THE PALEOGENE MAMMALIAN FAUNA OF SANTA ROSA, AMAZONIAN PERU

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This volume describes most of the known mammalian fauna of the Santa Rosa local fauna of eastern Peru, the first Paleogene vertebrate fauna to be reported from the forested, tropical lowlands of the Amazon Basin. It represents the work of many investigators, some of whom had a much more difficult task than others because of the unequal representation of the different mammalian groups present in the paleofauna. The articles are heavily weighted toward taxonomic descriptions of species new to science, but there is also much discussion of the relationships of the new forms and what they might indicate about the evolution of the South American mammalian fauna. As the first description of a Paleogene fauna from Amazonia, this publication presents critical baseline studies that will be of value to all students of South American vertebrate paleontology. I consider it a privilege to have served as both an editor and a contributor for this publication, and I hope its contents will prove as exciting to the reader as they have been to me.

This work is the culmination of the first phase in efforts to describe the mammalian paleofauna from Santa Rosa. I say first phase because, although the Santa Rosa local fauna has been sampled, the sample has not been thorough. These papers provide a detailed look at an abundant and diverse mammalian paleofauna, but they are based on a relatively small sample. Future excavations at the Santa Rosa site, including more rapid processing of screen-washed matrix using heavy liquid techniques, will undoubtedly yield both a vast collection of vertebrate specimens and many more species new to science.

Any work as extensive as this cannot include many of the more recent advances that have occurred in South American vertebrate paleontology. For example, work continues in Argentina on refining the dates of Paleogene South American Land Mammal Ages (SALMAs); a second rodent, one much more derived than any from Santa Rosa, has been reported from the Tinguirirican faunas of Chile; formal recognition of a Tinguirirican SALMA has been proposed; and preliminary studies of armored edentates from Santa Rosa appear to support an Eocene age for the Santa Rosa paleofauna. None of these developments alter the taxonomic conclusions presented herein, but some of them might be important for a future age assignment for the Santa Rosa local fauna.

Field research in vertebrate paleontology in the vast tropical lowlands of the Amazon Basin is challenging, but the obstacles are probably no greater than comparable research taking place in other parts of the world, such as Antarctica or the Sahara. What is really difficult is overcoming the deeply entrenched view that paleontological research in Amazonia is bound to fail because there is nothing there to discover. Our research dispels this notion. Moreover, the specimens described herein are significant not just because they represent species new to science. As the first Paleogene vertebrate fauna for half of the South American continent, the Santa Rosa local fauna has provided wonderful new perspectives on early South American mammals and opened the door to entirely new considerations of the evolution of major lineages of South American mammals. Equally important, if not more so, is the impetus given to the search for new Paleogene sites in Amazonia. The outcrops are there. As in paleontological fieldwork anywhere, it is only necessary to find the right ones.

I wish to take this opportunity to thank all the contributors for their enthusiasm and commitment to this multifaceted project, as well as acknowledge their patience during the long process of bringing the results of their research to fruition. I thank all of the many reviewers for their gracious contributions of time and effort, which contributed to the overall improvement of this volume.

I also wish to thank those who have contributed in so many other ways to this work. John G. Wigmore has been an especially enthusiastic supporter of our Amazonian field work. He participated in the Santa Rosa discovery expedition and in following years provided funding that supported additional expeditions. Additional funding for fieldwork came from the National Geographic Society, Winifred Rhodes, and Richard Seaver. Encouragement for our field efforts in western Amazonia came from the Instituto Geologico, Minéro, y Metalúrgico (INGEMMET) of Peru, and especially Ing. Hugo Rivera Mantilla, Director Técnica of INGEMMET, and Ing. Oscar Palacios, Director General de Geologia de INGEMMET. Without their desire to seek basic information on the geological resources of Peru, coming from whatever discipline, we would never have succeeded in our efforts to find such a site as Santa Rosa. Critical logistical support for airlifting field equipment and many heavy bags of matrix from the isolated outpost of Breu to Pucallpa was provided by the Peruvian army. Last, but certainly not least, I thank my field companions of many years of slogging through the mud of Amazonia, Carl David Frailley and Lidia Romero-Pittman. Ultimately, it must be recognized that it was their indefatigable efforts and good cheer, as well as their sharp eyes for tiny fossils, that made this work possible.

