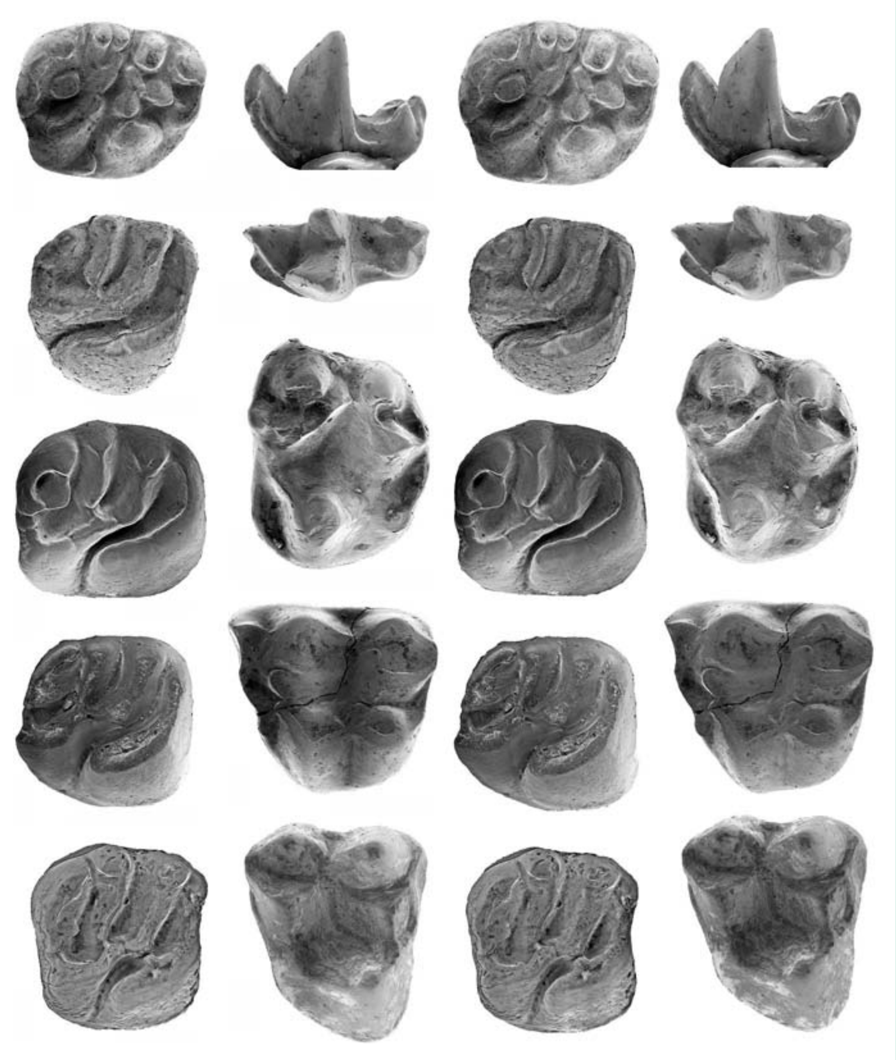
The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru

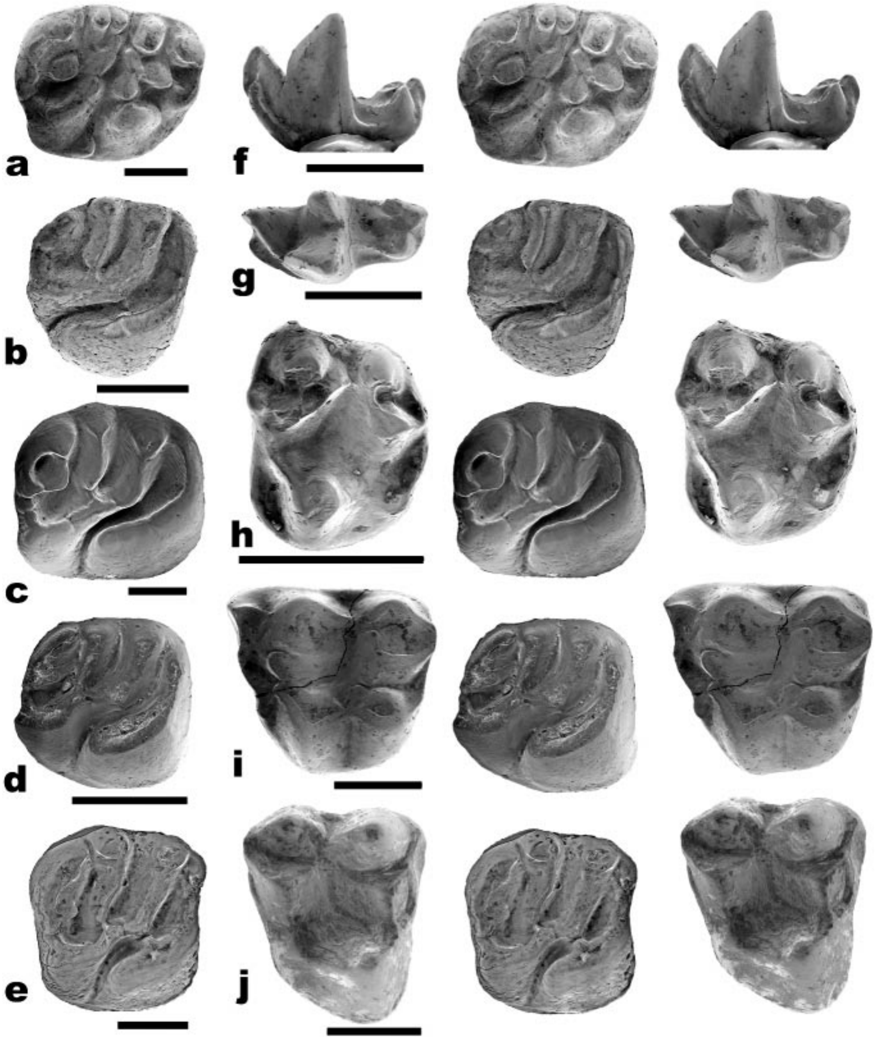
Edited By Kenneth E. Campbell, Jr.



Natural History Museum of Los Angeles County

Science Series 40 December 27, 2004

THE PALEOGENE MAMMALIAN FAUNA OF SANTA ROSA, AMAZONIAN PERU



Cover Illustration and Plate I (above): SEM stereopairs of representative molar teeth of new genera and species from Santa Rosa local fauna. **a–e**, Rodents: **a–c**, family Agoutidae, three gen. et spp. nov.; **d, e** (reversed), family Echimyidae, two gen. et spp. nov. Upper left molars; anterior to right, labial at top. **f–j**, Marsupials: **f–g**, Didelphimorphia, ?Herpetotheriidae gen. et sp. nov., last lower left molar; **f**, occlusal view; **g**, labial view; **h**, Polydolopimorphia, family indet., gen. et sp. nov., upper left molar, occlusal view; **i**, Paucituberculata, Caenolestidae gen. et sp. nov., upper left molar, occlusal view; **j**, Polydolopimorphia, family Prepidolopidae, gen. et sp. nov., right upper molar. Scale bars = 1 mm.

THE PALEOGENE MAMMALIAN FAUNA OF SANTA ROSA, AMAZONIAN PERU

Edited By
Kenneth E. Campbell, Jr.

NO. 40
SCIENCE SERIES
Natural History Museum
of Los Angeles County

Natural History Museum of Los Angeles County
Los Angeles, California 90007
ISSN 1-891276-27-1
Published on 27 December 2004
Printed in the United States of America

PREFACE

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 Tinguiririca faunas of Chile; formal recognition of a Tinguiririca 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 paleonotology 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 perspectivies 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 Geológico, Minéro, y Metalúrgico (INGEMMET) of Peru, and especially Ing. Hugo Rivera Mantilla, Director Técnica of INGEMMET, and Ing. Oscar Palacios, Director General de Geología 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 Frailey 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.
August 2004
Los Angeles, California

CONTENTS

The Paleogene Santa Rosa Local Fauna: Introduction 1
Kenneth E. Campbell, Jr.

The Paleogene Santa Rosa Local Fauna of Amazonian Perú: Geographic and Geologic Setting 3
Kenneth E. Campbell, Jr., Carl David Frailey, and Lidia Romero-Pittman

New Paleogene Marsupials from the Amazon Basin of Eastern Perú 15
Francisco J. Goin and and Adriana M. Candela

Paleogene Notoungulates from the Amazon Basin of Peru 61
Bruce J. Shockey, Ralph Hitz, and Mariano Bond

Paleogene Rodents from Amazonian Peru: The Santa Rosa Local Fauna 71
Carl David Frailey and Kenneth E. Campbell, Jr.

Incisor Enamel Microstructure of South America's Earliest Rodents: Implications for Caviomorph Origin and Diversification 131
Thomas Martin

A Possible Bat (Mammalia: Chiroptera) from the ?Eocene of Amazonian Perú 141
Nicholas J. Czaplewski and Kenneth E. Campbell, Jr.

Enigmatic Mammal from the Paleogene of Perú 145
Francisco J. Goin, Emma Carolina Vieytes, María Guiomar Vucetich, Alfredo A. Carlini, and Mariano Bond

The Santa Rosa Local Fauna: A Summary 155
Kenneth E. Campbell, Jr.

Science Series, Number 40, pp. 1–163
Natural History Museum of Los Angeles County, 2004

The Paleogene Santa Rosa Local Fauna: Introduction

Kenneth E. Campbell, Jr.[1]

The physiographic region known as lowland Amazonia comprises approximately 40 percent of the South American continent. Yet, prior to the discovery of the Santa Rosa local fauna of eastern Peru, absolutely nothing was known of the fauna that inhabited this portion of the continent in the Paleogene. Although the eastern Amazonian lowlands of Peru are known to have numerous paleontological sites containing vertebrates, some of which have produced some major paleontological surprises (e.g., Willard, 1966; Frailey, 1986; Kay and Frailey, 1993; Campbell et al., 2000), these sites all date from the Neogene. Remarkably, because of the diversity of the mammalian taxa represented in the collection from Santa Rosa and the abundance of specimens of so many of the taxa in the paleofauna, an exceptionally good first picture of mammalian life during the slice of time represented by the Santa Rosa local fauna has emerged. Although still incomplete, this picture provides us with a wealth of data about certain groups of mammals. In time, as we secure more specimens, the nonmammalian vertebrates are studied, and we better understand the data available, the Santa Rosa local fauna will provide much crucial information for paleoecological reconstructions of the Paleogene of Amazonia.

To many, perhaps the most surprising aspect of Amazonian vertebrate paleontology is that there are *any* fossils to be found in these vast tropical lowlands. This attitude may well be derived from the false assumption that fossils are not to be found in tropical areas, which is based in large part, perhaps, on the erroneous assumption that fossils are not preserved under tropical conditions. This line of reasoning ignores the fact that many of western North America's fossiliferous lower Tertiary sites were formed in tropical settings. The only difference is that today the Amazon Basin is covered with tropical vegetation, whereas western North America now encompasses many arid and semiarid regions where extensive rock exposures are common, long stratigraphic sections are exposed, and fossils can be found with relative ease. In lowland Amazonia, outcrops are found only along river cutbanks and good exposures are few. Nonetheless, fossil vertebrates are fairly common in certain formations underlying the thick cover of tropical vegetation of modern Amazonia.

In the tropical lowlands of western Amazonia, two factors make paleontological investigations possible. The first is that most of western Amazonia has undergone slight, broadscale uplift as a consequence of the latter phases of the Andean Orogeny, and a few limited areas have seen significant local folding and faulting as well. The overall uplift has not been great, averaging perhaps only a few tens to a hundred meters, but it has facilitated exposure of Neogene deposits throughout the region. Older deposits are exposed in more limited areas, where local uplift has exceeded several hundred meters. In some instances, the entire Tertiary sequence may crop out along rivers crossing anticlinal structures formed during late Tertiary/Quaternary uplift in western Amazonia (Kummel, 1948). This is because of the fairly shallow depth to underlying basement rock and the relatively unconsolidated nature of the Tertiary sediments. The largest of these uplifted areas is the Sierra de Divisor, a narrow, folded and faulted zone that extends over a linear distance of about 240 km along the border region between Peru and Brazil. The Santa Rosa locality was found within this structural zone.

The second factor is that, because of the establishment of the modern Amazonian drainage system in the late Neogene, the rivers in the region flow in entrenched valleys. This means that when the rivers come into contact with the sides of their valley, they usually form cutbanks where one can observe the stratigraphic column and where fossiliferous deposits are exposed. The height of the cutbanks in the valley walls varies considerably, but it seldom exceeds 80 m. Cutbanks are difficult to work because they are often nearly vertical, but in many areas, broad shelves occur near the waterline during the low water periods of the dry season.

The common image of the Amazon Basin as a vast, waterlogged swampland is highly overrated, and mostly erroneous, because the areas subjected to flooding are almost all within the entrenched river valleys of the basin and approximately 80 percent of the basin is never flooded. The fact that there are large areas subject to flooding is a result of the large size of many of the Amazonian rivers and because these rivers have formed large floodplains in broad valleys carved into largely unconsolidated sediments. In Amazonia, larger rivers inevitably have broader floodplains, which results in fewer cutbanks into older rock formations on the sides of the valley. More exposures of valley walls per river kilometer are to be found in the smaller rivers and headwater streams that have very small or no floodplains because their channels have yet to reach base level and they are constantly cutting into the rock formations that form the valley sides. Unfortunately, these rivers are logistically the most

---

[1] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: kcampbel@nhm.org

Science Series, Number 40, pp. 1–2
Natural History Museum of Los Angeles County, 2004

difficult to work because they shallow rapidly during the dry season and are subject to blockage by tree falls, both factors that can make them impassable.

The Santa Rosa local fauna was discovered in July 1995 in a cutbank of only a few meters height along the Río Yurúa, Perú (Río Juruá in Brazil) (Campbell et al., 1996). About 400 kg of sediments were screen-washed as a test that year, using ordinary fiberglass window screen. The concentrated matrix produced hundreds of microvertebrate specimens. A return visit to the Santa Rosa locality in 1998 resulted in a much larger sample. Only a small portion of the matrix from that expedition has been picked for microfossils, but that portion has proven to be as productive as the 1995 sample. The remainder of that matrix will undoubtedly yield thousands of specimens. However, the small particle size of this matrix, all of which is less than 4 mm diameter, precludes finding additional mammalian specimens bearing more than a single tooth, except for possibly the very smallest of the taxa represented. There will undoubtedly be additional reports of new mammalian taxa from the Santa Rosa local fauna in the future, but it is probably fair to say that they will represent the rarer, although potentially more interesting, components of the paleofauna.

The Santa Rosa local fauna contains a few large vertebrates, represented mostly by bone fragments, but its significance lies in its rich and diverse microfauna. Although mammals are the thrust of the collection of papers presented in this volume, fish, amphibians, reptiles, and birds are also present in the microfauna. The majority of the taxa present are represented only by isolated teeth, but they nonetheless give us a very informed first glimpse of an early Tertiary, low latitude, tropical vertebrate fauna of South America.

The most abundant, and probably diverse, of all the vertebrates are the fish. At least five families are present (J. Lundberg, personal communication), represented by thousands of small to tiny teeth. The fish fauna is being described separately and will undoubtedly provide important information for paleoecological reconstruction at the site. Reptiles are represented by crocodilians, turtles, and possibly lizards. There are many hundreds of small, isolated teeth of crocodilians of various types, and they represent the second most common group of vertebrates in the paleofauna, after the fish. Unfortunately, these numerous teeth cannot be identified to species, so they do not provide more than general information on environmental conditions. Isolated turtle osteoscutes are not uncommon in the paleofauna, but they are also insufficient for identification. A few fossil specimens are considered to be possible lacertilian jaws, but as yet, they have not been studied. The rarest vertebrates in the paleofauna are amphibians and birds. Both of these latter groups are to date represented by fewer than a dozen specimens, and, unfortunately, these are too fragmentary to provide taxonomic characters that would assist in identification. That both groups are represented, however, does indicate the breadth of the fauna preserved at Santa Rosa and its potential for preserving additional components of the mammalian paleofauna not yet identified.

The only invertebrate fossils found at Santa Rosa to date are crab claws, probably of taxa belonging to the family Pseudothelphusiidae (J. Martin, personal communication). These fossils are fairly abundant and display a wide size distribution. Charophytes are also reported to occur in the deposits at Santa Rosa (M. Aldana, personal communication; personal observation), but they have not been described in the literature.

The papers in this volume describe the mammalian portion of the Santa Rosa local fauna; its importance for understanding early Tertiary mammalian faunas of low latitude, tropical South America; and, on a larger scale, its significance to our understanding of mammalian evolution in the early Tertiary in South America. This research would not have been possible without the enthusiastic cooperation and participation of our Peruvian colleagues at the Instituto Geológico, Minéro, y Metalúrgico (INGEMMET). On behalf of all the authors in this volume, I thank them. To facilitate the research on the Santa Rosa local fauna, specimens have been catalogued into the collections of the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County. Following completion of the research on the Santa Rosa local fauna, all holotypes and representative series of all taxa will be returned to Peru.

LITERATURE CITED

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 1996. The first Paleogene fauna from the Amazon Basin and its bearing on the first occurrence of rodents in South America. *Journal of Vertebrate Paleontology* 16(3)(Suppl.):25A.

———. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: Implications for the Great American Faunal Interchange. *Instituto Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín* 23:1–152.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Río Acre region, western Amazonia. *Contributions in Science* 374:1–46.

Kay, R.F., and C.D. Frailey. 1993. Large fossil platyrrhines from the Rio Acre local fauna, late Miocene, western Amazonia. *Journal of Human Evolution* 25:319–327.

Kummel, B. 1948. Geological reconnaissance of the Contamana Region, Peru. *Geological Society of America, Bulletin* 59:1217–1265.

Willard, B. 1966. *The Harvey Bassler collection of Peruvian fossils*. Bethlehem, Pennsylvania: Lehigh University, 255 pp.

Received 2 July 2003; accepted 29 December 2003.

The Paleogene Santa Rosa Local Fauna of Amazonian Perú: Geographic and Geologic Setting

Kenneth E. Campbell, Jr.,[1] Carl David Frailey,[2] and
Lidia Romero-Pittman[3]

ABSTRACT. The Santa Rosa local fauna of eastern Perú is the first low-latitude, low-elevation, early Tertiary vertebrate paleofauna known for the tropical regions of South America. The paleofauna is derived from coarse-grained fluvial deposits within the massive series of clay-dominated continental red beds of eastern Perú. Here, we summarize the geologic history and rock formations of the western Amazon Basin and describe the geologic features of the Río Yurúa and the locality where the Santa Rosa local fauna was found. The age of the Santa Rosa local fauna is estimated as late Eocene on the basis of the stage of evolution of the marsupials and rodents in the fauna. This age is consistent with that of the Paleocene–Eocene Yahuarango Formation, one of the oldest of the continental red beds of eastern Perú.

RESUMEN. La fauna local de Santa Rosa, del Perú oriental, es la primera paleofauna mamífera del Terciario temprano de baja latitud y baja elevación conocida para las regiones tropicales de Sudamérica. Aquí la historia geológica y las formaciones rocosas del oeste de la cuenca Amazonica son resumidas y las características geológicas del Río Yurúa y de la localidad de Santa Rosa son descritos. La edad estimada de la fauna local de Santa Rosa es eoceno tardío basado en el estado de evolución y la combinación de taxa presentes en la fauna. Una edad eoceno conforme a la edad paleoceno–eoceno de la Formación Yahuarango, una de las mas antiguos de las capas rojas continentales del Perú oriente.

