of New York Press.
- Paula Couto, C.D.e. 1952. Fossil mammals from the beginning of the Cenozoic in Brasil: Condylartha, Litopterna, Xenungulata and Astrapotheria. *Bulletin of the American Museum of Natural History* 99(6): 355–394.
- Petersen, C.S. 1946. Estudios geológicos en la región del río Chubut medio. *Dirección General de Minas y Geología (Buenos Aires) Boletín* 59: 1–137.
- Rapela, C., L. Spalletti, J. Merodio, and E. Aragón. 1984. El vulcanismo Paleoceno-Eoceno de la provincia volcánica Andino-Patagónica. *Relatorio 9° Congreso Geológico Argentino* 1(8): 189–213.
- Rohlf, F.J. 1977. Computational efficiency of agglomerative cluster-ing algorithms. *IBM Watson Research Center RC* 6831: 1–36.
- Roth, S. 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretaceo superior y Terciario inferior de la Patagonia. *Revista del Museo de La Plata* 11: 135–158.
- Russell, D.E., P. Louis, and D.E. Savage. 1973. Chiroptera and Dermoptera of the French Early Eocene. *Palaeovertebrata Mémoir Extraordinaire*: 1–77.

- Scott, W.B. 1913. A history of the land mammals in the Western Hemisphere. New York: Macmillan.
- Simmons, N.B., and J.H. Geisler. 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bats lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bulletin of the American Museum of Natural History* 235: 1–182.
- Simpson, G.G. 1935a. Early and Middle Tertiary geology of the Gaiman region, Chubut, Argentina. *American Museum Novitates* 775: 1–29.
- Simpson, G.G. 1935b. Occurrence and relationships of Rio Chico fauna of Patagonia. *American Museum Novitates* 818: 1–21.
- Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: i–xvi, 1–350.
- Simpson, G.G. 1948. The beginning of the age of mammals in South America. Part 1. Introduction. Systematics: *Marsupialia*, *Edentata*, *Condylarthra*, *Litopterna* and *Notioprogonia*. *Bulletin of the American Museum of Natural History* 91(1): 1–232, pls. 1–19.
- Simpson, G.G. 1967a. The Ameghino's localities for Early Cenozoic mammals in Patagonia. *Bulletin of the Museum of Comparative Zoology* 136(9): 63–76.
- Simpson, G.G. 1967b. The beginning of the age of mammal in South America. Part 2. Systematics: *Notoungulata*, concluded (*Typrotheria*, *Hegetotheria*, *Toxodonta*, *Notoungulata* incertae sedis), *Astrapotheria*, *Trigonostylopoidea*, *Pyrotheria*, *Xenungulata*, Mammalia incertae sedis. *Bulletin of the American Museum of Natural History* 137: 1–260, pls. 1–46.
- Simpson, G.G., J. L. Minoprio, and B. Patterson. 1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. *Bulletin of the Museum of Comparative Zoology* 127(4): 239–293.
- Sneath, P.H.A., and R.R. Sokal. 1973. Numerical taxonomy. San Francisco: Freeman.
- Somoza, R., G. Cladera, and S. Archangelsky. 1995. Una nueva Tafloflora Paleocena de Chubut Patagonia: su edad y ambiente de depositación. *Actas 6 Congreso Argentino de Paleontología y Bioestratigrafía*, Trelew: 265–269.
- Soria, M.F. 1980 a. Una nueva y problemática forma de ungulado del Casamayorensis. *Actas 2 Congreso Argentino de Paleontología y Bioestratigrafía y 1er Congreso Latinoamericano de Paleontología* (Buenos Aires, 1978): 193–203.
- Soria, M.F. 1980 b. Las afinidades de *Phoradiadus divortiensis* Simpson, Minoprio y Patterson, 1962. *Circular Informativa Asociación Paleontológica Argentina* 4: 20.
- Soria, M.F. 1984 a. Noticia preliminar sobre los Amilnedwardsidae, fam. nov. (Mammalia) del Eoceno temprano de Patagonia, República Argentina. *Resúmenes las Jornadas Argentinas de Paleontología de Vertebrados*, La Plata: 19.
- Soria, M.F. 1984 b. Notopterna: un nuevo orden de mamíferos ungulados del Terciario inferior de Sudamérica. *Resúmenes las Jornadas Argentinas de Paleontología de Vertebrados*, La Plata: 23.
- Soria, M.F. 1989. Notopterna: un nuevo orden de mamíferos ungulados Eógenos de América del Sur. Parte 1. *Los Amilnedwardsidae*. *Ameghiniana* 25(3): 245–258.
- Soria, M.F. 2001. Los Proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales* 1: 1–167.
- Tejedor, M.F., N.J. Czaplewski, F.J. Goin, and E. Aragón. 2005. The oldest record of South American bats. *Journal of Vertebrate Paleontology* 25: 990–993.
- Ubilla, M., D. Perea, and M. Bond. 1999. Two new records of Notoungulates (Isotemnidae; Oldfieldthomasiidae n.g., n. sp.) from Fray Bentos Fm. (Deseadan SALMA, Oligocene) in the Santa Lucia Basin, Uruguay. *Congreso Internacional Evolución Neotropical del Cenozoico* (La Paz, 1999) *Resúmenes*: 43.
- Vizcaino, S.F., R. Pascual, M.A. Reguero, and F.J. Goin. 1998. Antarctica as background for mammalian evolution. *In* *Paleógeno de América del Sur y de la Península Antártica*. *Asociación Paleontológica Argentina Publicación Especial* 5: 199–209.
- Volkheimer, W., and L. Lage. 1981. Descripción geológica de la Hoja 42 c, Cerro Mirador, provincia del Chubut. *Servicio Geológico Nacional Boletín* 181: 1–71.
- Wilf, P., N.R. Cúneo, K.R. Johnson, J.F. Hicks, S.L. Wing, and J.D. Obradovich. 2003. High plant diversity in the Eocene South America: evidence from Patagonia. *Science* 300: 122–125.
- Wilf, P., C.C. Labandeira, K.R. Johnson, and N.R. Cúneo. 2005. Richness of plant-insect associations in Eocene Patagonia: a legacy for the South American biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 102: 8944–8948.

- Woodburne, M.W. 1977. Definition and characterization in mammalian chronostratigraphy. *Journal of Paleontology* 51(2): 220–234.
- Wyss, A.R., J.J. Flynn, M.A. Norell, C.C. Swisher III., M.J. Novacek, M.C. McKenna, and R. Charrier. 1994. Paleogene mammals from the Andes of central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. *American Museum Novitates* 3098: 1–31.
- Zinsmeister, W.J. 1979. Biogeographic significance of the Late Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. *In* J. Gray and A. Boucot (editors), *Historical biogeography, plate tectonics, and changing environment. Proceedings of the Annual Biological Colloquium and Selected Paper 37*: 349–355. Corvallis: Oregon State University Press.
- Zinsmeister, W.J. 1982. Late Cretaceous-early Tertiary molluscan biogeography of the southern Circum-Pacific. *Journal of Paleontology* 56: 84–102.