Kenneth E. Campbell, Jr.
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Paleogene Notoungulates from the Amazon Basin of Peru

Bruce J. Shockey,¹ Ralph Hitz,² and Mariano Bond³

ABSTRACT. Paleogene-grade notoungulates (order Notoungulata) from the Santa Rosa local fauna of eastern Peru are documented and described. The specimens include at least two species of toxodont notoungulates (suborder Toxodontia) and the first record of an interatheriid (suborder Typotheria) from the Amazon Basin. The toxodont specimens include isolated teeth from a sheep-sized animal and a tooth from perhaps the smallest known toxodont. The larger toxodont specimens include an upper molar having distinctive, open, multiple cristae; a leontiniid-like upper premolar; and a lower molar with the general morphology of toxodontids, leontiniids, and Deseadan or younger notohippids. The interatheriid specimen is a lower jaw with molars morphologically similar to the “Tinguirirican” Eopachyrucos plicifera and an unnamed, small interatheriid from Salla, Bolivia (Deseadan South American Land Mammal Age). The toxodont specimens, as well as the interatheriid, are comparable to known notoungulates ranging in age from “Tinguirirican” to Deseadan (31.5–24 Ma). These specimens offer tantalizing hints regarding the notoungulate fauna of the Amazon Basin and suggest a region to explore for clues regarding the rapid radiation of advanced notoungulates in the late Paleogene and early Neogene.

INTRODUCTION

Despite the relatively good mammalian record for the Cenozoic of South America, there remain significant gaps in our knowledge of the evolutionary history of notoungulates. These gaps are both spatial and temporal; that is, a large geographic region (Amazonia) is underrepresented in the fossil record and depositional hiatuses are present, even in the well-explored higher latitudes. Thus, the discovery of Paleogene-grade notoungulates in the Amazon Basin of Peru is noteworthy, despite their limited nature.

The notoungulate remains from Santa Rosa include several isolated teeth referable to the suborder Toxodontia and a single mandibular fragment with molars referable to the family Interatheriidae, suborder Typotheria. The toxodont teeth are of two distinct size classes. Most of the specimens are from a roughly sheep-sized animal, but one specimen is much smaller. The interathere specimen is also
quite small. Although none of the notoungulate specimens from Santa Rosa can be confidently referred to any known genus, they are similar to taxa that lived in the time interval after the Mustersan South American Land Mammal Age (SALMA) and into the Deseadan SALMA.

Paleogene notoungulates have been virtually unknown from the Amazon Basin. Even early Neogene, that is, Miocene, notoungulates are poorly known from this region. A single upper molar, the holotypical and only known specimen of *Purperia cribatidens* (Paula Couto, 1981), was referred to the Notohippidae (*Purperia* Paula Couto, 1982a), a replacement for the preoccupied generic name *Megahippus* Paula Couto, 1981). Restudy of this specimen by Ribeiro and Bond (1999) indicates that it is not referable to this family. It may be a leontiniid, but it can only be confidently referred to the subordinal level (Toxodontia). A single, lower molar tooth fragment noted by Paula Couto (1982b) apparently is the only other evidence of notohippids in the Amazon Basin. However, a variety of toxodontids are known from Amazonia. Paula Couto (1981) reported the middle Miocene nesodontine toxodontid *Nesodon* sp. from the western Amazon. He also reported (Paula Couto, 1982b) a dozen other genera of toxodontids that came from western Amazonia, all of which were referred to the more derived and geologically younger subfamilies Toxodontinae and Haplodontheriinae of the family Toxodontidae. The presence of interatheriids in the Amazon Basin had been unrecorded, but they are known from the mid-Miocene of La Venta, Colombia (Stirton, 1953) farther to the north.