INTRODUCTION

The Santa Rosa local fauna of eastern Perú is the first Paleogene vertebrate fauna known from the tropical lowlands of the Amazon Basin (Campbell et al., 1996). Unfortunately, a significant factor limits our placement of the Santa Rosa paleofauna into an overall scheme for the evolutionary development of the South American vertebrate fauna: we cannot place the paleofauna within a stratigraphic context with any great degree of certainty. The requisite geologic data that would facilitate dating of the fauna are just not currently available for the remote region in which the Santa Rosa locality lies. It might even be argued that the historic lack of Paleogene vertebrate faunas from the lowland tropical regions of South America has contributed to the overall lack of detailed knowledge about the geologic evolution of the Amazonia. We include here a brief summary of the geologic history of eastern Perú because the region may be unfamiliar to many. This also allows us to place the discussion of the geology of the Río Yurúa into a broader regional context. The stage of evolution of the most abundant mammalian taxa provides an approximate age for the fauna, and from that point, we discuss the possible stratigraphic context of the Santa Rosa local fauna.

GEOGRAPHIC SETTING

The Santa Rosa locality occurs on the left bank of the Río Yurúa, at 9°29′39″ S, 72°45′48″ W (Fig. 1), Provincia Atalaya, Departamento de Ucayali, Perú. The site is approximately 7.0 km (by air) north of the small community and army post of Breu (also known under the older name of Tipishca), approximately 7.5 km (by air) due south of the Perú–Brazil border, and 230 km (by air) east-southeast from Pucallpa (on the Río Ucayali), the closest Peruvian city of any size. The elevation of the airstrip at Breu is approximately 235 m above mean sea level, whereas the elevation at the Santa Rosa locality is estimated to be approximately 215 m above mean sea level on the basis of Sheet 2352 [Santa Rosa] of the Perú 1:100,000 topographic series. The fossil

---

[1] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: kcampbel@nhm.org

[2] Johnson County Community College, Overland Park, Kansas 66210; Museum of Natural History, University of Kansas, Lawrence, Kansas 66045; Research Associate, Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: cfrailey@jccc.net

[3] Instituto Geológico, Minéro, y Metalúrgico (INGEMMET), Av. Canadá 1470, San Borja, Apartado 889, Lima 41, Perú. Email: lromero@ingemmet.gob.pe

Science Series, Number 40, pp. 3–14
Natural History Museum of Los Angeles County, 2004

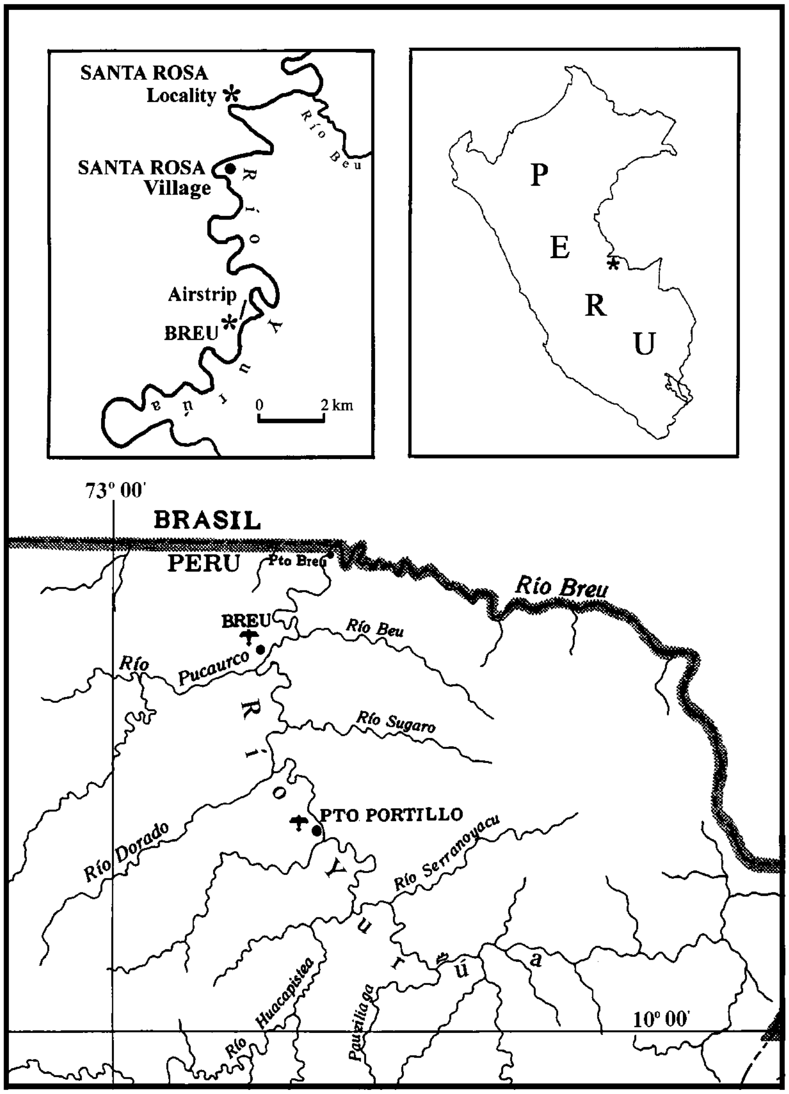


Figure 1 Map showing the location of the Santa Rosa fossil locality in eastern Perú. **Inset. Upper left:** map showing the Santa Rosa locality on a detailed outline of the Río Yurúa river channel as it appears on the Perú 1:250,000 Río Torolluc map, 1984, based on LANDSAT imagery. **Inset. Upper right:** map of Perú, showing location of lower map.

locality takes its name from the small village of Santa Rosa, which is located on the right bank of the river 2.0 km due south of the locality and between the locality and the community of Breu farther upriver (Fig. 1). It should be noted that on Sheet 2352 [Santa Rosa] (first edition; undated) and on the corresponding geologic map, the village of Santa Rosa is misplaced. It is mapped on the curve of the river exposing the Santa Rosa locality, on the bank opposite the locality, but it should be mapped 2.0 km due south. Another anomaly is that on both the 1995 and 1998 expeditions, our GPS unit placed the locality at 9°29′39″ S, but calculating the latitude from Sheet 2352 [Santa Rosa] places the locality at 9°28′39″ S. We cannot explain the one minute difference, and we do not know which is the correct figure.

LOCALITY DESCRIPTION

The fossiliferous deposits occur in a long (>100 m) cut bank. About 5 m of red clay (thickness dependent on river level) are unconformably overlain by unconsolidated, buff sands (Figs. 2, 3). Above the sands, which appear to be of fairly recent origin and probably represent terrace deposits, the forested riverbank slopes steeply away from the river to a higher terrace level. The fossiliferous horizons are

Figure 2 View of the Santa Rosa fossil locality from the east. A coarse-grained fossiliferous lens can be seen at the feet of C. Frailey (left) and J. Wigmore (opening sample bag). The primary site of the locality is located near the west end of the outcrop, approximately over the head of Wigmore. The top of the Yahuarango Formation can be seen at the shoulder level of L. Romero-Pittman (walking on right).

a number of small fluvial deposits, which we interpret as bed load deposits (Figs. 4, 5), composed of coarse sand of mixed composition, calcareous nodules, and small clay pebbles. The largest fossils present are turtle shell fragments and fragments of larger vertebrate limb bones. The coarse fluvial deposits lie in horizons, or lenses, that are all less than 30 cm thick, are of variable lengths, and, in the outcrop, usually feather out laterally. These lenses, and particularly the longer, more pebbly horizons that can be meters in length, slope from left to right across the face of the outcrop (Figs. 3, 4). Whether this slope reflects the original slope of deposition or is the result of uplift is unknown. The lenses may be closely stacked vertically, or they may occur as quite isolated lenses in the mass of red clay. On the left side of the outcrop, a number of the lenses end abruptly, as if at a fault, or at the edge of a large, subsequent paleochannel incision (Fig. 3). The small area exposed and the lack of detailed geologic data for the region make interpretation of structural geology at the site difficult.

The fossils from Santa Rosa are *in situ* and show no signs of being reworked. It is unlikely that the many small, fragile dentigerous mandibles and maxillae could have withstood reworking, and many of the delicately edged, isolated microfossils show no wear. In addition, many of the microclasts and microfossils show signs of having undergone extreme shear stresses that resulted in many visible fractures, especially in the microclasts (Fig. 6) and the mammal teeth, as can be seen in photographs of specimens in the papers that follow. Many of the clasts (e.g., Figs. 6A–B) have intersecting planes of fractures that can be interpreted to delineate the greatest principal stress axis. As a consequence of these fractures, and because there was no subsequent natural cementation at the fracture sites, in the process of recovery many of the fossils break into fragments following fracture lines, just as they would have broken had they been reworked in transport from deposits in higher terrain. The fracturing of the clasts and fossils indicate that the fossiliferous beds must have been subjected to extreme pressure, most probably resulting from the multiple phases of tectonism that gave rise to the Andes (see "Geologic Setting"). The presence of similar microfractures has not been observed in any of the Miocene microfaunas we have obtained from Amazonia.

GEOLOGIC SETTING

GEOLOGY OF EASTERN PERÚ

The modern Amazon Basin formed as a consequence of the Andean Orogeny, a series of orogenic episodes that began in the Cretaceous (Mégard, 1984, 1987; Sébrier and Soler, 1991). These epi-

Figure 3 The most thoroughly sampled portion of the Santa Rosa locality as seen from across the Río Yurúa. The slightly sloping conglomeratic lenses that bear the fossils stand out in relief against the surrounding clays in the center and toward the right of the photograph. The lenses terminate abruptly on the left, either at a fault or at the edge of a large paleochannel. The top of the Yahuarango Formation is near the top of the photograph (in shadows).

sodes were a result of the subduction of the Nazca Plate under the western continental margin of South America as the continent moved westward, away from Africa. As the Western Cordillera of the Andes began to emerge in the Cretaceous, a flood of clastic sediments began accumulating in the broad area between the shield rocks of the Brazilian and Guianian highlands and the rising Andes. The estimated thickness of the accumulated Tertiary deposits varies from 1700 to 2000 m (Jenks, 1956;

Figure 4 A view of the primary fossiliferous portion of the Santa Rosa locality, including the cleft seen in the right of Figure 3. The top of the Yahuarango Formation is at the top of this photograph. Note the decrease in the quantity of the conglomeratic lenses to the right. The water level in this view is about 1 m higher than in Figure 3, covering the shelf seen in the latter figure.

Figure 5 A close-up of the excavated face of the outcrop reveals that, in this area, the conglomeratic lenses are dominant over the pure clay horizons, one of which is seen directly above the scale running across the width of the photograph. This view is of a small area just to the left of the cleft in the right of Figure 3, where the conglomeratic lenses appear to be quite thick.

Rüegg, 1956) to 10,000 m (Campbell and Bürgl, 1965). Kummel (1948) gives a thickness of about 3000 m for the post-Cretaceous Contamana Group in north central Perú, which includes all but the very youngest of the Tertiary formations. The Tertiary deposits thin eastward as they overlap the basement rocks of the Brazilian shield. The Peruvian Andes appear to have experienced six relatively short phases of compression as the subducting plate squeezed the continental crust against the shield rocks (Mégard, 1984, 1987; Sébrier and Soler, 1991). Each new phase saw the zone of compression move eastward as the continental crust was shortened, with the last major compressional phase, which formed the Sub-Andean Thrust and Fold Belt, occurring during the late Miocene (~7 Ma; the Quechua III phase of Mégard, 1984; Pardo, 1982).

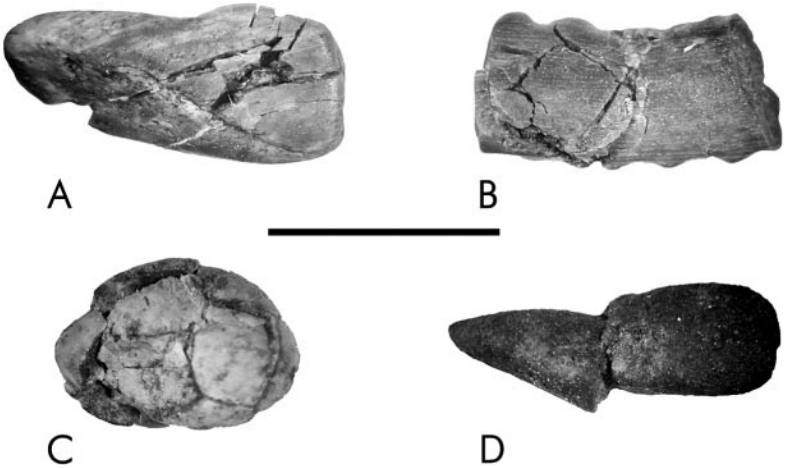


Figure 6 A high-pressure environment resulted in the fracturing of many microclasts and mammal teeth found in the fossiliferous horizons of the Yahuarango Formation. **A,** Well-rounded bone fragment; **B,** fish spine; **C,** possible seed; **D,** elongated pebble. Scale = 5 mm.

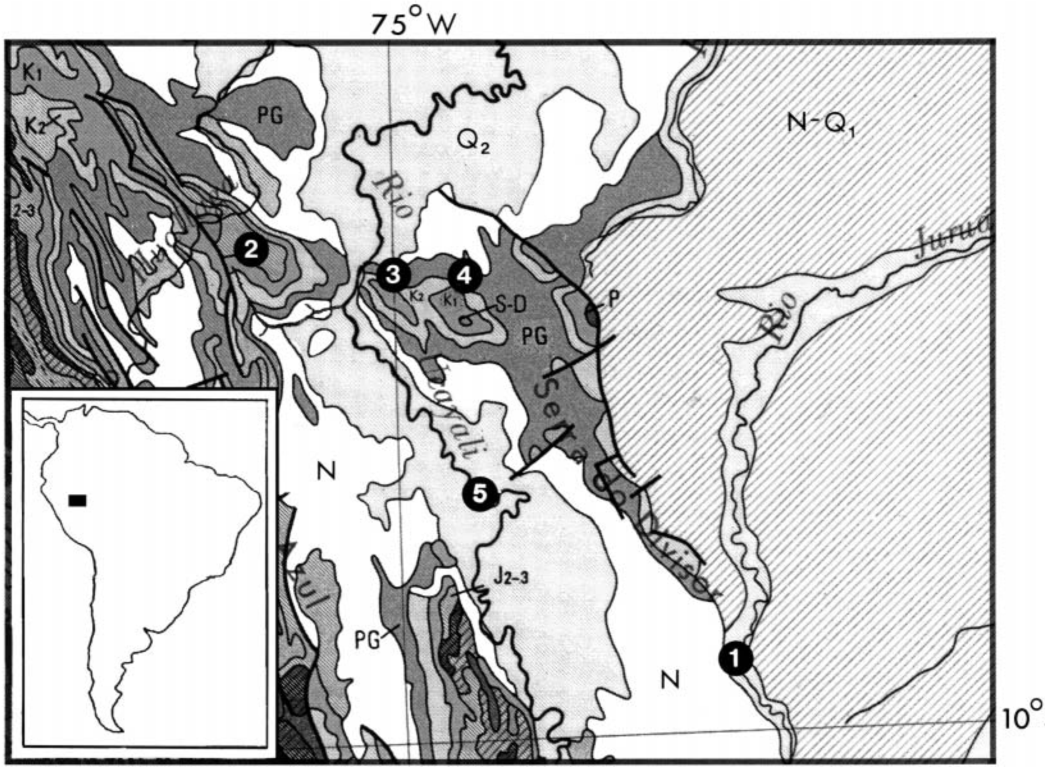


Figure 7 Geologic map of a portion of the western Amazon Basin and the Eastern Cordillera of Perú showing location of the Santa Rosa locality (**1**) on the Río Yurúa (Río Juruá in Brazil). The Cushabatay (**2**) Mountains form the spur of the Eastern Cordillera leading into the Contamana (**3**) and Contaya (**4**) Mountains and the Sierra de Divisor. The anticlinal structure of the long, folded and faulted belt running east-southeast from the Eastern Cordillera is clear, although the map is not particularly detailed because of its scale. The city of Pucallpa (**5**) is on the Río Ucayali. Geologic units identified on this map: J_{2-3} = Jurassic, K_1 and K_2 = Cretaceous, N = Neogene, Q_1 = Pleistocene, Q_2 = Holocene, P = Permian, PG = Paleogene, S-D = Silurian/Devonian. Adapted from Choubert and Faure-Muret (1976).

The last major marine incursion into Amazonian Perú from the Pacific occurred in the Oligocene and resulted in the deposition of the Pozo Formation. The lowland connection between the Amazon Basin and the Pacific Ocean through which this marine incursion passed, and which probably served for the later westward drainage of the basin, is generally assumed to have been closed in the Miocene, although there are no data that bear on the actual time of closure. The most likely time for this event was during uplift of the Eastern Cordillera during the latter part of the Quechua I phase of the Andean orogeny [bracketed between 20 and 12.5 Ma by Mégard (1984, 1987); placed at 25–17 Ma by Noble et al. (1990)] or, less likely, early in the Quechua II phase [placed at 12–8 Ma in northern Perú by Noble et al. (1990) and at 9.5–8.5 Ma by Mégard (1984, 1987)]. The closure of the western connection may have created a freshwater "interior sea" within the basin (Putzer, 1984), with drainage northward into the Caribbean until the eastward drainage pattern of the Amazonian river system was established (Hoorn et al., 1995). During the late Tertiary the Amazon Basin was never far above sea level, and transgressions of marine/brackish water from the Caribbean region may have reached central Amazonia in the Miocene, and possibly even in the Pliocene (Ihering, 1927; Sheppard and Bate, 1980; Nuttall, 1990; Hoorn, 1994; Räsänen et al., 1995). Sedimentation within lowland Amazonia is currently very limited (Dumont et al., 1990; personal observation), with most modern rivers flowing in entrenched valleys.

In addition to the Sub-Andean Thrust and Fold Belt, several anticlinal and domal structures in the Andean Foreland Basin of eastern central Perú were uplifted during the late Miocene Quechua III phase of the Andean orogeny (Pardo, 1982; Mégard, 1984), and most of these uplifted areas occur in a fairly narrow, curving structural zone extending east-southeast from the Eastern Cordillera (Fig. 7). The northernmost structural feature that forms part of this structural zone is a spur of the Eastern Cordillera, the Cushabatay Mountains. The Contamana and Contaya Mountains, separated from the Cushabatay Mountains by the Río Ucayali, continue the structural zone southeastward and form the connecting link to the Sierra de Divisor. The Sierra de Divisor is a long group of narrower anticlinal structures that run south-southeastward and that form the basis of the border between Perú and Brazil for a distance of almost 240 km. These structures are fault bounded, in part, on their eastern flanks, and transverse faulting has also been reported. Portions of these uplifted areas remain today as topographic highs in the Amazonian lowlands. Cretaceous strata are reported to crop out where the tops of some of these structures have been eroded away (e.g., Kummel, 1948; Valenzuela and Zavala, 1998), and rare instances of even older rocks are recorded (Fig. 7). On the geologic map of Perú (INGEMMET, 1975), the Santa Rosa locality is located about 50 km south of the mapped limit of the series of uplifted anticlinal structures that comprise the Sierra de Divisor. However, ONERN (1980) and Valenzuela and Zavala (1998) describe Paleogene strata closer than 50 km from the Santa Rosa area.