To facilitate the discussion of the possible age of Santa Rosa, we will informally refer to the interval after the Mustersan SALMA and before the Deseadan SALMA as "Tinguirirican" (Wyss et al., 1994; Flynn and Swisher, 1995), an age roughly equivalent to Ameghino's "Astraponoteen plus Astrapotheriinae" (see Bond et al., 1996; Kay et al., 1999; and Hitz et al., 2000). With respect to the geochronology of the Tinguirirican faunal interval, Wyss et al. (1994) reported an isotopic age of 31.5 Ma for the fossil-bearing horizons at the principal locality of Tinguiririca, Chile. They provided an additional isotopic date from below the fossiliferous sequence that suggested that the duration of the Tinguirirican interval might have extended to 37.5 Ma. Recent isotopic dates reported by Kay et al. (1999) from the Sarmiento Formation at the Gran Barranca, Argentina, however, appear to better constrain the duration of the Tinguirirican faunal interval. Kay et al. (1999) provided isotopic age data from the Barrancan substage of the Casamayoran SALMA, the upper age limit of which is about 35.3 Ma. This limit dictates that the Mustersan must fit between 31.5 and about 35 Ma, implying that the duration of the Tinguirirican faunal interval cannot extend as far back in time as previously conceived. Because of the present flux in our understanding of the duration of the Tinguirirican interval, we will simply refer to the isotopic age of the Tinguirirican fauna as 31.5 Ma, with the understanding that it extends an unknown, but probably short, amount of time, into the earlier Oligocene.

The toxodont specimens are not referable to any known genera, but they are too incomplete to serve as useful holotypes (see Pascual, 1965). The referral or naming of the interatheriid specimen is also deferred until more complete material becomes available.

All specimens discussed herein came from Natural History Museum of Los Angeles County (LACM) locality 6289, about 2 km north of the village of Santa Rosa, Peru, on the west bank of the Rio Yurúa near its confluence with the Rio Beu, in Provincia Atalaya, Departamento Ucayali, eastern Peru (9°29′39″ S, 72°45′48″ W; see Campbell et al., 2004).

Abbreviations of the museums from which comparative notoungulates were examined are as follows.

- **LACM** Natural History Museum of Los Angeles County, Los Angeles, California, USA
- **UF** Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida
- **FMNH** Field Museum of Natural History, Chicago, Illinois

**SYSTEMATIC PALEONTOLOGY**

Order Notoungulata Roth, 1902

Suborder Toxodontia Owen, 1853

Toxodontia is one of the three currently recognized suborders of the Notoungulata (Cifelli, 1993; McKenna and Bell, 1997). It includes five families: the Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, and Toxodontidae. The phylogenetic analysis of Cifelli (1993) suggests that the Isotemnidae is basal to the "advanced Toxodontia" and that the Homalodotheriidae were derived from a specialized lineage of isotemnids. The "advanced Toxodontia" include the leontiniids, notohippids (*sensu* Simpson, 1945), and toxodontids. All of the toxodont specimens noted in this work are referred to the "advanced Toxodontia" (*sensu* Cifelli, 1993).

None of the toxodont specimens from Santa Rosa were found in an association that would suggest that they represent a single individual. Most are of a similar size, such that they could have come from the same species. At this time it is more prudent to describe the larger toxodont specimens as individual teeth rather than distinct taxa.

One toxodont specimen (LACM 140570), however, is so small that it is very distinct, not just from the other toxodont specimens from Santa Rosa, but from all other known taxa of this suborder. It is described and discussed separately.
Figure 1 Occlusal views of notoungulate teeth from Santa Rosa, Peru. A, LACM 140569, left M₁ or M₂; B, LACM 144304, left P; C, LACM 144305, right M₁, illustrating the 7|9 morphology discussed in the text; D, LACM 140570, left lower molar of small ?notohippid; E, LACM 140571, interatheriid molars of partial mandible, M₁-trigonid of M₂.

LARGER SPECIMENS OF TOXODONTIA

The larger notoungulate teeth recovered from Santa Rosa are from a medium-sized (more or less sheep-sized) toxodont. They are well preserved and instructive; thus, they are described and discussed below.

**MATERIAL.** LACM 140569, left M₁ or M₂; LACM 144304, left upper premolar; LACM 144305, right M₁ or M₂; LACM 144307, left M₁ or M₂ (missing the hypoconid) is comparable to LACM 144305. Collected by K.E. Campbell, C.D. Frailey, L. Romero-Pitman, and M. Aldana in 1995, 1998.