Almost all of the Tertiary deposits of western Amazonia are referred to as the "Capas Rojas," or "red beds," and four formations of red beds are recognized in Perú. Of these, three [the Huchpayacu Formation (Cretaceous–?Paleocene), the Yahuarango Formation (Paleocene–Eocene), and the Chambira Formation (Miocene) (Fig. 8)] are all similar in that they are lithologically monotonous, consisting of alternating beds of sands, silts, mudstones, unconsolidated clays, and occasional evaporites. Stratification is irregular, with abundant cross-bedding, channeling, and lenticulation (Rüegg, 1947, 1956; Kummel, 1948). There is little size sorting of the clasts, which are mineralogically heterogeneous and unaltered, suggesting both an Andean origin and rapid deposition. This interpretation is reinforced by an overall decrease in clast size to the east. Despite the gross similarities among these formations, Rüegg (1947, 1956) states that, with experience, the lower Tertiary (Paleogene), or pre-Pozo Formation, red beds can be distinguished in the field from the upper Tertiary (Neogene), or post-Pozo Formation, red beds. We have also arrived at this conclusion.

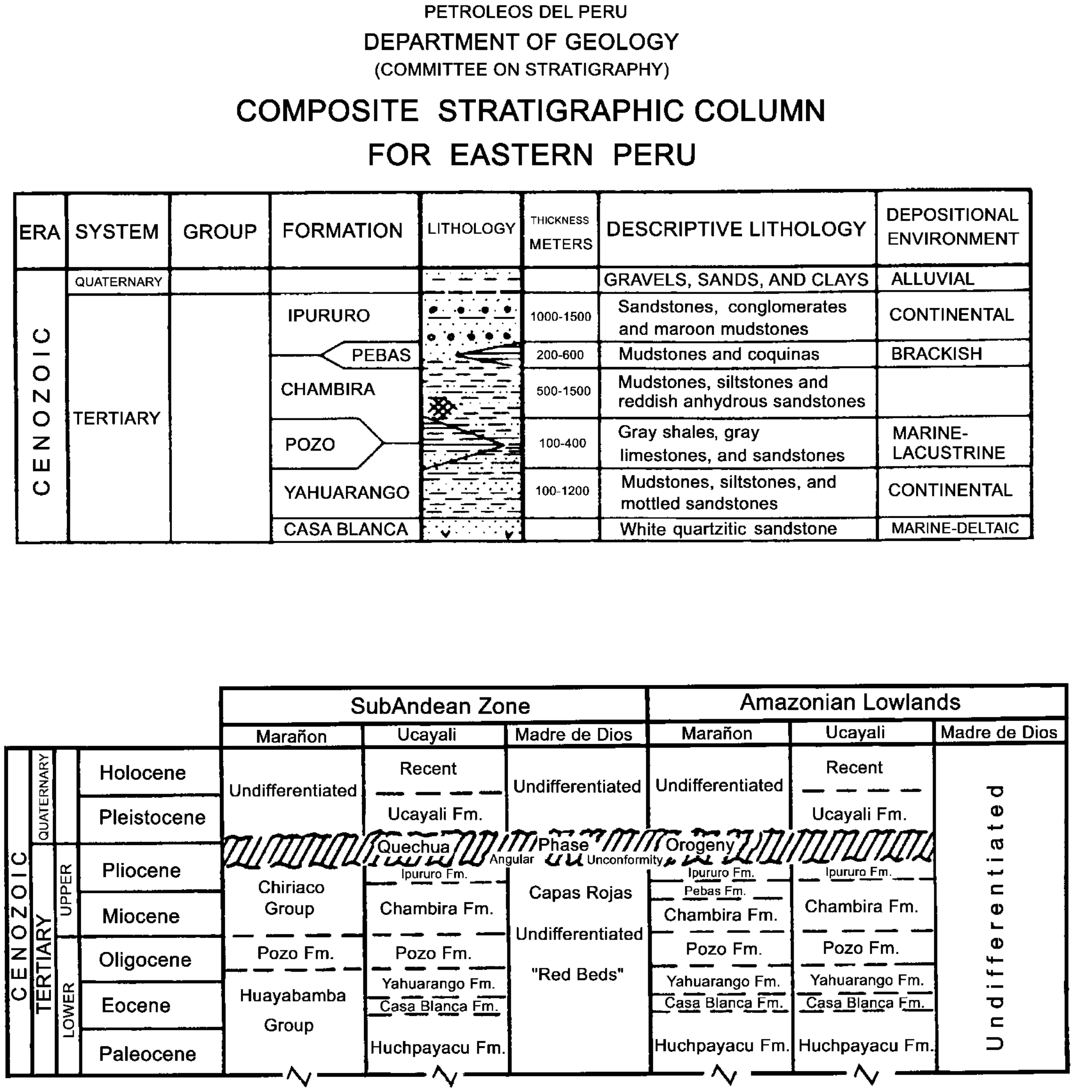
A fourth "red bed" formation is the Miocene Ipururo Formation, the lithologic characteristics of which set it off from the three older red bed formations (Kummel, 1948). There is a possibility that the lithologic change between the red beds of the Chambira Formation and those of the more variable, darker sediments of the younger Ipururo Formation is a result of the blockage of the westward flow of the Amazonian drainage and its reorganization into a northward, and, later, west- to east-flowing drainage system, but this remains to be confirmed. This suggestion assumes that the drainage reorganization would have dramatically affected environments of deposition within the basin.

Two key lower Tertiary formations (Pardo and Zuñiga, 1976) occur within the red bed sequence and serve as markers to separate the red bed formations in many areas in northern and eastern Perú. The first of these marker beds is the Casa Blanca Formation (Kummel, 1948), which consists of about 60 m of massive, white, quartzose sandstones at its type locality. This formation is of uniform lithology, has a wide areal distribution in eastern Perú, and separates the upper Cretaceous–?Paleocene Huchpayacu Formation and the Paleocene–Eocene Yahuarango Formation. The Casa Blanca Formation signifies a period when the source area for sediments being deposited in western Amazonia shifted from the emerging Andes to the eastern Brazilian shield. This formation is considered essentially isochronous because it is rather thin, but a reliable age for this unfossiliferous formation has not been established.

The second key formation is the ?Eocene–Oligocene Pozo Formation (Williams, 1949), a 400-m-thick marine sequence at the type locality, with fossils of foraminiferans, ostracodes, and marine mollusks. This formation separates the Paleocene–Eocene Yahuarango Formation from the Miocene Chambira Formation. It is well known from Ecuador south to Yurimaguas, Perú (Pardo and Zuñiga, 1976), and it has been identified in well cores in the Río Ucayali valley (Martínez, 1975). However, it is less well known farther to the southeast, and it was not reported in the Santa Rosa area by ONERN (1980) or Valenzuela and Zavala (1998). As pointed out by Flynn and Swisher (1995), there are few instances in the Cenozoic of South America where fossiliferous marine strata intertongue with fossiliferous terrestrial sequences; thus, this important means of dating strata and correlating among disparate regions is seldom available.

Although the sequence of Tertiary formations in eastern Perú is fairly well known, the lack of numerical age dates for most of these formations remains a problem for interpreting the ages of their contained faunas. This problem becomes clear when comparing the stratigraphic charts of Guizado (1975) (Fig. 8), Pardo and Zuñiga (1976) (Fig. 8), and Valenzuela and Zavala (1998) (chart not included here), and when comparing these charts with the age assignments of Kummel (1948) for the formations of eastern Perú. There are datable sequences within these older strata (Kummel, 1946; Rüegg, 1947, 1956), but to our knowledge there have been no efforts to date them by modern radiometric methods. Securing numerical age dates for stratigraphic horizons near the key marker formations is necessary for anchoring the stratigraphic column of eastern Perú and for resolving conflicting interpretations related to the chronologic occurrence of these beds. The only numerical age dates for strata of lowland Amazonia are those of Campbell et al. (2001), and these pertain only to the youngest of the Neogene strata.

On the basis of the stage of evolution of the marsupials and rodents, the age of the Santa Rosa local fauna is placed at ?Eocene [Mustersan South Amer-



PETROLEOS DEL PERU
DEPARTMENT OF GEOLOGY
(COMMITTEE ON STRATIGRAPHY)

COMPOSITE STRATIGRAPHIC COLUMN
FOR EASTERN PERU

ERA	SYSTEM	GROUP	FORMATION	LITHOLOGY	THICKNESS METERS	DESCRIPTIVE LITHOLOGY	DEPOSITIONAL ENVIRONMENT
CENOZOIC	QUATERNARY					GRAVELS, SANDS, AND CLAYS	ALLUVIAL
	TERTIARY		IPURURO		1000-1500	Sandstones, conglomerates and maroon mudstones	CONTINENTAL
			PEBAS		200-600	Mudstones and coquinas	BRACKISH
			CHAMBIRA		500-1500	Mudstones, siltstones and reddish anhydrous sandstones	
			POZO		100-400	Gray shales, gray limestones, and sandstones	MARINE-LACUSTRINE
			YAHUARANGO		100-1200	Mudstones, siltstones, and mottled sandstones	CONTINENTAL
			CASA BLANCA			White quartzitic sandstone	MARINE-DELTAIC

				SubAndean Zone			Amazonian Lowlands		
				Marañon	Ucayali	Madre de Dios	Marañon	Ucayali	Madre de Dios
CENOZOIC	QUATERNARY		Holocene	Undifferentiated	Recent	Undifferentiated	Undifferentiated	Recent	Undifferentiated
			Pleistocene		Ucayali Fm.			Ucayali Fm.	
				Quechua Phase Orogeny Angular Unconformity					
	TERTIARY	UPPER	Pliocene	Chiriaco Group	Ipururo Fm.	Capas Rojas	Ipururo Fm. Pebas Fm.	Ipururo Fm.	
			Miocene		Chambira Fm.	Undifferentiated	Chambira Fm.	Chambira Fm.	
		LOWER	Oligocene	Pozo Fm.	Pozo Fm.	"Red Beds"	Pozo Fm.	Pozo Fm.	
			Eocene	Huayabamba Group	Yahuarango Fm. Casa Blanca Fm.		Yahuarango Fm. Casa Blanca Fm.	Yahuarango Fm. Casa Blanca Fm.	
			Paleocene		Huchpayacu Fm.		Huchpayacu Fm.	Huchpayacu Fm.	

Figure 8 These two charts illustrate the recognized Cenozoic stratigraphic column in eastern Perú. The two key marker beds—the white sandstone Casa Blanca Formation and the marine Pozo Formation—are seen to bracket the Paleocene–Eocene Yahuarango Formation, although this is clearly the case only in the northern portion of the Ucayali Valley. The age of the Santa Rosa local fauna, on the basis of taxa present and their stage of evolution, is estimated to be Eocene, which would place the fossiliferous deposit within the Yahuarango Formation. **Above,** adapted from Guizado (1975). **Below,** adapted from Pardo and Zuñiga (1976). (Both translated from Spanish).

ican Land Mammal Age (SALMA) (see Campbell, 2004)]. If this age estimation is correct, it can be hypothesized that the fauna must come from the Yahuarango Formation, which lies between the two key marker formations cited above. Although Pardo and Zuñiga (1976) illustrate the Yahuarango Formation as passing from the mid-Eocene into the Oligocene, Guizado (1975) suggested that deposition of the overlying Pozo Formation was initiated in the late Eocene, thereby limiting the Yahuarango Formation to the Eocene. Cruz et al. (1997) also dated the Pozo Formation to the Eocene on the basis of its abundant microfossils. Cruz et al. (1997) assigned a Paleocene age to the Yahuarango Formation on the basis of the presence of age-indicative charophytes, whereas Valenzuela and Zavala (1998) suggested an age of upper Maestrichtian to mid-Eocene. Thus, primarily on the basis of microfossil data unknown to earlier workers, more recent authors have tended to assign an older age to the Yahuarango Formation.

Termination of deposition of the Pozo Formation and the beginning of deposition of the Chambira Formation is placed at about the Oligocene–Miocene boundary (Martinez, 1975; Pardo and Zuñiga, 1976; Cruz et al., 1997). If this age assignment is correct, the Chambira Formation is far too young to host the Santa Rosa local fauna.

One difficulty in referring the Santa Rosa locality to the Paleocene–Eocene Yahuarango Formation with complete confidence is that if the Pozo Formation does not occur as far southeast as the Santa Rosa locality, then the fossiliferous deposits there might have been deposited contemporaneously with the Pozo Formation as a continuation of the Yahuarango Formation into the Oligocene, or as an older portion of the Chambira Formation. If this were the case, then it might be more difficult to separate the Yahuarango Formation from the overlying Chambira Formation because of lithologic similarities, and it might also be more difficult to determine the time of initiation of deposition of the Chambira Formation in southeastern Perú. Although the Pozo Formation has been reported in subsurface logs of wells drilled in the Río Ucayali valley to the west of the Santa Rosa locality at approximately the same latitude (Martinez, 1975), and Cruz et al. (1997) reported it in the Sierra de Divisor about 200 km north-northwest of Santa Rosa, we know of no data that document its distribution close to the Santa Rosa locality.

GEOLOGY OF THE RÍO YURÚA

The only published studies of the geology of the Río Yurúa are those of ONERN (1980) and Valenzuela and Zavala (1998). ONERN's (1980) geological work concentrated on geomorphology and stratigraphy, whereas that of Valenzuela and Zavala (1998) concentrated on stratigraphy with summaries of geomorphology and historical geology. We disagree with several aspects of these interpretations, as detailed below and as summarized in our generalized stratigraphic column for the region (Fig. 9).

The red beds comprising the stratigraphic sequence along the Río Yurúa were identified by ONERN (1980) as the lower Tertiary Huayabamba Formation (also known as the lower red beds, lower Capas Rojas, lower Puca, Huchpayacu Formation, and Yahuarango Formation), the upper Tertiary Chambira Formation (also known as the upper red beds, upper Capas Rojas, and upper Puca), and the Ipururo Formation. We refer to the Yahuarango Formation those strata cropping out along the Río Yurúa that ONERN (1980) referred to the lower Tertiary Huayabamba Formation and the upper Tertiary Chambira Formation.

Valenzuela and Zavala (1998) interpreted the deposits cropping out along the Río Yurúa to comprise, in their terms, the Miocene Chambira Formation, the Mio-Pliocene Ipururo Formation, and the capping Plio-Pleistocene Ucayali Formation. The Chambira Formation is described as the basal unit exposed along the river, and they include the locality of the Santa Rosa local fauna in this formation, even providing a photograph of the Santa Rosa locality (Valenzuela and Zavala, 1998; foto 16). Thus, what they refer to as the Chambira Formation, we interpret as the Yahuarango Formation.

Along the Río Yurúa, the Yahuarango Formation consists of moderately indurated massive clays and mudstones, with occasional bedding visible. Thin horizons a few centimeters thick of unconsolidated, variously colored fine sand of mixed composition are frequently encountered. Also frequently encountered are calcareous and hematitic conglomeratic lenses, the latter appearing to replace the former. The calcareous conglomerates appear to correspond to channel or bed load deposits that vary in thickness from 2 to 30 cm, separated by beds of clay. The channel and bed load deposits comprise clasts that range from very fine-grained to 12 cm in longest dimension, with fine and medium-sized grains predominating. Most of the larger clasts correspond to calcareous concretions, clay balls, fragments of bone, and plant matter, with much clay matrix and calcareous cement. Small pebbles are also found. The calcareous fluvial deposits are the fossiliferous horizons at the Santa Rosa locality.

At the top of the Yahuarango Formation along the Río Yurúa is a clear unconformity that separates it from the overlying formation (Fig. 9). This unconformity is found throughout western Amazonia, and it was called the Ucayali Peneplane by Kummel (1948). The Ucayali Peneplane apparently formed as a consequence of regionwide erosion following the uplift associated with the early late Miocene Quechua II Andean compressional event (see review of this topic in Campbell et al., 2000). Kummel (1948) referred to the strata overlying the unconformity as the Ucayali Formation, but for reasons of priority, we prefer the designation of Madre de Dios Formation (Campbell et al., 2000). Both ONERN (1980) and Valenzuela and Zavala (1998) call the formation overlying the unconformity the Ipururo Formation, the next youngest formation after the Chambira Formation in the recognized stratigraphic sequence of eastern Perú. However, from their descriptions of the lithology of the formation, it is clear that it is the Mio-Pliocene Madre de Dios Formation. Unfortunately, Valenzuela and Zavala (1998) also applied the name Ucayali Formation to unnamed Plio-Pleistocene terrace gravels unrelated to the name-bearing formation of Kummel (1948).

The Madre de Dios Formation comprises the youngest part of the stratigraphic column along the upper Río Yurúa. This is a very complex formation, with numerous gradual and abrupt facies changes. The deposits include soft beds of clay that vary from narrowly laminar to massive in form; clayey silts and silty sands; and cross-bedded, medium- to coarse-grained, well-sorted, unconsolidated sandstones. Paleochannels are often clearly visible. The basal horizons, which appear to be prograding del-

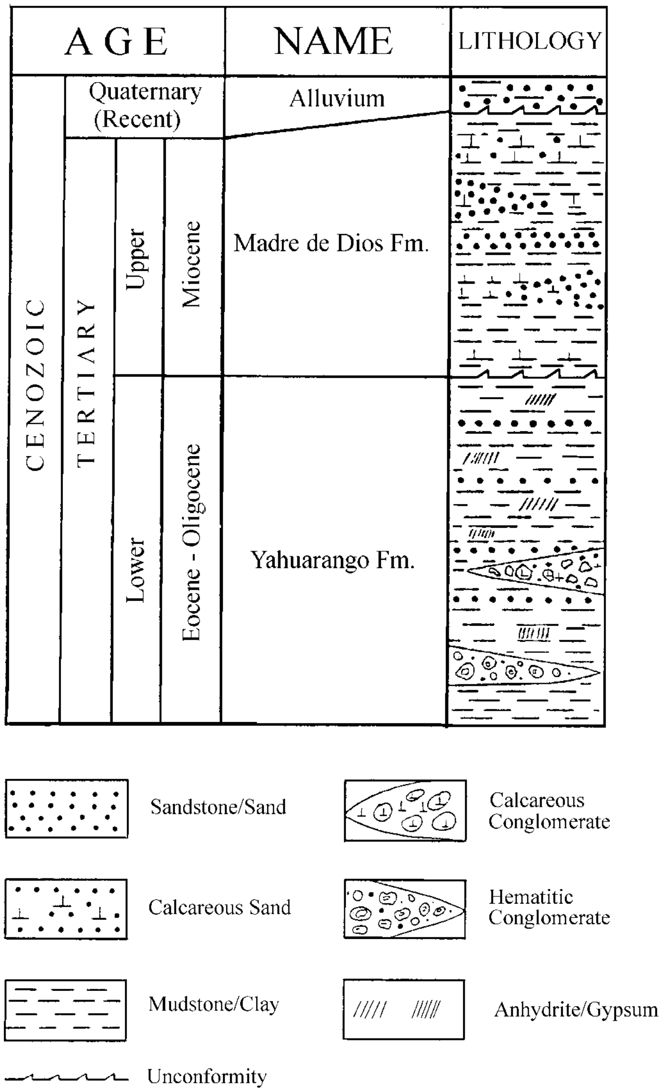


Figure 9 The general lithostratigraphic column for the Río Yurúa. The only Quaternary deposits seen along the Río Yurúa are those covering the river terraces and the Recent alluvium of the modern floodplains.

taic deposits (i.e., foreset beds) are primarily conglomeratic, grading rapidly upward into sands and silts. The basal conglomeratic horizons are often very fossiliferous, producing both micro- and macromammal fossils. On the basis of an ^{40}A/^{39}A ash date of 9.01 ± 0.28 Ma (Campbell et al., 2001) and the fossil taxa found in the basal horizons of the Madre de Dios Formation (Frailey, 1986), the age of the older portion of the formation is interpreted as upper Miocene (Huayquerian SALMA; 9–6 Ma). The uppermost horizon of this formation was dated to 3.12 ± 0.02 Ma (Campbell et al., 2001), but this horizon did not crop out along that portion of the Río Yurúa studied. For a more detailed review of the Madre de Dios Formation, see Campbell et al. (2000).