**Family Indeterminate**

**Genus and Species Indeterminate**

**Figure 1A**

**MATERIAL.** LACM 140569.

**DESCRIPTION.** This upper left molar (M₁ or M₂) is distinctive in having multiple and open cristae. It is mesodont and has an oblique protoloph that is significantly longer than the transversely oriented metaconid. The anteroposterior dimension of the tooth is 18.7 mm and the transverse diameter is 18.4 mm. The crown height at the paracone ridge is 17.2 mm. Enamel is missing from the posterior portion of the ectoloph, but the dentine border is complete enough so that its form is unambiguous; that is, it is not strongly undulated. The paracone ridge is weak, and the shape of labial dentine suggests only a slight bulge at the metacone. Three major cristae project from the anterior half of the ectoloph toward the medial sagittal plane of the tooth. Two smaller cristae lie posterior to the third; none unite with the crochet. These five cristae give the labial side of the infolding of enamel a complex branching appearance. This infolding has not been isolated as a fossa, suggesting that the tooth is minimally worn. Another millimeter or so of wear would have isolated this infolding as the major fossa. The short posterior cingulum forms an oval-shaped fossa that is partially bisected by a posterior enamel projection, giving the fossa somewhat of a figure eight appearance. There is no external cingulum, but a distinct anterolingual cingulum is present. The lingual portion of this cingulum forms a cusplet. The tooth lacks any trace of cementum.

**COMMENTS.** The most distinctive feature of LACM 140569 is the supernumerary cristae, of which none unite with the crochet, or with either medially. Although the tendency to develop cusplets adjacent to the ectoloph is pronounced in notoungulates (Patterson, 1934), such cusplets are typically minute and disappear or unite rapidly with wear. Rarely do they form more than two distinct cristae. The "advanced Toxodontia" typically have only two cristae in their upper molars, with the posterior one uniting with the crochet. However, multiple cristae are present in the molars of many leontiniids [e.g., *Huilatherium pluriplicatum* Villarroel and Guerrero, 1983; *Colpodon* Burmeister, 1885 (personal observation of FMNH 13310); *Taubatherium major* Soria and Alvarenga, 1989; and *T. paulacoutoi* Soria and Alvarenga, 1989], but they unite and form multiple labial fossettes (or "enamel-lined pits" of some authors, e.g., Villarroel and Colwell Danis, 1997).
The cristae of LACM 140569 are not united (do not form fossettes); thus, they are more similar in appearance to those of *Plexotemnus complicatissimus* Ameghino, 1904, and closely related taxa that Simpson (1967) united under a single genus, *Acolobryx* Ameghino, 1902 (this synonymy and use of the generic name *Acolobryx* has been disputed; see Bond and Lopez, 1993). These *Plexotemnus*-like taxa have well-formed multiple cristae that, like LACM 140569, give the medial margin of the ectoloph an undulating appearance. Also, the cristae tend to remain distinct from the crochet. Distinctive undulated medial margins of the ectoloph are present in *Plexotemnus* (Casamayoran SALMA) and *Psuelia coarctatus* (Ameghino, 1901) (Mustersan SALMA). However, LACM 140569 differs from these taxa by lacking the medial bulge of the posterior cingulum and by being a little larger and higher crowned. LACM 140569 differs from molars of known leontiniids by its smaller size, by its relatively smaller transverse dimension, and by not having cristae and crochet united.

Genus and Species Indeterminate

**Figure 1B**

**MATERIAL.** LACM 144304.

**DESCRIPTION.** The size of this upper premolar suggests that it came from an animal a little larger than the animal from which came the upper molar discussed above (LACM 140569).

The occlusal view of this premolar (Fig. 1B) has a roughly square appearance, with a longer transverse than anteroposterior dimension (length = 16.2 mm; width = 18.5 mm). There is a sharp groove in the ectoloph between the parastyle and the paracone ridge and a slight bulge at the metacone. Otherwise, the ectoloph is fairly straight. The paracone ridge is distinctly shorter than the paracone and metacone, which are about the same height. An external cingulum covers the base of the ectoloph, running from the posterior margin of the paracone to the posterior border of the tooth. The paracone ridge, including the external cingulum, is 17.2 mm tall.

The occlusal surfaces of the paracone and metacone show some wear, which has left subtle, but unmistakable oblique (posteroalabial to anterolingual) wear lines. The metaloph and the medial border of the posterior cingulum reach the protocone. Tiny cuspules cover the enamel between the posterior cingulum and the metacone ridge. A deep central valley separates the protocone from the ectoloph. There is no protoloph.

The protocone is robust and, though it is nearly as high as the paracone and metacone, it is very little worn, remaining completely covered in enamel. There is a vertical groove of the protocone similar to, but weaker than, that of *Leontinia* Ameghino, 1895 (see Patterson, 1934). An anterior cingulum rings the anterior base of the protocone and extends to the parastyle. The center of the lingual surface of the protocone lacks a cingulum.

**COMMENTS.** The lack of a protoloph, combined with the reasonably well-developed anterolingual cingulum, is suggestive of the “leontiniid depression” (sensu Colwell, 1965; see also Villarroel and Colwell Danis, 1997) of leontiniid premolars. LACM 144304 is much smaller than premolars of *Leontinia gaudryi* Ameghino, 1895, and *Scarrittia canquenesis* Simpson, 1934, but its anteroposterior dimension is within the size range of Ps. In the lower end of the size range of Ps of *Ancylococelus frequens* Ameghino, 1893. It is almost as large as the P3 of a small, unnamed leontiniid from Salla, Bolivia (Shockey, 1997b:fig. 3.1). Not only does the form of the tooth suggest a leontiniid referral, but also something of the function is demonstrated with the oblique macrowear marks on the tooth. This is a conspicuous feature seen in virtually all specimens examined of *Leontinia*, *Scarrittia* Simpson, 1934, and a currently unnamed leontiniid genus from Salla (Shockey, 1997b). We provisionally refer this tooth to the *Leontiniidae*.

Genus and Species Indeterminate

**Figure 1C**

**MATERIAL.** LACM 144305.

**DESCRIPTION.** LACM 144305, a right M1, has a length of 16.8 mm and a width of 6.8 mm. In occlusal view, it appears as a seven-over-nine (7/9; Fig. 1C), the trigonid having the shape of the number seven and the talonid forming a nine (the entolophid fossettid being the hole in the circle part of the nine). This 7/9 morphology (with an entolophid fossettid) is typical of right lower molars of Deseadan notohippids (except *Morphippus* Ameghino, 1897, and *Eurygenium* Ameghino, 1895), Deseadan-to-Santacrucian toxodontids, and all known leontiniids (left lower molars of these animals appear as the mirror image of 7/9). This 7/9 morphology is a putative synapomorphy for the “advanced Toxodontia” (Gifelli, 1993). The molar at hand is smaller than those of most leontiniids, and it is most comparable in size to those of neosodentine toxodontids and Deseadan notohippids.

Like the previous specimens described, LACM 144305 is little worn. The trigonid is less worn than the talonid, having its occlusal area on a plane 3 mm higher than that of the talonid. The lingual infolding of enamel is deep, but it would have become very shallow with 1-2 mm of wear and disappear with just 3-4 mm of wear. The most distinctive feature of the trigonid is the sharp, vertical ridge along the protocone just anterior to the infolding of labial enamel at the trigonid–talonid border.

The talonid is more deeply worn, and little remains of the lingual infolding of enamel that separates it from the trigonid. With about another 1 mm of wear, the trigonid and talonid would have united, leaving just a trigonid–talonid fossettid. The
entolophid is robust and has a crescent-shaped entolophid fossettid. The hypolophid is distinct from the entolophid, but these would have merged with another 1 mm of wear.

LACM 144305 is very similar in size, crown height, and morphology to the M₃ from a nearly complete mandible of a nesodontine toxodontid, *Proadinotherium* sp. of Salla (UF 149222; see Shockey, 1997b:fig. 3.12). Most of the few differences in the two may be attributed to the greater wear of the trigonid of the Salla specimen. However, the labial surface of the trigonids of the molars of the Salla specimen are rounded, lacking the distinctive, sharp, vertical ridge seen on LACM 144305.

COMMENTS. Although LACM 144305 is nearly identical to the *Proadinotherium* sp. specimen from Salla, the 7/9 morphology of the lower molars of the “advanced Toxodontia” is seen in Deseadan-grade notohippids and leontiniids, as well as nesodontine toxodontids, so it is of little value in determining phylogenetic position more precisely than as unspecialized “advanced Toxodontia.” The labial vertical ridge of the trigonid, however, is frequently seen in specimens of leontiniids.