SUMMARY

We recognize two formations cropping out along the Río Yurúa at the southern end of the Sierra de Divisor structural zone, as opposed to the three formations previously described as being present. The two formations we recognize, which are separated by the Ucayali Unconformity, are the Paleocene–Eocene Yahuarango Formation and the Mio-Pliocene Madre de Dios Formation. Recognition of the Yahuarango Formation as the fossiliferous stratum is tentative, pending more detailed stratigraphic data. The fossiliferous horizons producing the Santa Rosa local fauna are coarse-grained to conglomeratic bed load or channel deposits that occur within the massive red clays of what we interpret to be

the Yahuarango Formation. On the basis of their stage of evolution, the marsupials and rodents appear to date to the late Eocene, or Mustersen SALMA, which is consistent with the age of portions of the Yahuarango Formation as presently interpreted. The Madre de Dios Formation is identified as cropping out along the Río Yurúa on the basis of its characteristic lithostratigraphy.

ACKNOWLEDGMENTS

We thank Ing. Hugo Rivera Mantilla, Director Técnica of INGEMMET, and Ing. Oscar Palacios, Director General de Geología de INGEMMET, who have been very supportive of our geological and paleontological studies in Perú. We thank Javier Guerro, Fritz Hertel, Carina Hoorn, and Michael Woodburne for helpful reviews of our manuscript. The National Geographic Society and John G. Wigmore provided financial support for the field work leading to the discovery of the Santa Rosa local fauna. Winifred Rhodes, Richard Seaver, and John Wigmore provided funding for the 1998 expedition to Santa Rosa.

LITERATURE CITED

Campbell, C.J., and H. Bürgl. 1965. Section through the Eastern Cordillera of Colombia, South America. *Geological Society of America, Bulletin* 76:567–590.

Campbell, K.E., Jr. 2004. The Santa Rosa local fauna: A summary. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, vol. 40, 155–163.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 1996. The first Paleogene fauna from the Amazon Basin and its bearing on the first occurrence of rodents in South America. *Journal of Vertebrate Paleontology* 16(3)(Suppl.):25A.

———. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: Implications for the Great American Faunal Interchange. *Instituto Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín* 23:1–152.

Campbell, K.E., Jr., M. Heizler, C.D. Frailey, L. Romero-Pittman, and D.R. Prothero. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. *Geology* 29(7):595–598.

Choubert, G., and A. Faure-Muret. 1976. *Atlas géologique monde. Geological World Atlas.* Paris: UNESCO.

Cruz, N. de la, J. Zedano-C., and A. Zapata-M. 1997. Geología de los cuadrángulos de San Roque, Río Callería, San Lucas, Pucallpa, Nuevo Utiquinia, Cantagallo y Divisor Yurúa Ucayali. *Instituto Geológico Minero y Metalúrgico, Serie A: Carta Geológica Nacional, Boletín* 102:1–155.

Dumont, J.F., S. Lamotte, and F. Kahn. 1990. Wetland and upland forest ecosystems in Peruvian Amazonia: Plant species diversity in the light of some geological and botanical evidence. *Forest Ecology and Management* 33/34:125–139.

Flynn, J.J., and C.C. Swisher III. 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. In *Geochronology time scales and global stratigraphic correlation,* ed. A. Berggren, D.V. Kent, and J. Hardenbol. Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication, 54:317–333.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Río Acre region, western Amazonia. *Contributions in Science* 374:1–46.

Guizado, J. 1975. Las molasas del pliocenico–cuaternarios del Oriente Peruano. *Boletín de la Sociedad Geológica del Peru* 45:25–44.

Hoorn, C. 1994. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (Early Miocene–early Middle Miocene, Colombia). *Paleogeography, Palaeoclimatology, Palaeoecology* 109:1–54.

Hoorn, C., J. Guerrero, G.A. Sarmiento, and M.A. Lorente. 1995. Andean tectonics as a cause for changing drainage pattern in Miocene northern South America. *Geology* 23:237–240.

Ihering, H. von. 1927. *Die Geschichte des Atlantischen Ozeans.* Jena, Germany: Fischer, 237 pp.

(INGEMMET) Instituto Geológico, Minéro, y Metalúrgico. 1975. Mapa Geológico del Perú. Lima, Perú: INGEMMET.

Jenks, W.F. 1956. Perú. *Geological Society of America, Memoir* 65:213–247.

Kummel, B. 1946. Estratigrafía de la región de Santa Clara. Estudio preliminar. *Boletín de la Sociedad Geológica del Perú* 19:133–152.

———. 1948. Geological reconnaissance of the Contamana Region, Peru. *Geological Society of America, Bulletin* 59:1217–1265.

Martínez, M. 1975. Tectónica del area Ucayali Central. *Boletín de la Sociedad Geológica del Perú* 45:61–82.

Mégard, F. 1984. The Andean orogenic period and its major structures in central and northern Peru. *Journal of the Geological Society of London* 141:893–900.

———. 1987. Structure and evolution of the Peruvian Andes. In *Anatomy of mountain ranges,* ed. J.-P. Schaer and J. Rodgers, 179–210. Princeton: Princeton University Press.

Noble, D.C., E.H. McKee, T. Mourier, and F. Mégard. 1990. Cenozoic stratigraphy, magmatic activity, compressive deformation, and uplift in northern Peru. *Geological Society of America Bulletin* 102: 1105–1113.

Nuttall, C.P. 1990. A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bulletin, British Museum of Natural History (Geology)* 45: 165–371.

(ONERN) Oficina Nacional de Evaluación de Recursos Naturales. 1980. *Inventario, evaluación e integración de los recursos naturales de la zona de los Rios Alto Yurúa—Breu.* Lima, Peru: ONERN.

Pardo, A.A. 1982. Características estructurales de la faja subandina del norte del Perú. In *Simposium "Exploración Petrolera en las cuencas subandinas de Venezuela, Colombia, Ecuador y Perú,"* 1–8. Bogotá, Colombia: Asociación Colombiana de Geólogos y Geofisicos de Petrol.

Pardo, A.A., and F. Zuñiga. 1976. Estratigrafía y evolución tectónica de la region de la selva del Perú. Parte II. Mesozoico y Cenozoico. *Segundo Congreso Latinoamericano de Geología, Memorias. Boletín Geológica, Caracas, Publicación Especial* 7:588–608.

Putzer, H. 1984. The geological evolution of the Amazon Basin and its mineral resources. In *The Amazon,* ed. H. Sioli, 15–46. Dordrecht, The Netherlands: Dr. W. Junk.

Räsänen, M.E., A.M. Linna, J.C.R. Santos, and F.R. Negri. 1995. Late Miocene tidal deposits in the Amazonian Foreland Basin. *Science* 269(5222):386–390.

Rüegg, W. 1947. Estratigrafía Comparada del Oriente Peruano. *Boletín de la Sociedad Geológica del Perú* 20:57–100.

———. 1956. Geología y Petróleo en la Faja Subandina Peruana. *Simposio Sobre Yacimientos de Petróleo y Gas, XX Congreso Geológico International IV, Mexico,* 89–139.

Sébrier, M., and P. Soler. 1991. Tectonics and magmatism in the Peruvian Andes from late Oligocene time to the Present. *Geological Society of America, Special Paper* 265:259–278.

Sheppard, L.M., and R.H. Bate. 1980. Plio-Pleistocene ostracods from the upper Amazon of Colombia and Peru. *Paleontology* 23(1):97–124.

Valenzuela-O., G., and B. Zavala-C. 1998. Geología de los cuadrángulos de Puerto Putaya 18-p, Río Shahuinto 18-q, Jacaya 19-p, Santa Rosa 19-q, Río Breu 19-r, Parantari 20-p, Breu 20-q, y Río Piquiyacu 20-r. *Instituto Geológico Minero y Metalúrgico, Serie A: Carta Geológica Nacional, Boletín* 109:1–137.

Williams, M.D. 1949. Depositos terciarios continentales del valle del Alto Amazonas. *Boletín de la Sociedad Geológica del Perú, Volumen Jubilar* 50(Parte II):1–13.

Received 2 July 2003; accepted 29 December 2003.

New Paleogene Marsupials from the Amazon Basin of Eastern Perú

Francisco J. Goin[1,2] and Adriana M. Candela[1]

ABSTRACT. An analysis of 79 fossil specimens, most comprising tiny, isolated upper and lower molars recovered from Paleogene levels near Santa Rosa in the Peruvian Amazon, led to the recognition of eight new genera and eleven new species of extinct marsupials: *Rumiodon inti* gen. et sp. nov. (Didelphimorphia, cf. Herpetotheriidae), *Patene campbelli* sp. nov. (Sparassodonta, Hathliacynidae), *Incadolops ucayali* gen. et sp. nov. (Polydolopimorphia, Prepidolopidae), *Wamradolops tsullodon* gen. et sp. nov. (Polydolopimorphia, family indeterminate), *Hondonadia pittmanae* sp. nov. (Polydolopimorphia, family indeterminate), *Perulestes cardichi* and *P. fraileyi* gen. et spp. nov. (Paucituberculata, Caenolestidae), *Sasawatsu mahaynaq* gen. et sp. nov. (Paucituberculata, cf. Palaeothentidae), *Kirutherium paititiensis* gen. et sp. nov. (Microbiotheria, Microbiotheriidae), *Wirunodon chanku* gen. et sp. nov. (order and family indeterminate), and *Kiruwamaq chisu* gen. et sp. nov. (order and family indeterminate). The marsupial that best resembles *W. chanku* is *Kasserinotherium tunisiense,* from the lower Eocene of Africa. *Perulestes* and *Sasawatsu* represent early stages in the evolution of the paucituberculatan quadrangular upper molar; their combined features confirm that paucituberculatans and polydolopimorphians do not belong to a natural group. *Wamradolops, Incadolops,* and *Hondonadia* add significant information on the evolution of several major polydolopimorphian lineages. A formal suprageneric taxonomy for the order Polydolopimorphia, included in a major (unnamed) taxon together with microbiotherians (and diprotodontians?) is proposed. Frugivorous or frugivorous–insectivorous adaptive types are dominant among the Santa Rosa marsupials, with *W. tsullodon* the most abundant, comprising almost half of all marsupial specimens. A comparative analysis of the Santa Rosa marsupials with those of other Paleogene South American faunas failed to correlate it with any known South American Land Mammal Age. We conclude that the age of this fauna is, most probably, middle to late Eocene, although the possibility of an early Oligocene age should not yet be discarded.

RESUMEN. El análisis de 79 especímenes fósiles consistentes en su mayor parte en molares superiores e inferiores de muy pequeño tamaño, procedentes de niveles paleógenos cercanos a la localidad de Santa Rosa, en la Amazonia peruana, permitió el reconocimiento de once nuevas especies de marsupiales extinguidos: *Rumiodon inti* gen. et sp. nov. (Didelphimorphia,? Herpetotheriidae), *Patene campbelli* sp. nov. (Sparassodonta, Hathliacynidae), *Incadolops ucayali* gen. et sp. nov. (Polydolopimorphia, Prepidolopidae), *Wamradolops tsullodon* gen. et sp. nov. (Polydolopimorphia, familia indet.), *Hondonadia pittmanae* sp. nov. (Polydolopimorphia, familia indet.), *Perulestes cardichi* y *P. fraileyi* gen. et spp. nov. (Paucituberculata, Caenolestidae), *Sasawatsu mahaynaq* gen. et sp. nov. (Paucituberculata, cf. Palaeothentidae), *Kirutherium paititiensis* gen. et sp. nov. (Microbiotheria, Microbiotheriidae), *Wirunodon chanku* gen. et sp. nov. (orden y familia indet.) y *Kiruwamaq chisu* gen. et sp. nov. (orden y familia indet.). El único marsupial conocido que recuerda a *W. chanku* es *Kasserinotherium tunisiense,* del Eoceno temprano de Africa. *Perulestes* y *Sasawatsu* representan estadíos tempranos en la evolución del patrón molar de los Paucituberculata; su combinación de caracteres confirma que los Paucituberculata y los Polydolopimorphia no constituyen un grupo natural. Los polidolopimorfios *Wamradolops, Incadolops* y *Hondonadia* agregan información significativa sobre la evolución de varios linajes de este orden. Se propone formalmente una nueva taxonomía supragenérica del Orden Polydolopimorphia, el cual se incluye en un grupo mayor (innominado) junto con los Microbiotheria (¿y los Diprotodontia?). Los tipos frugívoros o frugívoro–insectívoros son dominantes en esta fauna, siendo *W. tsullodon* el más abundantemente representado, con casi la mitad de los es-

---

[1] Departamento Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. Email: fgoin@museo.fcnym.unlp.edu.ar and acandela@museo.fcnym.unlp.edu.ar

[2] Correspondence

Science Series, Number 40, pp. 15–60
Natural History Museum of Los Angeles County, 2004

pecímenes. Un análisis comparativo de los marsupiales de Santa Rosa con aquéllos de otras faunas paleógenas sudamericanas no permite correlacionarla con ninguna de las edades-mamífero reconocidas para el Paleógeno sudamericano. Sin embargo, se concluye que la edad de esta fauna es, más probablemente, Eoceno medio a tardío, aunque tampoco debería descartarse una edad Oligoceno temprano.

INTRODUCTION

There is a strong bias in our knowledge of South American Paleogene land mammals resulting from two main factors: most early Tertiary fossil sites are located in the southernmost part of the continent (e.g., Patagonia, Argentina; see Fig. 1), and a large proportion of the known mammals are of moderate to large size. This bias partially reflects both the history of South American paleomammalogy, beginning with the Ameghinos' pioneering studies in central and southern Argentina, and the collecting techniques traditionally employed (naked-eye search for fossils). This bias is especially important in regard to South American marsupials for two reasons. First, as far as living marsupials are concerned, the majority of taxa is presently distributed in tropical, warm, and wet regions of South America. This suggests that, even though environmental conditions were probably different from those of the present during Paleogene times, an important diversity of extinct taxa that is not presently recorded should be expected in tropical South America. Second, most South American marsupials are, and most probably have always been, very small to medium-sized forms. This is not reflected in the known Paleogene fossil record of marsupials. A quick review of the literature on Paleogene mammals from Argentina is illustrative. From four Patagonian localities of the Riochican (late Paleocene) South American Land Mammal Age (SALMA; Bajo de la Palangana, Cañadón Hondo, Cerro Redondo, and Pan de Azúcar; see Fig. 1), Marshall et al. (1983) listed several medium-sized sparassodonts and a few polydolopines, which are the largest polydolopimorphians. Among Casamayoran SALMA (conventionally, early Eocene, but see below), mammals from Patagonia, which form one of the best known Tertiary faunas of South America, are five sparassodont genera, three polydolopines, a squirrel-sized caroloameghiniid, and one didelphimorphian opossum (*Coona pattersoni* Simpson, 1938, similar in size to the largest of living marmosines), and only one, very small, microbiotheriid opossum (*Eomicrobiotherium gaudryi* Simpson, 1964). Mustersan SALMA (conventionally, early to middle Eocene, but see below) marsupials from Patagonia are, in turn, very poorly represented, with only two sparassodonts and one polydolopine known. Divisaderan SALMA (?early Oligocene) mammals are known mostly from the type locality, Divisadero Largo, in western Argentina. Marsupial remains from this locality are restricted to a few specimens referable to the extremely specialized, rat-sized taxa of the family Groeberiidae. Finally, Deseadan SALMA (middle to late Oligocene) marsupials from Argentina include three medium-sized (*Notogale* Loomis, 1914) to very large (*Pharsophorus* Ameghino, 1897; *Proborhyaena* Ameghino, 1897) sparassodonts and three rat-sized paucituberculatans (see Marshall et al., 1983; Pascual et al., 1996).

In recent years, the use of screen-washing techniques applied to fossil prospecting and collecting has changed our perception of the diversity of South American fossil mammals. For example, in one Patagonian locality, the middle Paleocene Las Flores Formation, the application of these techniques helped R. Pascual, M. McKenna, C. Tambussi, and A. Carlini recover an impressive variety of mammal remains, mostly isolated molars, ranging from tiny to moderately large-sized specimens. Among the marsupials, there seem to be no fewer than 30 species representative of all major lineages of South American metatherians (Goin et al., 1997). The diversity of this fauna suggests that a very significant part of South American marsupial history, especially that of the Paleogene, is still to be discovered.

The second aspect that precludes a better understanding of mammalian diversity and evolution during the Tertiary is the already mentioned lack of tropical, mammal-bearing, stratigraphic levels. In southern South America during the Paleogene, there was a shift in environmental conditions, beginning in the Eocene. Commenting on their "Prepatagonian Faunistic Cycle" (Casamayoran to Divisaderan SALMAs), Pascual et al. (1996:285–286, italics ours) mention that, "By its own, the Patagonian mammal record testifies to the climatic and related environmental shifting trend that occurred throughout this Cycle: the ratio of hypsodont to brachydont 'ungulates' increased from the early to the later part. . . . This trend is compatible with the progressive shift from forested warm habitats to extensive temperate grassland plains. . . . Those vertebrates indicative of warm environments disappeared from middle Patagonian latitudes already from the middle part (Mustersan SALMA) of this Cycle. . . . Even most of those 'ungulate' species representing the end of this cycle (Divisaderan SALMA) recorded in latitudes (33° S) not far from northern Patagonia . . . *curiously show primitive states with respect to their Patagonian counterparts.*" Moreover, even the Divisadero Largo mammals may represent a relatively marginal fauna in the whole South American context for that age. In discussing why the extremely specialized groeberiid marsupials were, by that time, solely recorded at Divisadero Largo, without known ancestors or de-

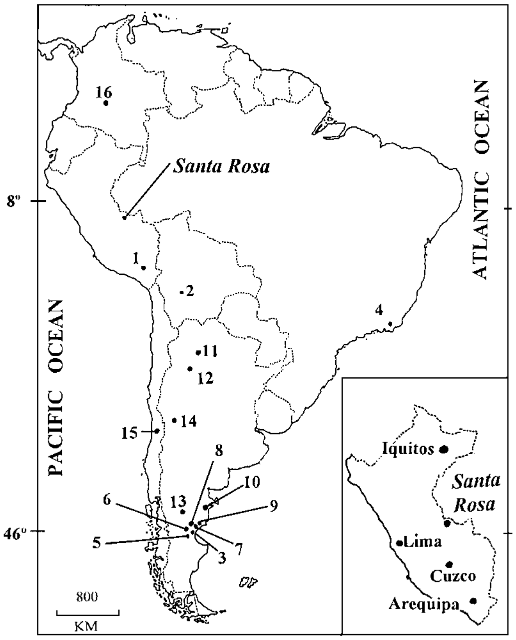


Figure 1 Map showing the fossil site near Santa Rosa, in eastern Perú, and other (mostly) Paleogene localities mentioned in the text (see "Introduction" and "Discussion"). **1,** Laguna Umayo (Perú; latest Cretaceous or earliest Paleocene); **2,** Tiupampa (Bolivia; Tiupampian SALMA, early Paleocene); **3,** Punta Peligro (Argentina; Peligran SALMA, early Paleocene); **4,** Itaboraí (Brazil; Itaboraian SALMA, middle Paleocene); **5,** Yacimiento Las Flores (Argentina; Itaboraian SALMA, middle Paleocene); **6,** Gran Barranca or Barranca Sur, Lago Colhué Huapi (Argentina; late Paleocene to Miocene); **7,** Bajo de la Palangana (Argentina; Riochican SALMA, late Paleocene); **8,** Cañadón Hondo (Argentina; Riochican SALMA, late Paleocene); **9,** Cerro Redondo (Argentina; Riochican SALMA, late Paleocene); **10,** Pan de Azúcar (Argentina; Riochican SALMA, late Paleocene); **11,** Lumbrera Formation (Argentina; Casamayoran SALMA, conventionally early Eocene, but see "Introduction"); **12,** Antofagasta de la Sierra (Argentina; Mustersan SALMA, conventionally middle Eocene, but see "Introduction"); **13,** Gran Hondonada (Argentina; Mustersan SALMA); **14,** Divisadero Largo (Argentina; Divisaderan SALMA, ?late Eocene–early Oligocene); **15,** Termas del Flaco (Chile; "Tinguirirican" age, early Oligocene); **16,** La Venta (Colombia; Laventan SALMA, middle Miocene).

scendants, Simpson suggested that they ". . . evolved in what are now (and quite likely were then) the tropics and [are] picked up in our record only when [they] spread rather briefly to what was for [them] a marginal area" (Simpson, 1970:17; cited also in Pascual et al., 1994:257). The recognition of different climatic–environmental conditions between southernmost South America and northern regions of the continent beginning in the middle Eocene implies that future prospecting in the latter will lead to the recovery of quite different faunas. These new faunas will probably include taxa representing generalized forms with respect to contemporary, related taxa recorded in Patagonia.