Discussion of Larger Specimens of Toxodontia

The toxodont specimens described above are of similar size, suggesting the possibility that they are from the same species, but there was no close association of any of these teeth upon collection that would suggest that they were from a single individual. LACM 144305 and the other lower molar (LACM 144307; not figured) are near-perfect mirror images of one another, and they certainly came from the same species, if not the same individual.

However, it is difficult to interpret the upper molar (LACM 140569) and the upper premolar (LACM 144304) as coming from the same species. The upper premolar is most likely that of a leontiniid, and it is within the size range of the P₃s of the smallest leontiniids and within the lower end of the size range of the P₃s of *Ancylocetus* Ameghino, 1895, and a small species of an unnamed genus at Salla (Shockey, 1997b). The upper molar (LACM 140569), however, is smaller than the M₁s of the smallest leontiniids. The undulated median surface of the ectoloph of the M₁ is exactly the morphology that one would expect to have led to the multiple, enamel-lined pits seen in a variety of leontiniid molars. Thus, it might represent a primitive leontiniid or an animal closely related to leontiniids. Likewise, the generalized toxodont morphology of the lower molars (LACM 144305 and LACM 144307) suggest that they are from an animal near the base of the “advanced Toxodontia” radiation and might, too, be from a primitive leontiniid or closely related taxon.

The relative lack of wear of these teeth may represent a sample bias or a bias in preservation; that is, young individuals died and were preserved. It may, however indicate environmental conditions in which nonabrasive forage was available to and consumed by these herbivores.

SMALL SPECIMEN OF TOXODONTIA

cf. *Notohippidae* Ameghino, 1895

Genus and Species Indeterminate

Figure 1D

MATERIAL. LACM 140570.

DESCRIPTION. This M₃ or M₂ is similar to, but distinctly smaller than, those of the “dwarf” notohippid *Rhynchippus pumilus* (Ameghino, 1897). It is also lower crowned than *R. pumilus*, or any known Deseadan or younger notohippid. The entolophid is distinct in having a somewhat undulated anterolingual border. The entolophid is fairly robust and contains a subtriangular fossettid. No other fossettids are present.

The anteroposterior dimension of the talonid is 5.9 mm at the occlusal level, and the estimated total occlusal anteroposterior length is about 7.5 mm. The greatest height of the crown is 7.3 mm.

COMMENTS. This specimen is much too small to belong to the same taxon as any of the toxodontid specimens described above. It has both primitive and derived characters, in that it is brachydont to mesodont, but it shows the derived entolophid fossettid. This entolophid fossettid is seen in most Deseadan notohippids, but not in pre-Deseadan genera such as *Eomorphippus* Roth, 1902 (see Simpson, 1967), or the *Plecostomennus*-like taxa. An entolophid fossettid appears in early toxodontids (and is lost in late Miocene and younger toxodontids), all known leontiniids, and most Deseadan or younger notohippids. It may represent a synapomorphy for leontiniids, toxodontids, and advanced notohippids. A phylogenetic analysis has shown, however, that it is just as likely for this trait to have evolved independently in leontiniids (Shockey, 1997a). If, indeed, the entolophid fossettid were a synapomorphy for these diverse Deseadan taxa, then it would have evolved at some time prior to the Deseadan.

SUBORDER TYPOTHERIA ZITTEL, 1893

Family Interatheriidae Ameghino, 1887

Subfamily Interatheriinae Simpson, 1945

Genus and Species Indeterminate

Figure 1E

MATERIAL. LACM 140571, partial left mandible with M₁₋₃ (only the trigonid of M₃ remains). DESCRIPTION. LACM 140571 is the only interathere specimen known from the Amazon Basin. Persistent labial and lingual sulci on the molars render them bilobed and identify this specimen as an interathere, although some basal interatheres have weakly developed sulci (Hitz, 1997). Additionally, the extremely hypsodont, or possibly hypselodont,
molars of LACM 140571 identify this specimen more narrowly as belonging to the subfamily Interatheriinae.

Compared with known interatherines, LACM 140571 is very small. The length and width of the $M_3$ is 4.3 by 2.4 mm and of the $M_2$ is 4.6 by 2.4 mm. The metaconids on $M_1$ and $M_2$ are pronounced and project lingually. On the lingual side of the talonid of both $M_1$ and $M_2$ there is a slight lingual extension, positioned just posterior to the metaconid. This feature is more pronounced on $M_1$. The trigonid of the $M_1$ is smaller than that of $M_1$ or $M_2$, and the metaconid is less pronounced than that of the preceding molars. The labial side of the mandible is smooth with no visible foramina. The lack of foramina labially supports the interpretation that these teeth are the $M_3$. Most interatheres observed by us have a mental foramen on the labial side of the mandible below the $P_4$. The lack of such on LACM 140571 suggests that the specimen represents a more posterior portion of the jaw than the premolar area. The lingual side of the mandible has a shallow excavation on the posterior end, interpreted here as the mandibular fossa.

By virtue of its size and the lingually projecting metaconids of the molars, LACM 140571 resembles *Eopachyrucos plicifer*a Ameghino, 1901, and an unnamed species from Salla, Bolivia (Hitz, 1997). Given its fragmentary condition, however, referral of this specimen to either taxon is premature.

COMMENTS. The upper Oligocene Salla beds of Bolivia preserve several interather taxae, the smallest of which ranges widely in size (MacFadden et al., 1985; Hitz, 1997). The dentition of LACM 140371 resembles a few of the more diminutive specimens (UF 91302, UF 91644, UF 91643, UF 49266) from this smaller taxon, both in size and general morphology. LACM 140571 also resembles a specimen of *Eopachyrucos plicifera* (MLP 12-1329), a taxon known from several localities from southern Argentina (Gran Barranca, Chubut; Cañadón Blanco, Chubut; Rocas Bayas, Río Negro). *Eopachyrucos plicifera* was first allocated to the Interatheriidae by Ameghino (1901), but a recent, emended diagnosis places it within the Interatheriidae (Hitz et al., 2000).

The upper Oligocene Salla beds have long been recognized as belonging to the Deseadan SALMA (MacFadden et al., 1985). The age of the deposits bearing *E. plicifera* is more problematic. Recent evidence (Bond et al., 1996), however, suggests that they fall within a hiatus in the SALMA sequence, between the Mustersan and Deseadan SALMAs. Bond et al. (1996) identified a stratigraphic level at the Gran Barranca, Chubut, that appears distinct from Deseadan and Mustersan deposits and termed this interval the “Astraponoteen plus supérieur level.” Several localities in Argentina have been tentatively correlated to the Astraponoteen plus supérieur level at the Gran Barranca, including Cañadón Blanco and Rocas Bayas (Hitz et al., 2000). Furthermore, the Astraponoteen plus supérieur level has been tentatively correlated to the Tinguiririca fauna of central Chile on the basis of faunal similarities [e.g., interatheres (see Hitz et al., 2000) and marsupials (Goin and Candela, personal communication)].

DISCUSSION

It is unclear whether the larger toxodont specimens represent one, two, or three species. Nothing regarding their collection or morphology clearly relates them to one another, but the similar size suggests the possibility.

The upper molar (LACM 140569) is distinctive in having ununited multiple cristae. This is similar to that seen in the Casamayoran to Mustersan *Plexotemnus*-like toxodontids, but LACM 140569 is larger, is higher crowned, and lacks the lingual bulge of the posterior cingulum seen in the *Plexotemnus*-like taxa. Alternatively, the multiple cristae may suggest a relationship with the leontinids, which tend to have multiple cristae, although they are expressed as labial fossettes or enamel pits. LACM 140569 also differs from leontinids by having linear dimensions that are only 90 percent of those of the smallest known leontinids. The upper premolar (LACM 144304) has a morphology (e.g., “leontiniid basin”) comparable to leontinids, although it is smaller than all but the smallest members of the family. Should LACM 140569 and LACM 144304 belong to a single species, it would likely be a primitive leontinid. The lower molar (LACM 144305) has the general morphology of the “advanced Toxodontia” (sensu Cifelli, 1993). Although it is almost identical to the M$_2$ of *Proadinotherium* sp. (a nesodontine toxodontid) of Salla, the single significant difference (the sharp vertical ridge of the labial trigonid) is a character suggestive of leontinids. Thus, all three of the larger specimens may have come from a very small and primitive leontinid.