In this work, we analyze a new marsupial fauna recovered from Paleogene levels in a fossil locality near Santa Rosa at a very low latitude in the eastern Amazonian lowlands of Perú. The fauna presented here consists of 79 specimens, most of them very small, isolated molars, representing ten genera, eight of which are new, and eleven new species referable to all major lineages (orders) of South American marsupials. Some of the new taxa, however, cannot be referred to any known lineage. The description of the new taxa, the analysis of their affinities, and the discussion of the probable age of the fossil association constitute the main goals of this study. As stated below, some of these taxa represent "missing links" in the evolution of South American marsupials. Other taxa comprise extremely derived, even aberrant marsupials that may never have been recorded before and possibly never will be again, whereas a few can be positively related to well-known taxonomic counterparts in southern South America. In this sense, this contribution adds knowledge about the regional differentiation of South American marsupials during a key period (middle to late Paleogene; see "Discussion") of their history.

Relevant to the discussion of the age of Santa Rosa mammals (see "Discussion") is the recent contribution by Kay et al. (1999), who reported the first radiometric age determinations and associated magnetic polarity stratigraphy for the Casamayoran SALMA. Their data indicate that the Barrancan subage of the Casamayoran is much younger than previously thought; that is, 36 Ma instead of 55–50 Ma. Thus, the Casamayoran SALMA would be late Eocene in age, whereas the Mustersan SALMA would be practically at the Eocene–Oligocene boundary. This means that no SALMAs are recognized for the early and middle, or most, of the Eocene. It could be that, whereas the Barrancan Subage is late Eocene, the Vacan Subage of the Casamayoran SALMA actually represents a fraction of the middle Eocene. This, however, has not been postulated on the basis of radiometric or paleomagnetic evidence.

The Santa Rosa locality (Provincia Atalaya, Departamento de Ucayali, Perú) is located approximately 2 km north of the village of Santa Rosa on the northwest bank of the Río Yurúa near the confluence between it and the Río Beu, at 9°29′39″ S, and 72°45′48″ W (Fig. 1). Campbell et al. (2004) suggest that the fossil-producing deposits at the site belong to the Paleocene–Eocene Yahuarango Formation (also known as the Huayabamba Formation, lower red beds, lower Capas Rojas, lower Puca, or Huchpayacu Formation). The fossiliferous beds at Santa Rosa correspond to calcareous, clayey channel deposits consisting of mostly fine-grained sediments with horizons containing large concentrations of calcareous concretions, bone, teeth, shell, and plant material. Most of the specimens studied in this work came from screen-washing of about 400 kg of matrix from these beds at Santa Rosa in 1995. Several additional specimens resulting from a return trip to the site in 1998 are also included. Available unsorted concentrate and additional field work have the potential to produce many dozens of additional specimens. Field work, unusually difficult compared with more "normal" paleontological work in higher latitudes, was carried out by Kenneth E. Campbell, Carl D. Frailey, Lidia Romero-Pittman, and Manuel Aldana.

ABBREVIATIONS AND TERMINOLOGY

LACM	Natural History Museum of Los Angeles County, California, USA
MLP	Departamento Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina
MNRJ	Museu Nacional de Rio de Janeiro, Brazil
SALMA	South American Land Mammal Age

Upper incisors	I^1, I^2, I^3, I^4, I^5
Upper canine	C^1
Upper premolars	P^1, P^2, P^3
Upper molars	M^1, M^2, M^3, M^4
Lower incisors	I_1, I_2, I_3, I_4
Lower canine	C_1
Lower premolars	P_1, P_2, P_3
Lower molars	M_1, M_2, M_3, M_4
Upper/lower molar (locus unknown)	M^x/M_x
Deciduous third upper/lower premolar	dp^3/dp_3
Stylar cusps A, B, C, D	StA, StB, StC, StD, respectively

Nomenclature for molar cusps and cristae used in this study is shown in Figure 2. All measurements are in millimeters; L = length, W = width; an asterisk (*) after some measurements indicates that they are approximate. When commenting on the inferred feeding habits of marsupials, we use the term faunivorous to refer to animals that eat both invertebrates and small vertebrates.

SYSTEMATIC PALEONTOLOGY

Supercohort Marsupialia Illiger, 1811

Order Didelphimorphia Gill, 1872

cf. Family Herpertotheriidae Trouessart, 1879

Rumiodon gen. nov.

TYPE SPECIES. *Rumiodon inti* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. From the Quechua *rumi,* "stone," and the Greek *odontos,* "tooth."

Rumiodon inti sp. nov.

Figures 3A–B

HOLOTYPE. LACM 144515, isolated right M^1.

HYPODIGM. The holotype; LACM 140661, isolated right $M^{?2}$; and LACM 140687, isolated left lower premolar.

DIAGNOSIS. *Rumiodon inti* differs from other didelphimorphians in the following combination of characters: upper molars much longer than wide, with reduced protocones and well-developed postmetacristae; centrocrista with labial vertex ending very close to labial face of the tooth; paracone and metacone well separated; paraconule vestigial or absent; metaconule reduced; stylar shelf reduced; StA, StB, StC, and StD, at least in M^1, anteroposteriorly aligned and labiolingually compressed; StB subequal to StD and larger than StC, which is, in turn, larger than StA.

MEASUREMENTS. LACM 144515: L = 1.50, W = 0.90; LACM 140661: L = 1.59, W = 1.19; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. From the Quechua *Inti,* "sun," supreme god of the Inca people.

DESCRIPTION. The holotype (LACM 144515) is complete and unworn. It is clearly longer than wide, with the protocone reduced and the postmetacrista well developed. The metacone is much larger and higher than the paracone; both cusps are placed well apart. The stylar shelf is high and reduced in its labiolingual width. The centrocrista is high and labially invasive. The preprotocrista connects labially with the anterobasal cingulum, whereas the postprotocrista extends basally past the metacone's posterolingual face. All stylar cusps, but especially the anterior ones, are labiolingually compressed. StA is small, but clearly distinct and well projected anteriorly. StB is slightly larger than StD in size and height; StC is smaller and equidistant to both. The paraconule is vestigial or absent; the metaconule is very reduced. StB and the paracone are very close to each other, and the postmetacrista is nearly parallel to the dental axis. These last two features suggest that the holotype is an M^1.

Several features present in LACM 140661, including the proximity of the paracone and StB, the orientation of the postmetacrista, and the very anterior placement of the protocone, suggest that this tooth is also an M^1. However, its large size and more robust protocone and metacone lead us to regard it as a possible M^2. LACM 140661 has strongly worn cusps and crests, especially the postmetacrista. The protocone is quite reduced and low relative to the stylar shelf. Consequently, the trigon basin is reduced, but deep. The protocone and the pre- and postprotocristae are strongly worn, though a small metaconule can be observed on the distal end of the latter. The metaconule is labiolin-

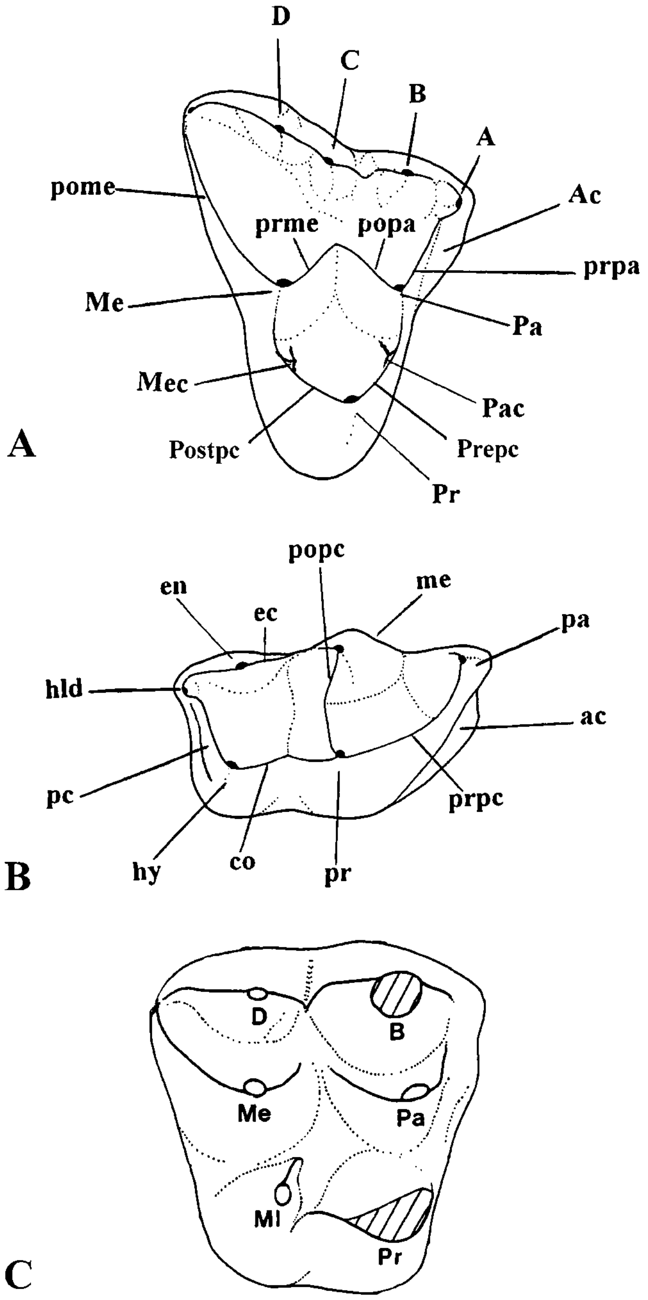


Figure 2 Nomenclature for molar teeth used in this study, exemplified by a didelphimorphian opossum (**A**, **B**) and by the generalized polydolopimorphian *Rosendolops primigenium* (from Goin and Candela, 1996) (**C**). **A**, **C**, Upper right molars; **B**, lower right molar. **Abbreviations for upper molars:** A, B, C, D, stylar cusps A, B, C, and D, respectively; Ac, anterior cingulum; Me, metacone; Mec, metaconule (in **C**, Ml is metaconule); Pa, paracone; Pac, paraconule; pome, postmetacrista (postparacrista + premetacrista = centrocrista); popa, postparacrista; Postpc, postprotocrista; Pr, protocone; Prepc, preprotocrista; prme, premetacrista; prpa, preparacrista. **Abbreviations for lower molars:** ac, anterior cingulum; co, cristid obliqua; ec, entocristid; en, entoconid; hld, hypoconulid; hy, hypoconid; me, metaconid; pa, paraconid; pc, postcingulum; popc, postprotocristid; pr, protoconid; prpc, preprotocristid. The preprotocristid and the postparacristid form the paracristid; the postprotocristid and the postmetacristid form the metacristid. Not to scale.

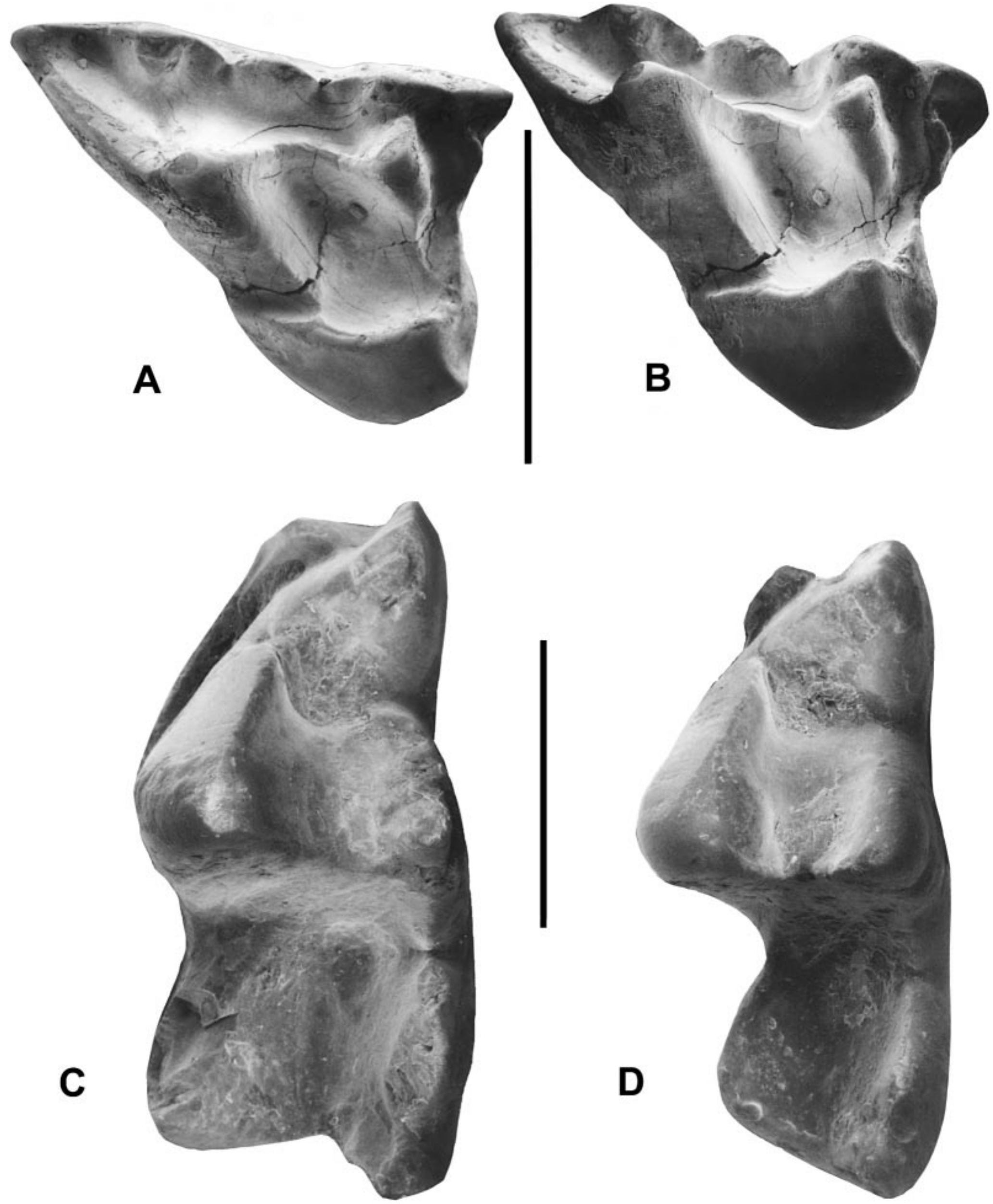


Figure 3 *Rumiodon inti* gen. et sp. nov. LACM 144515 (holotype), isolated right M^1: **A,** occlusal view; **B,** occlusal-lingual view. *Rumiodon* sp. LACM 140583: **C,** left M_3; **D,** M_4. Scale = 1 mm.

gually compressed and develops a posterior crest that does not end in the base of the metacone but, instead, runs a short distance at the base of this cusp, parallel to the postmetacrista. The paracone is clearly smaller and lower than the metacone, and it is very close to and paired with StB. However, the preparacrista does not seem to have connected with this stylar cusp at its lingual slope, but instead at its frontal face. Both the postparacrista and the premetacrista penetrate deeply to the stylar shelf so that, in occlusal view, the vertex of the centrocrista ends very close to StC. The postmetacrista is quite developed, and it is almost as long as the anterior width of the tooth. The metacone is strong and high, about twice the size of the paracone, although both cusps are very worn. StC is small and rounded. StD is larger and higher than StB, and it develops an anterior and a posterior crest. The anterolabial end of the tooth is broken, so the presence or absence of a StA cannot be determined. A narrow anterior cingulum is present.

LACM 140687 is an isolated left lower premolar, broken in its anterior portion. Apparently it was unicuspid, with a sharp central cusp. The whole premolar is strongly compressed labiolingually. The posterior crest is sharp edged, ending at the base in a narrow posterior cingulum

COMMENTS. *Rumiodon inti* is a didelphimorphian opossum not larger than medium-sized living marmosines. The strong development of the cutting crests of the upper molars and the reduction of the protocone of M^1 probably reflect faunivorous or even carnivorous feeding habits.

Despite general morphological similarities between *R. inti* and some Neogene didelphids, several features suggest closer affinities with Paleogene rather than with Neogene opossum groups (see also, "Discussion"). *Rumiodon inti* differs from Neogene marmosines and didelphines in the following combination of characters.

1. In both marmosines and didelphines the para- and metaconules, if present, are extremely small or vestigial; in *Rumiodon,* the paraconule is vestigial, but the metaconule is distinct, although reduced, in at least one molar (LACM 140661).
2. The stylar shelf is very narrow in *Rumiodon,* unlike in most Neogene taxa of Didelphimorphia. When it is very narrow among the latter, as in species of the carnivorous Sparassocynidae or in didelphines that have specialized toward a carnivorous diet (e.g., *Hyperdidelphys* Ameghino, 1904), it occurs together with the reduction or loss of the stylar cusps. In *Rumiodon,* as in several Paleogene opossums, the stylar shelf is narrow, but there is no reduction of the stylar cusps.
3. The centrocrista penetrates the stylar shelf deeply labially in *Rumiodon,* as in the Paleogene Derorhynchidae and Herpetotheriidae, but not in Neogene opossums.
4. Although an StC is present in *R. inti,* as in several Neogene opossums, this cusp is clearly equidistant from StB and StD, an infrequent feature in Neogene didelphines (but not in some marmosines in which StC is present).
5. The extent of the reduction of the protocone and the great development of the postmetacrista and its orientation relatively parallel to the dental axis are infrequently seen in Neogene opossums.