The diminutive ?notohippid, LACM 140570, is comparable to Deseadan taxa, but it is lower crowned. The interatherid, LACM 140571, is most comparable to the early Oligocene “Tinguirirican” *Eopachyrucos plicifera* and an unnamed interather from the upper Oligocene (Deseadan) of Salla, Bolivia.

The toxodont specimens discussed above are higher crowned than those of Mustersan species of Toxodontia, but generally lower crowned than those of the Deseadan (see Shockey, 1997a). Although there appears to be a strong relationship between crown height and the geological age of at least notohippids (Shockey, 1997a), some caution should be exercised before extrapolating this principle to tropical regions. For example, Cifelli and Guerrero (1997) noted that proterotheriid litopterns from the low-latitude, middle Miocene La Venta fauna of Colombia actually had significantly lower crowned cheek teeth than geologically older
proterotheriids from the Santacrucian faunas of southern Patagonia. This suggests that regional environmental differences influence the evolution of hypsodonty.

The problems associated with the use of high-latitude fossils to estimate the age of tropical faunas were reviewed by Madden et al. (1997). These investigators found that correlation by faunal resemblance or by "guide" fossils tended to overestimate the age of the La Venta fauna. For example, Kay et al. (1987) correlated the La Venta fauna with the Santacrucian SALMA by using the Simpson coefficient of faunal similarity (Simpson, 1960). Also, some "guide" fossils (e.g., Prothoatherium, Pachybiototherium) suggested a Colhuehuapian "age" for the considerably younger La Venta fauna.

Although much of the La Venta fauna appears archaic for its age, it should be noted that some relatively "advanced" lineages are also found there. For example, the first records of Dasypodini and Tolypeutinae armadillos occur at La Venta (Carlini et al., 1997). The general lack of similarity between the La Venta and Patagonian faunas of similar age suggests that there was little faunal exchange between the northern and southern extremes of the continent, at least during the middle Miocene. We optimistically note, however, that Stirton's (1953) original estimate of a "Friissan" age for the La Venta fauna (see Madden et al., 1997, for discussion) was within a couple million years of its actual age (13.5–11.6 Ma; Flynn et al., 1997).

Given the caveats noted above, we offer an imprecise, first-order estimate of a "Tinguirirican" to Deseadan SALMA age for the notoungulates of Santa Rosa on the basis of their comparative morphology with notoungulates of known age and on their degree of hypsodonty. Other, better represented faunal members of the Santa Rosa local fauna [e.g., marsupials (Goin and Candela, 2004) and rodents (Frailey and Campbell, 2004)] appear to constrain this age further.

CONCLUSIONS

This work records the occurrence of Paleogene-grade notoungulates from the Amazon region of eastern Peru. They include toxodonts of two distinct size classes and the first record of an interarchthere from the Amazon Basin. These notoungulates, on the basis of their degree of hypsodonty and similarity to known taxa, appear to date from the early Oligocene ("Tinguirirican" age) to the late Oligocene (Deseadan SALMA), or, in absolute terms, from about 31.5 to 24 Ma. The larger toxodont specimens share features with the early "advanced toxodontida," suggesting that they represent taxa near the base of the radiation of leontiniids, Deseadan notouhippids, and toxodontids. LACM 140569 presents characters suggestive of an advanced Pleso-temnus-like toxodont or a primitive leontid, or, curiously, both. These limited specimens cannot narrowly constrain the age of the Santa Rosa fauna, but the older end of the age estimate is close to the age estimates derived from the numerous marsupial and rodent specimens from Santa Rosa.

Although the notoungulates described in this work are fragmentary, they offer tantalizing hints of taxa unknown in the rest of the Neotropics. Given the tremendous gap in our knowledge of the taxa that gave rise to the explosive radiation of notoungulates in the Deseadan, the discovery of these Paleogene-grade notoungulates at Santa Rosa compels further exploration in tropical South America. Such endeavors have the potential to fill both the geographic and temporal gaps in our knowledge of the history of life in South America.

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LITERATURE CITED


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