Most of the features mentioned above relate *Rumiodon* with several Paleogene species of Didelphimorphia of both South America and the Holarctic region. Particularly interesting are the following: (a) Several features are shared by *Rumiodon* and some European Herpetotheriidae of the genera *Amphiperatherium* Filhol, 1879, and *Peratherium* Aymard, 1850 (see "Discussion"). In the M^1 of *Amphiperatherium minutum* (Aymard, 1846), for example, stylar cusps B, C, and D are clearly set apart from each other, the protocone is reduced, the postmetacrista is well developed, and the metaconule is more developed than the paraconule, which is vestigial or absent (see Crochet, 1980). These species also show several similarities between their lower molars and those of *Rumiodon* (e.g., unreduced hypoconulids, anterobasal cingula well developed, little reduced paraconids, and entoconids large and very compressed laterally). Most of these characters are also shared by *R. inti* and two European species of the genus *Peratherium*: *P. matronense* Crochet, 1979, and *P. monspeliense* Crochet, 1979. (b) The deep centrocrista, high stylar shelf, distinct StC that is aligned with StB and StD, and reduction of the protocone are all features suggesting affinities with *Derorhynchus* Paula Couto, 1952a, and allied taxa from the middle Paleocene of South America (Oliveira, 1998). In fact, many of these features are shared between South American derorhynchids and European herpetotheriids. A review of the Itaboraian "opossum-like" marsupials from Brazil led Oliveira (1998) to assign several taxa to the Herpetotheriidae. Marshall (1987) originally regarded derorhynchines as a subfamily of Didelphidae, the Derorhynchinae, which Goin et al. (1999) raised to family rank. Affinities between derorhynchids and herpetotheriids have been mentioned previously by one of us (Goin, 1991, 1995). Goin (1991) suggested that both lineages, together with several additional taxa from the Paleogene of South America, might constitute a natural group, having a sister group relationship to Neogene and Recent South American didelphimorphians.

We find more affinities among *R. inti* and Paleogene opossums not belonging to the Didelphidae (Marmosinae + Didelphinae), such as European herpetotheriids and South American derorhynchids, than with any known group of South American Neogene didelphimorphians. As already stated, we are inclined to consider that a relationship with the Herpetotheriidae may be a plausible systematic hypothesis. Pending a review of these and other Paleogene didelphimorphians, we provisionally regard *R. inti* as a probable herpetotheriid.

Rumiodon sp.

REFERRED SPECIMENS. LACM 140583, left mandibular fragment with almost complete M_{3-4} (Figs. 3C–D), and LACM 144518, isolated left trigonid.

MEASUREMENTS. LACM 140583: LM_3 = 2.4, WM_3 = 1.12, LM_4 = 2.12, WM_4 = 1.08; mm.

DESCRIPTION. LACM 140583 is a left mandibular fragment with the two last molars, shown separately in Figs. 3C–D. The horizontal ramus is typically didelphimorphian, with the origin of the ascending ramus behind the M_4. Both molars have strong, well-developed preprotocristids and wide anterobasal cingula that continue posteriad almost to the base of the hypoconids. Paraconids are well developed and have a lingual position. Protoconids

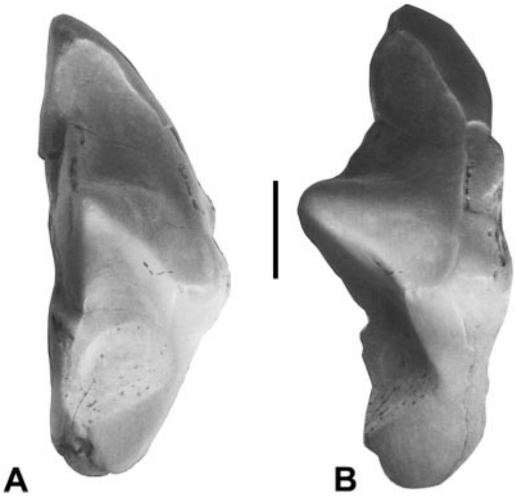


Figure 4 *Patene campbelli* sp. nov. LACM 140628 (holotype), isolated left M^4: **A,** occlusal view; **B,** posterior view. Scale = 1 mm.

are very high and robust. Metaconids are intermediate in height between para- and protoconids. Talonids are shorter than trigonids. Hypoconulids are well developed in both molars, and the entoconids are higher than the hypoconids and very compressed labiolingually, developing sharp entocristids. Hypoconulids are placed almost immediately behind the entoconids. The talonid basin is shallow in both molars, and the hypoconids are not very prominent. The talonid of M_4 is somewhat more reduced than that of M_3. The postprotocristids are even, high, and perpendicular to the talonid plane. At the base of this crest, lingually and behind the metaconid, is a small crest projecting posteriad, having a deep notch at its contact with the entocristid. The entoconid of M_4 (Fig. 3D) is displaced somewhat posteriorly with respect to that of M_3 (Fig. 3C), in which it forms a distinct wall lingual to the talonid.

LACM 144518, an isolated left trigonid, is even larger than the trigonids of LACM 140583. The protoconid is broken, but its relative size at the base indicates that it was larger than the metaconid and the paraconid. The paracristid is well developed, as is the hypoconulid notch. The anterobasal cingulum is moderately developed. At the metacristid, it is evident that the cristid obliqua ended anteriorly at a point below the tip of the protoconid. Behind the metaconid is a small crest, possibly connected to the pre-entocristid.

COMMENTS. Although comparable features suggest rather strongly that the holotype of *Rumiodon inti,* LACM 140661, and LACM 140583 belong to the same taxon, it must be pointed out that the upper molars of *R. inti* are somewhat smaller than what might be expected from the size of the preserved M_{3-4} referred to *Rumiodon* sp. It could be argued that the holotype of *R. inti* is, in fact, a deciduous molar (dp^3). However, the paracone of that specimen is not fused to StB, a common feature in dp^{3}s of species of the Didelphimorphia, and the proportions of the holotypical specimen are similar to those of the M^{1}s of many other didelphimorphians.

Although the lower molars in the mandibular fragment assigned here to *Rumiodon* sp. are larger than the upper counterparts of *R. inti,* the cusp and crest development of both lower molars seem to agree with the lower molar morphology one might expect on the basis of the upper molars. The observed differences in size may simply reflect intraspecific variability. However, the size differences seem significant to us. In the absence of more complete materials of upper and lower molars, we provisionally refer the mandibular fragment with M_{3-4} to *Rumiodon* sp.

Order Sparassodonta Ameghino, 1894

Family Hathliacynidae Ameghino, 1894

Patene Simpson, 1935

Patene campbelli **sp. nov.**

Figure 4

HOLOTYPE. LACM 140628, isolated left M^4.

HYPODIGM. The holotype only.

DIAGNOSIS. Differs from *Patene simpsoni* Paula Couto, 1952b, in its smaller size and by the presence, in M^4, of a more reduced metacone and less developed anterobasal cingulum. It differs from *Patene colhuapiensis* Simpson, 1935, by its smaller size and by having M^4 with persistent anterobasal cingulum, paraconule and metacone more developed, and trigon basin wider.

MEASUREMENTS. L = 4.92, W = 2.0; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. Honoring Kenneth E. Campbell, codiscoverer of the Santa Rosa local fauna of eastern Perú, in recognition of his paleontological research in tropical South America.

DESCRIPTION. The holotype is an almost complete, somewhat worn, isolated left M^4. The paracone is, by far, the highest cusp of the tooth (Fig. 4B). It is followed in size by the metacone, which is very reduced and fused to the paracone at the base, and then by the paraconule, which is slightly higher than the protocone. The metacone is more lingually placed than the paracone, and it develops a narrow labial cingulum that extends from almost the fusion point with the paracone to the parastylar corner of the tooth (Figs. 4A–B). The preparacrista is straight and sharp. It does not reach the parastylar corner, but only to a more lingual point within the stylar shelf, at the base of which the anterior cingulum of the tooth originates. This cingulum is very narrow and disappears before contacting the anterior crest of the paraconule (Fig. 4A). The paraconule is moderately developed and, at the point where it fuses with the paracone, it develops a small cutting crest. The trigon basin is relatively wide.

COMMENTS. This new species of Amazonian marsupial is referable to the genus *Patene,* and it appears most closely related to its most generalized species, *P. simpsoni* from the middle Paleocene–lower Eocene of Argentina and Brazil. *Patene campbelli* is a very generalized hathliacynid, as shown by the relatively wide trigon basin, the persistence of the paraconule, the presence of a vestigial metacone basally fused with the paracone, and the persistence, although reduced, of an anterobasal cingulum. All of these features are well developed in *P. simpsoni,* whereas they are almost absent in *P. colhuapiensis* from the Riochican (upper Paleocene) of central Patagonia. Consequently, the new species *P. campbelli* is morphologically intermediate between *P. simpsoni* and *P. colhuapiensis,* but closer to the former. The size of a domestic cat, *P. campbelli* is the smallest species of this genus, and it is almost the smallest of the known sparassodonts, with only the oldest representatives of the order, *Allqokirus australis* Marshall and Muizon, 1988, and *Mayulestes ferox* Muizon, 1994, both from the lower Paleocene of Tiupampa, Bolivia, being smaller.

Order Polydolopimorphia Ameghino, 1897

Family Prepidolopidae Pascual, 1980

Incadolops gen. nov.

TYPE SPECIES. *Incadolops ucayali* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. *Inca,* after the Inca civilization and people, and *dolops,* a Greek term meaning "ambusher," and a common ending of several polydolopimorphian generic names.

Incadolops ucayali sp. nov.

Figure 5

HOLOTYPE. LACM 144513, isolated left M^x.

HYPODIGM. The holotype only.

DIAGNOSIS. Differs from other prepidolopids (*Prepidolops* Pascual, 1980a, and *Punadolops* Goin et al., 1998) in the following features: upper molars with less difference in height between the protocone and the paracone–metacone; centrocrista less open, with premetacrista and postparacrista longer and closer to each other at their labial ends; metaconule clearly distinct and bearing small postcingulum at its base; anterobasal cingulum present (vestigial or absent in other prepidolopids), paracone and StB not as close to each other (especially relative to their positions in *Prepidolops didelphoides* Pascual, 1980a), and trigon basin relatively larger (especially relative to that of *Prepidolops didelphoides*).

MEASUREMENTS. L = 1.50; W = 1.79; mm.

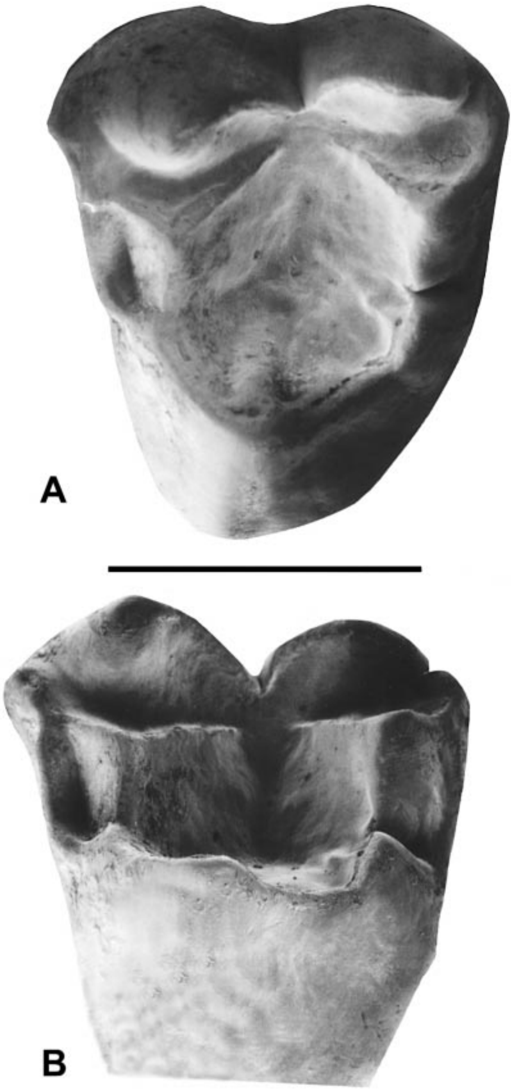


Figure 5 *Incadolops ucayali* sp. nov. LACM 144513 (holotype), left upper molar: **A,** occlusal view; **B,** lingual view. Scale = 1 mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Ucayali,* for the Departamento de Ucayali, in eastern Perú, wherein is found the type locality.

DESCRIPTION. LACM 144513 is subtrapezoidal in shape, wider than long, and with bunoid cusps. The protocone is strong and high, with its anterior face flat, supporting a large trigon basin. The metaconule is well developed, and it is only slightly displaced posterolingually. The premetaconular crest does not meet the base of the metacone; instead, it points anteriad, toward the trigon basin. The metacone is larger and higher than the paracone. Stylar cusps B and D are large and connected to each other by sharp cristae. The posterior crest of StB and the anterior crest of StD are long and sharp edged. At the anterolabial corner of the tooth is a small, anteroposteriorly compressed StA that is connected with a short and wide anterior cingulum. The centrocrista is open (Fig. 5A): the postparacrista ends labially near the posterior crest of StB, whereas the premetacrista ends near the anterior crest of StD. The preparacrista ends at the lingual base of StA. The postmetacrista is short and poorly developed.

COMMENTS. The following features that are present in *Incadolops ucayali* are diagnostic of the Polydolopimorphia: pairing of the paracone and metacone with the StB and StD, respectively, and only relative enlargement of the StB and StD (see Goin and Candela, 1996; and below). In turn, the absence of a "hypocone" (enlarged, displaced metaconule) and the presence of a large trigon basin are distinctive features of the Prepidolopidae.

Incadolops is more generalized than other prepidolopids (*Prepidolops* and *Punadolops*) in the following features: a lower paracone and metacone relative to the protocone, persistence of stylar cusps A and E, better developed metaconule, persistence of the anterior cingulum, less open centrocrista; that is, the labial ends of the postparacrista and the premetacrista are set closer to each other.

Order Polydolopimorphia

Family Indeterminate

Wamradolops gen. nov.

TYPE SPECIES. *Wamradolops tsullodon* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. From the Quechua *wamra,* "child," and the Greek *dolops,* "ambusher," a common ending of several polydolopimorphian generic names; in reference to the small size of the type species in comparison to other polydolopimorphian marsupials.

Wamradolops tsullodon sp. nov.

Figures 6–9

HOLOTYPE. LACM 140590, a right maxilla fragment with complete P^3–M^2 (Fig. 6).

HYPODIGM. The holotype; LACM 140584, right horizontal ramus with M^{1-3} and alveoli of M^4 (Fig. 8); LACM 140640, isolated left P^3; LACM 140601, isolated left ?dp_3; LACM 140654, isolated right M_1 (Figs. 9A–C); LACM 140645, isolated right M_1; LACM 140657, isolated left M_1; LACM 140660, isolated left M_1; LACM 140656, isolated right M_1 (Figs. 9D–F); LACM 140672, isolated fragmentary right M_2; LACM 140655, isolated right M_2; LACM 140658, isolated right M_2 (Figs. 9G–I); LACM 140609, isolated right M_2; LACM 140659, isolated left M_2; LACM 140648, isolated M_2; LACM 140588, isolated left M_3; LACM 140626, isolated left M_3 (Figs. 7B–C); LACM 140587, isolated left M_3; LACM 140586, isolated right M_3; LACM 140589, isolated left M_3; LACM 140608, isolated left M_4; LACM 140594, isolated right P^2; LACM 140595, isolated left P^2; LACM 140591, partial left maxilla with P^3–M^1; LACM 140597, isolated right M^1, very worn; LACM 140616, fragment of an isolated right M^1, without the anterior portion; LACM 144510, isolated left M^1; LACM 140593, isolated right M^1 (Fig. 7A); LACM 140585, isolated right M^2 (Figs. 7D–E); LACM 140596, isolated right M^3; LACM 140592, isolated left M^3 (Figs. 7F–G); LACM 140625, isolated left M^4; LACM 144512, isolated left M^4.

DIAGNOSIS. Upper molars strongly heterodont, with large, posterolingually displaced metaconule; M^1, and to a lesser extent M^2, with very reduced trigon basin as a consequence of the more labial and posterior position of protocone; protocone slightly lower than labial cusps; St?C, intermediate, but far labial to StB and StD, present only in M^1; and (preprotoconal?) cingulum strong, anterolingual to protocone, especially in M^1.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

MEASUREMENTS. See Table 1.

ETYMOLOGY. From the Quechua *tsulla,* "unequal," and the Greek *odontos,* "tooth," in reference to the strong heterodonty of the molar teeth.

DESCRIPTION. Specimens LACM 140594 and LACM 140595 are P^2s, a right and left, respectively. The anterior root of P^2 is more compressed than the posterior root, although it supports the larger and taller cusp of the tooth, which has a long anterior edge. The posterior root supports a very much shorter lobe that also forms a cusp, which is connected with the anterior cusp by means of a sharp crest. The anterior and posterior lobes of P^2 are separated by vertical ridges on both the lingual and labial sides, with the lingual ridge being higher. The posterior face is flat, and the enamel appears thicker on the labial face than on the lingual face. The P^2 is smaller than the P^3.

The holotype, LACM 140590, is a right maxilla with complete P^3–M^2 (Fig. 6). In the P^3, the anterior and posterior lobes are similar in size, and the lingual groove that separates them is wide and deep. Where the cusps merge, they form a continuous anteroposterior ridge, very compressed labiolingually.

The M^1 is much wider than the M^2, and it shows the greatest differences with respect to the generalized tribosphenic pattern. It is suboval in occlusal view, and the protocone is very close to the para- and metacone, being oddly placed between and lingual to them. Consequently, it does not take part in the anterolingual corner of the tooth. The trigon basin is almost absent. A strong ?preprotoconal cingulum develops in this corner and continues be-

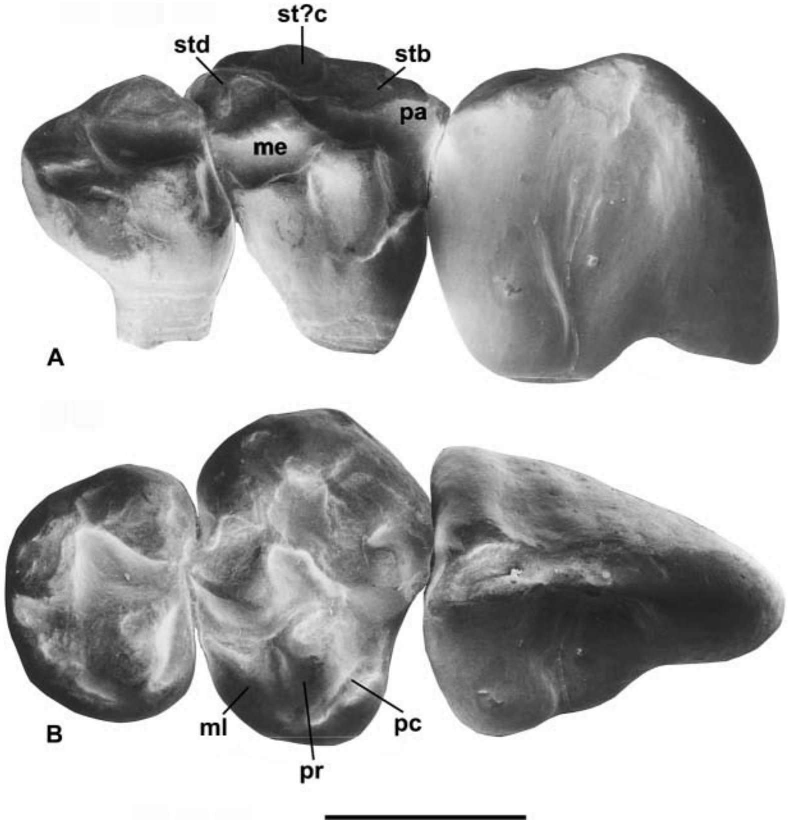


Figure 6 *Wamradolops tsullodon* gen. et sp. nov. LACM 140590 (holotype), partial right maxilla (bone not shown) with complete P^3–M^2: **A,** lingual view; **B,** occlusal view. **Abbreviations:** me, metaconid; ml, metaconule; pa, paraconid; pc, ?preprotoconal cingulum; pr, protoconid; stb, stylar cusp B; st?c, possible stylar cusp C; std, stylar cusp D. Scale = 1 mm.

low and lingual to the protocone. There are no traces of StA or StE. St?C (see below) is present and found on the labial side of the tooth. On the other hand, StB and StD are much more lingually placed on the stylar shelf, being opposite and paired to the paracone and metacone, respectively. A pair of very short crests connect the paracone with StB (the preparacrista?), and StB with St?C. The postparacrista is well developed. It does not connect immediately with the labial end of the premetacrista, but does so instead by means of a short ridge. In turn, StD develops anterior and posterior crests, the former connecting with the premetacrista, whereas the latter connects with the postmetacrista at the posterior side of the tooth. The metaconule is placed in the posterolingual corner of the tooth; it is smaller and lower than the proto- and metacone, and it develops a short anterior crest toward the protocone. In some of the preserved molars, the preprotoconal cingulum reaches the base of the metaconule posteriorly. The whole molar is bunoid, with a short crown and very low cusps, subequal in height. In short, the odd shape of the M^1 is mainly a result of the unequal location of the stylar cusps (quite labial St?C, whereas StD and StB are lingually displaced, almost paired to the metacone and paracone, respectively) and to the very unusual location of the protocone (Figs. 6, 7A).

The M^2 is clearly smaller than M^1. In the M^2, the St?C is absent; StB and StD have a more labial position within the stylar shelf than in M^1, and the metaconule is proportionally larger than in M^1. The preprotocrista connects with a long cingulum that, running along the anterolabial half of the tooth, continues on the labial side almost to the base of StD. The preprotoconal cingulum is somewhat less developed than in M^1. The metaconule is not united to the protocone by a crest; instead, a lingual flex separates the metaconule and protocone. A vestigial postprotoconal cingulum links the metaconule and protocone at their bases. Posteriorly and labially, the cingulum develops a crest that reaches the base of the metacone. The paracone is somewhat smaller than StB, and it is firmly attached to that cusp. The preparacrista is absent. The metacone is slightly larger and taller than StD, and it is located slightly posterior to StD. The centrocrista is open. The postmetacrista is very short. The premetacrista

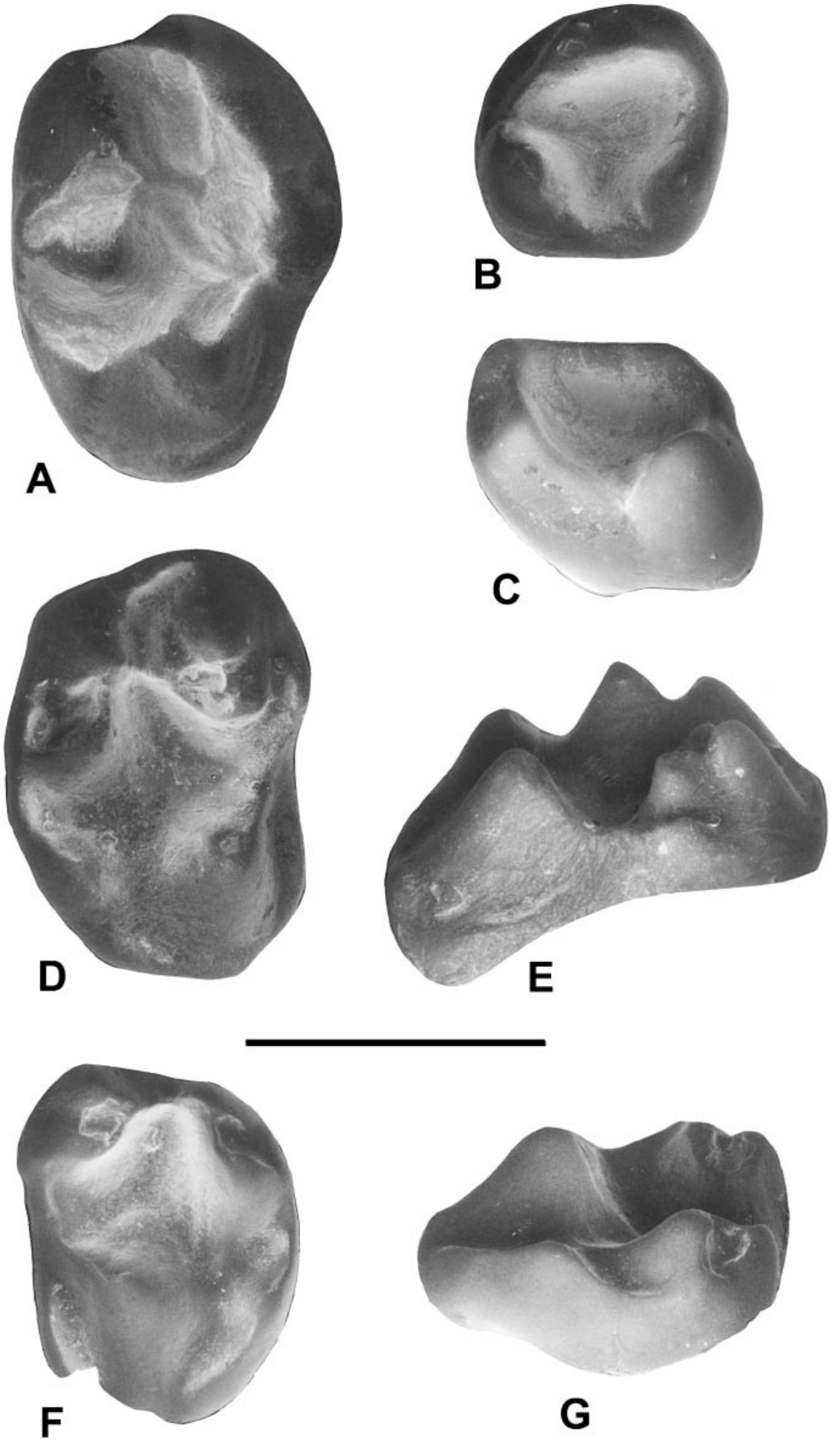


Figure 7 *Wamradolops tsullodon* gen. et sp. nov. LACM 140593, right M^1: **A,** occlusal view. LACM 140626, right M_3: **B,** occlusal view; **C,** labial view. LACM 140585, right M^2: **D,** occlusal view; **E,** anterior view. LACM 140592, left M^3: **F,** occlusal view; **G,** anterior view. Scale = 1 mm.

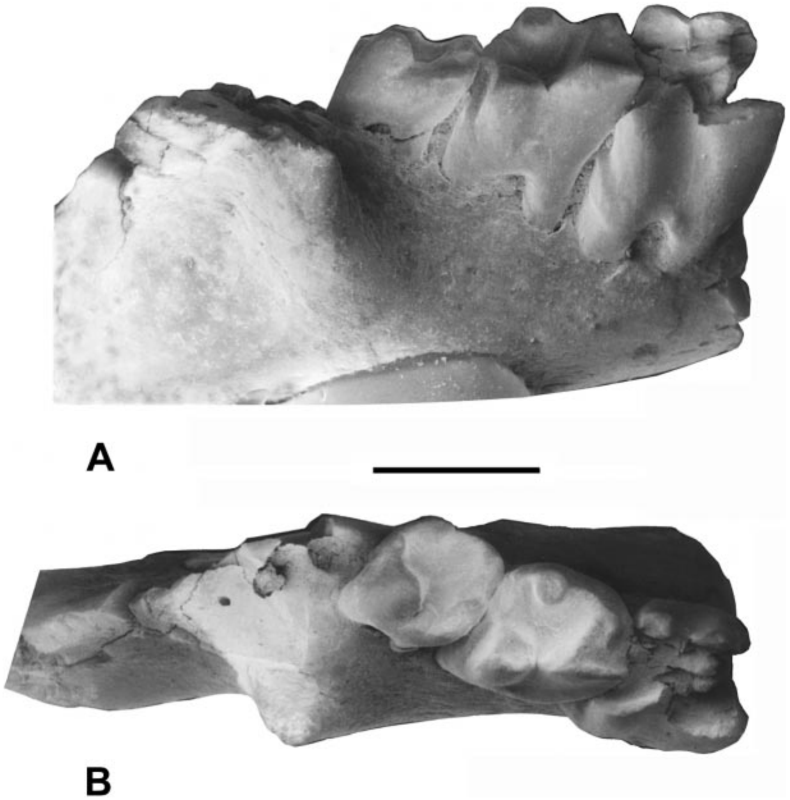


Figure 8 *Wamradolops tsullodon* gen. et sp. nov. LACM 140584, right mandible with M_{1-3}: **A,** labial view; **B,** occlusal view. Scale = 1 mm.

is longer and oriented toward the apex of StD. As the position of the protocone in this molar is more "normal," that is, more lingually placed, the trigon basin is wider than that of M^1.

The M^3 is somewhat smaller than the M^2, although essentially similar to the latter. It differs from the M^2 in the larger size of the protocone; in having the anterior face of the tooth more planar, whereas the posterior side is more rounded; by the weaker development of the metaconule; and by the presence of a continuous and broad lingual cingulum between the protocone and the metaconule. There is no labial cingulum, and the protocone is even more "normally" placed than in the M^2.

The M^4 is smaller than the M^3 and subtriangular in outline because of the absence of a metaconule. The StB is completely fused to the paracone. It is much taller and robust than StD, which is apparently fused to the metacone. The protocone is a low cusp, and the trigon basin is proportionally wide.

The only preserved lower premolar is LACM 140640, a left P_3. It is a large and robust tooth, much larger than the M_1. The anterior half of the P_3 is much more compressed than the posterior half, and its anterior edge is not very sharp. The posterior half develops a cutting edge at its apex. The posterior face of this tooth is almost flat.

The horizontal ramus is thick and robust, with a very deep masseteric fossa and the ascending ramus beginning just behind the M_3. As the ramus decreases in height from back to front, molars are increasingly higher from M_4 to M_1; thus, the top of the tooth row appears horizontal, as is also the case in the Bonapartheriidae.

The M_1 is a relatively high-crowned tooth, with the trigonid very compressed laterally and the talonid short and subequal in width to the trigonid. Its labial side is more than twice as high as the lingual side. This feature, known as "unilateral hypsodonty" in several rodents, is similar to, but much more pronounced than, that seen in prepidolopid or bonapartheriid polydolopimorphians. The anterior and posterior faces of M_1 are flat. The protoconid is very high and pointed, and its anterior and posterior cristae are aligned. The metaconid is much smaller and fused at its base to the protoconid. The paraconid is very small, not connected to the straight preprotocristid, and in a lingual position, almost on the anterior side of the tooth. In several unworn first molars, a small crest,

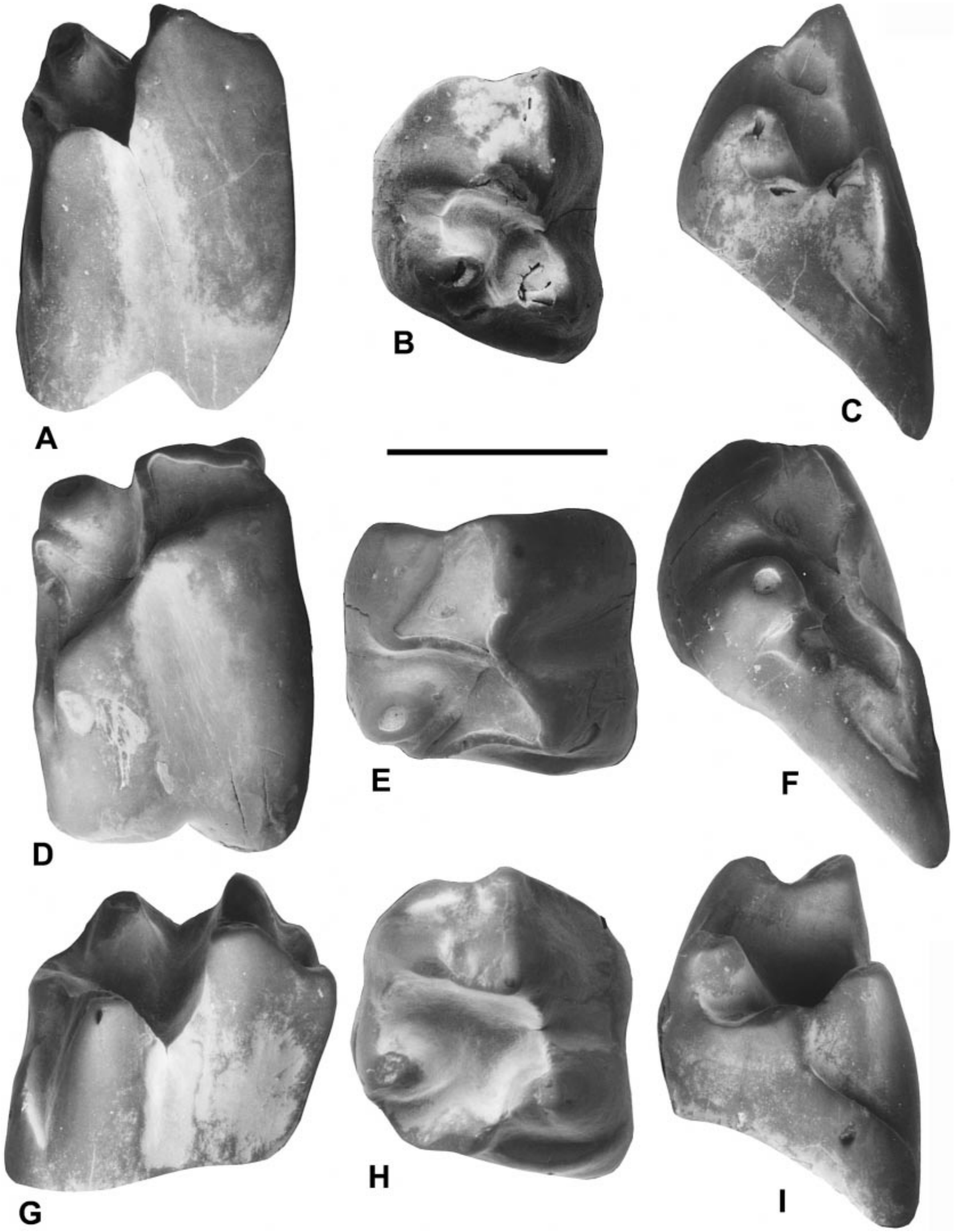


Figure 9 *Wamradolops tsullodon* gen. et sp. nov. LACM 140654, right, unworn M_1: **A,** labial view; **B,** occlusal view; **C,** posterior view. LACM 140656, right, worn M_1: **D,** labial view; **E,** occlusal view; **F,** posterior view. LACM 140658, right M_2: **G,** labial view; **H,** occlusal view; **I,** posterior view. Scale = 1 mm.

Table 1 Measurements (mm) of upper and lower molars of *Wamradolops tsullodon* gen. et sp. nov. L = length, W = width.

	Measurement (mm)							
	M^1		M^2		M^3		M^4	
Specimen	L	W	L	W	L	W	L	W
Upper molars								
LACM 140590	1.20	1.68	0.84	1.20				
LACM 140591	1.12	1.48						
LACM 140616		1.52						
LACM 140597	1.08	1.44						
LACM 140593	1.12	1.44						
LACM 140585			0.96	1.20				
LACM 140596					0.84	1.28		
LACM 140592					0.92	1.16		
Lower molars								
LACM 140584		0.76	1.00	0.72	0.84	0.68		
LACM 140660	1.20	0.80						
LACM 140654	1.16	0.88						
LACM 140656	1.08	1.04						
LACM 140645		0.76						
LACM 140657	1.16	0.88						
LACM 140658			1.12	0.64				
LACM 140655			1.04	0.80				
LACM 140659			0.96	0.68				
LACM 140609			1.12	0.68				
LACM 140589					0.84	0.88		
LACM 140588					0.96	0.80		
LACM 140587					0.96	0.80		
LACM 140626							0.80	0.64

resulting from the fusion of the para- and metaconid slopes, can be observed on the lingual face of the protoconid. The postprotocristid is atypical. Instead of connecting directly with the metaconid, thus forming, in occlusal view, an angle with the preprotocristid, it extends along the posterior side of the protoconid and then turns abruptly toward the metaconid. The entoconid is conical and higher than the hypoconid. The talonid basin is very narrow. The hypoconulid is well developed and placed posterolingually to the entoconid. A narrow postcingulum extends along the posterior side of the tooth. There is a vestigial anterobasal cingulum.

The M_2 is smaller than M_1, and the difference in height between the higher labial and the lower lingual side is less than in M_1. In the trigonid, the paraconid is very compressed anteroposteriorly as a consequence of the shortening of the trigonid on its lingual face, and it is closer to the metaconid than in M_1. The anterior side of the tooth is not flat but, instead, shows a concavity known as the hypoconulid fossa. The preprotocristid is shorter and directed downward, and the protoconid and the metaconid are subequal in height and more separate from each other than they are on the M_1. The talonid basin is somewhat broader than on M_1, and the entoconid and hypoconid are subequal in height. The hypoconulid is centered on the posterior side of the tooth, and it is more compressed dorsoventrally. The postcingulum is also broader than that of the M_1. There is a slightly differentiated anterobasal cingulum.

The M_3 is subquadrangular in outline and limited to four cusps: the metaconid, which is apparently fused with the paraconid, the protoconid, the entoconid, and the hypoconid. The protoconid is lower than the metaconid, and the hypoconid is larger and taller than the entoconid. The trigonid is notably anteroposteriorly compressed, forming, in fact, a crest transverse to the dental axis (the postprotocristid). There is a short anterobasal cingulum labial to the protoconid that continues posteriad basal to it. The talonid basin is proportionally larger than in the anterior molars. The hypoconulid is very reduced.

The M_4 is probably represented by LACM 140608. It is a small tooth, clearly longer than wide, both at the trigonid and at the talonid. The metaconid is taller than the protoconid, and, at its anterior face, it is partially fused to the paraconid. The entoconid is somewhat taller and stronger than the hypoconid. The hypoconulid is very small and low, and it occupies a central position on the posterior face of the talonid. The talonid basin is proportionally very wide.

LACM 140601 seems to represent an incomplete left dp_3. Its morphology is closely similar to that of M_1, except for the greater proximity of the entoconid to the trigonid and the vestigial size of the metaconid. Consequently, the trigonid is shaped almost exclusively by the protoconid and a strong preprotocristid.

COMMENTS. Among all the polydolopimorphians compared with *Wamradolops tsullodon,* the new taxon shows affinities with several groups that hitherto were known exclusively from the South American Paleogene: Prepidolopidae, Bonapartheriidae, Groeberiidae, Polydolopidae (but restricted to Polydolpinae *s.s.*; see below), and, belonging to an undetermined family, *Roberthoffstetteria* Marshall, Muizon, and Sigé, 1983. Affinities with the first two families seem particularly close. In some features, *Wamradolops* seems to be an intermediate form between *Prepidolops* and *Bonapartherium* Pascual, 1980a. In the bonapartheriids, as in the most specialized prepidolopids, the upper and lower molars are strongly heterodont. In the uppers, the metaconule forms a well-developed hypocone-like structure, and the para- and metacone are basally fused to StB and StD, respectively. In turn, the anterior lower molars, $M_{1–2}$, are notably compressed labiolingually to the point where there is practically no talonid basin, and they are relatively high crowned (Fig. 9). Finally, the mandibular ramus is very high (i.e., dorsoventrally deep), and the two last molars, $M_{3–4}$, are placed on the ascending surface of the ramus together with the origin of the masseteric crest (Fig. 8A). Upper and lower premolars are deeply modified as cutting blades, even though they develop a moderate talon at their lingual sides. In the Prepidolopidae the molars are somewhat less heterodont and more low crowned, and the mandibular ramus is robust and thick, but dorsoventrally shallow. The upper molars have only a weakly developed, and sometimes absent, metaconule without forming a "hypocone." The lower molars are shorter, less compressed, and preserve a slightly reduced talonid basin. Finally, the premolars, although hypertrophied and sharp edged, are somewhat more generalized than those of *Bonapartherium.* In *Wamradolops,* there is a mixture of characters of both families, as well as some other features, both primitive and derived, that are exclusive to this genus. Among the primitive characters, the persistence of postparacrista, pre- and postmetacrista, and a stylar cusp (St?C) in M^1 is noteworthy. Among the derived characters is the peculiar position of the protocone, especially in the M^1, in that it is very close to the para- and the metacone and almost leaves no space for the trigon basin (see above). In addition, a peculiar lingual cingulum extends across the base of the protocone.

In other features, *Wamradolops* also seems to be intermediate between *Prepidolops* and *Bonapartherium.* For example, a well-differentiated metaconule is in the position of a "hypocone," but it is less developed than in *Bonapartherium*; the trigonid of the M_1 is very compressed labiolingually, much more than in *Prepidolops,* although not reaching the degree of compression seen in *Bonapartherium* where the trigonid cusps are indistinguishable. The mandibular ramus is robust, broad, and short, as in *Prepidolops,* although the last lower molars ($M_{3–4}$) are placed in an ascending manner following the origin of the masseteric crest, as in *Bonapartherium.* The upper third premolar is very compressed, as in *Bonapartherium,* but without the lingual "talon" characteristic of the P^3 of the latter.

In short, although it is difficult to decide to which family *Wamradolops* belongs, it seems that the new Amazonian taxon is closer to prepidolopids and bonapartheriids, especially to the latter, than to any other known polydolopimorphian. However, several features show the resemblance of *Wamradolops* to other South American Paleogene marsupials as well. These are as follows.

1. One of the most unusual derived features present in the upper molars, and especially in the first upper molar, of *W. tsullodon* is the somewhat posterolabial "shifting" of the protocone (Figs. 6, 7A). As a consequence of this, the trigon basin is reduced relative to the size of the molar. This same feature is also present, though less extreme, in all upper molars of *Roberthoffstetteria nationalgeographica* Marshall, Muizon, and Sigé, 1983, a peculiar marsupial from the lower Paleocene (Tiupampian SALMA) of Bolivia, originally regarded by Marshall and Muizon (1988) as a caroloameghiniid. *Roberthoffstetteria* also shows a somewhat lingual position of StB and StD with respect to StC. The former are, as a consequence, relatively close to the paracone and metacone, respectively (Figs. 6B, 7A), but not as close as in *Wamradolops.*
2. The "shifting" of the protocone as mentioned above is also present in the first two upper molars of *Groeberia minoprioi* Patterson, 1952, from upper Eocene (Divisaderan SALMA) levels in western Argentina. As in *Wamradolops, Groeberia* has its protocone clearly displaced labially in M^1, less displaced in M^2, and almost in a "normal" position in M^3. As a consequence, in the first two upper molars of *Wamradolops* and *Groeberia,* the most lingual cusp is the "hypocone," or displaced metaconule. Finally, both *Wamradolops* and groeberiids have teeth with a very thick enamel layer (see Figs. 9D–F). This feature is also present, but to a lesser extent, in bonapartheriids. Several derived features in common between *Wamradolops* and the recently described, basal argyrolagoid *Klohnia charrieri* Flynn and Wyss, 1999, from lower Oligocene levels of central Chile are also relevant at this point, as discussed below (see "Discussion"). These and other considerations argue in favor of the polydolopimorphian affinities of the groeberiids (and of argyrolagids and patagoniids as well, see below).
3. Several of the above-mentioned derived features

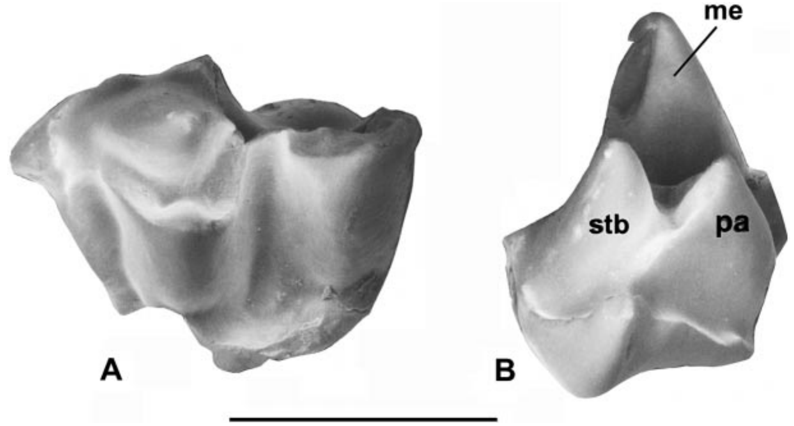


Figure 10 *Hondonadia pittmanae* gen. et sp. nov. LACM 140615 (holotype), isolated upper left molar: **A,** occlusal view; **B,** anterior view. **Abbreviations:** me, metaconid; pa, paraconid; stb, stylar cusp B. Scale = 1 mm.

> are also present in polydolopine polydolopimorphians. These features include the short, dorsoventrally shallow and thick horizontal ramus, strong heterodonty, bunoid crowns with very low cusps, the presence of a strong labial cingulum in the most anterior upper molars and, in the anterior upper molars, an unusually sloped labial face as a consequence of the lingual displacement of StB and StD. In fact, several of the most notable derived features of *Wamradolops* may constitute the plesiomorphic condition for the aberrantly specialized molar pattern of polydolopines. For instance, the "shifted" protocone, together with the strongly developed preprotoconal cingulum, could anticipate the trilobed lingual pattern of the upper molars of polydolopines. And the most labial stylar cusp present in the first upper molar of *Wamradolops* may not be homologous to StC of other marsupials; instead, it might be an accessory cusp that has emerged from the labial cingulum. The latter is the case with the labial accessory cusps and cuspules present in polydolopines.

Leaving aside the question as to what lineage *W. tsullodon* belongs, this taxon is important for our understanding of the Polydolopimorphia as a whole. The assemblage of derived features present in the dentition of *Wamradolops* strongly suggests that it, plus numerous other taxa such as *Roberthoffstetteria, Gashternia* Simpson, 1935; prepidolopids; bonapartheriids; epidolopines; polydolopines; groeberiids; patagoniids; and argyrolagids belong to a monophyletic group (see "Discussion").

Hondonadia Goin and Candela, 1998

Hondonadia pittmanae **sp. nov.**

Figure 10

HOLOTYPE. LACM 140615, an isolated, broken left M^x.

HYPODIGM. The holotype and LACM 144516, a partial ?left M^x.

DIAGNOSIS. Differs from *Hondonadia feruglioi* Goin and Candela, 1998, by having paracone unreduced, but rather high and styliform, subequal to StB; metacone larger than paracone and positioned even more labially.

MEASUREMENTS. LACM 140615: L = 1.52*; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. In honor of our colleague Lidia Romero-Pittman, of INGEMMET, Perú, codiscoverer of the Santa Rosa local fauna and collector of the first marsupial specimen from Santa Rosa.

DESCRIPTION. The holotype is highly fragmented, as it lacks almost the entire lingual half and part of the stylar shelf behind StB and labial to the metacone. In occlusal view, both the anterior and posterior edges of the tooth converge lingually, suggesting that if there had been any metaconule, it was not developed enough to change the subtriangular pattern of the tooth. Only the anterior half of the stylar shelf is preserved, where a small but conspicuous StA and a tall, pointed, and suboval in section StB can be observed (Figs. 10A–B). On the posterior side of this cusp is a small cutting crest, with a minute cusp on its apex, almost fused to the StB. The paracone is in front of the StB; it is well developed, subequal in height, and very close to this cusp. The preparacrista connects with the StA. The postparacrista seems to meet the premetacrista in a very labial point, immediately behind the StB. The metacone is larger and taller than the paracone, and it is much more labially placed than the latter. Both the paracone and the metacone are strongly asymmetric in their labial and lingual sides. Both have convex lingual sides descending smoothly toward the protocone (Fig. 10B), but on the other hand, the labial side of both cusps is planar, almost concave. Labial to StB is a relatively undeveloped cingulum. The anterior cingulum of the tooth is well developed, extending lingually along the base of the paracone.

COMMENTS. The twinning of the paracone and StB and, almost surely, of the metacone and StD, constitutes a polydolopimorphian synapomorphy (Goin and Candela, 1996). Among representatives of this order, the few assessable features of the Santa Rosa species agree well with those of *Hondonadia,* whose type species, *H. feruglioi,* comes from Mustersan SALMA (now recognized as late Eocene/early Oligocene; Kay et al., 1999) levels at Gran Hondonada, in central Patagonia (Goin and Candela, 1998). Derived features shared by *H. feruglioi* and the Amazonian species include: upper molars with trapezoidal outline in occlusal view, preparacrista connecting with StA, open centrocrista, metacone more labially placed than the paracone, and paracone somewhat reduced. In turn, almost all derived features of both species of *Hondonadia* suggest close affinities with the generalized polydolopimorphian *Rosendolops primigenium* Goin and Candela, 1996. That is, the labial sides of the para- and metacone are flat, almost concave; in both genera, the anterior cingulum of the upper molars is well developed, and StB has a posterior, but not an anterior, crest; the preparacrista connects with StA, and the metacone is more labial than the paracone. On the other hand, the genera differ in that *Hondonadia* has its paracone less reduced; the centrocrista is, apparently, not as open as in *Rosendolops*; and StA is more developed. The labial displacement of the metacone (Fig. 10A) with respect to the paracone is a unique, derived feature, incipiently present in *Rosendolops* and more obviously developed in *Hondonadia,* especially in *H. pittmanae.*

In our original description of the holotypical, and until now only known, species of the genus, *H. feruglioi,* we regarded it as a "?Polydolopimorphia" (Goin and Candela, 1998:81). Even though we noted its similarities with *Rosendolops,* the large size of StD (reduced or subequal to StB in other polydolopimorphians, larger than StB in many paucituberculatans) raised doubts about its ordinal assignation. The recognition of new taxa of generalized paucituberculatans in the Santa Rosa fauna sheds much light on the early phases in the evolution of representatives of both orders (see below), and confirms the assignment of *Hondonadia* to the Polydolopimorphia. Additionally, several upper and lower molars referable to a new, still undescribed species of *Hondonadia* have been recovered recently from ?post-Mustersan–?pre-Deseadan levels of the southern cliffs of Lake Colhué Huapi, in central Patagonia (Goin and Candela, 1997). These better preserved specimens have a set of derived features that add decisive evidence in favor of the polydolopimorphian affinities of this genus (see also Goin et al., 1998b).

Rosendolops primigenium was originally, and tentatively, referred to the Prepidolopidae by Goin and Candela (1996). Its affinities with *Hondonadia,* as well as the new information provided by the generalized prepidolopid *Incadolops ucayali* from Santa Rosa, raises doubts regarding its familial assignment. In our present state of knowledge, we prefer to regard both *Rosendolops* and *Hondonadia* as belonging to an as yet undetermined family of Bonapartherioidea (see Table 5).

Order Paucituberculata Ameghino, 1894

Family Caenolestidae Trouessart, 1898

Perulestes gen. nov.

TYPE SPECIES. *Perulestes cardichi* sp. nov.

INCLUDED SPECIES. *Perulestes cardichi* sp. nov. and *P. fraileyi* sp. nov.

DIAGNOSIS. *Perulestes* gen. nov. differs from all other genera of caenolestids in the following features: lower molars with shorter and narrower anterobasal cingula, M_1 with protoconid much higher than metaconid and paraconid more reduced, $M_{2–4}$ with trigonids having metaconids less anteriorly displaced and with very small paraconids, hypoconulids reduced. Upper molars with anterior cingula and paracone present, though very reduced and basally fused to the StB in $M^{1–2}$ and absent in M^4; StB clearly larger than StD in M^1, though subequal in height in $M^{2–4}$; metacone paired with StD but clearly visible; postmetacrista and StA persistent.

ETYMOLOGY. *Peru,* for Perú, the country of origin of the two known species of this genus, and the Greek *lestes,* meaning "robber" or "pirate" and, by extension, "carnivorous," a common ending for generic names of paucituberculatan marsupials.

COMMENTS. See comments under *Perulestes cardichi* sp. nov.

Perulestes cardichi sp. nov.

Figures 11, 12

HOLOTYPE. LACM 140649, a complete, isolated right M^1 (Figs. 11A–B).

HYPODIGM. The holotype; LACM 140606, almost complete, isolated left M_2 (Fig. 12); LACM 140604, almost complete, isolated right M_2; LACM 140652, isolated right M_2 with talonid broken; LACM 149364, isolated left M_2; LACM 140603, isolated right trigonid of M_3; LACM 140605, isolated left M_3; LACM 140599, isolated right talonid of M_4; LACM 140610, isolated left $M_{?3}$, broken in its lingual half; LACM 140624, fragment of left M^1 with only its parastylar corner; LACM 140650, isolated right M^1, complete, but very worn; LACM 140686, fragment of left M^2 with only parastylar corner; LACM 149363, isolated left M^2; LACM 140703, isolated, very worn left M^2; LACM 140613, complete, isolated right

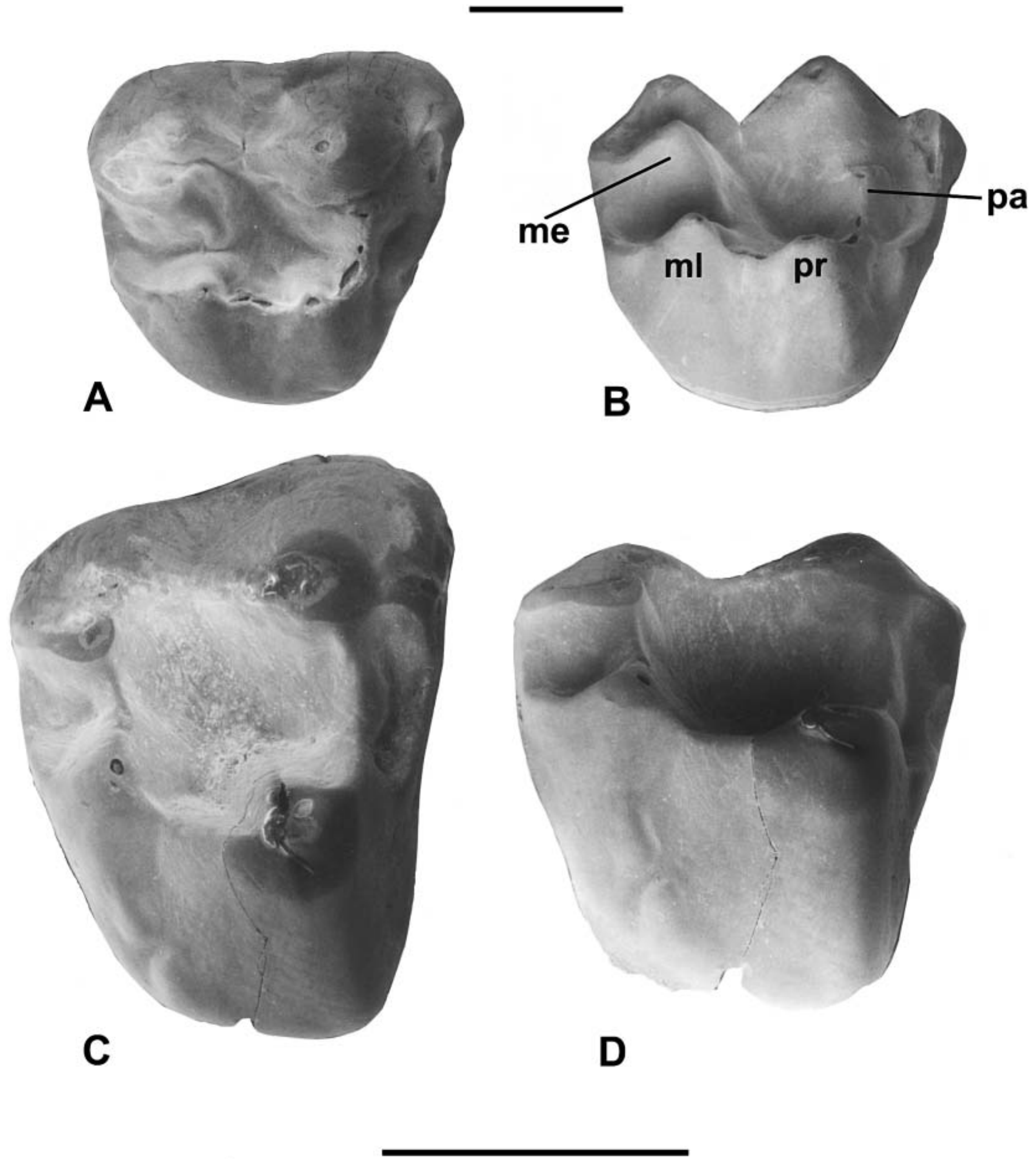


Figure 11 *Perulestes cardichi* gen. et sp. nov. LACM 140649 (holotype), right M^1: **A,** occlusal view; **B,** lingual view. LACM 140613, right M^4: **C,** occlusal view; **D,** lingual view. **Abbreviations:** me, metaconid; ml, metaconule; pa, paraconid; pr, protoconid. Scale = 1 mm.

M^4 (Figs. 11C–D); LACM 140618, partial right M^4 with only posterior half; and LACM 140614, partial left M^4 with only posterior half.

DIAGNOSIS. *Perulestes cardichi* sp. nov. differs from the other species of the genus, *P. fraileyi* sp. nov., in its smaller size and by having lower molars with hypoconulid less developed and less prominent posteriorly and metacone less displaced posteriorly with respect to StD of upper molars.

MEASUREMENTS. See Table 2.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. Honoring Ing. Augusto Cardich, Peruvian Professor of Andean Archaeology at the Museo de La Plata, for his contributions to the knowledge of the South American past.

DESCRIPTION. *Perulestes cardichi* is similar in size to *Pichipilus centinelus* Marshall and Pascual,

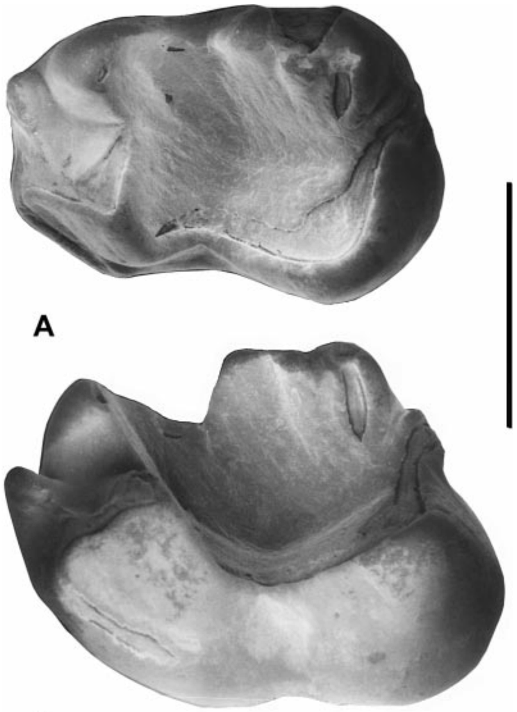


Figure 12 *Perulestes cardichi* gen. et sp. nov. LACM 140606, left M_2: **A,** occlusal view; **B,** labial view. Scale = 1 mm.

1977, from the middle Miocene of Patagonia. On the basis of the preserved remains, the reduction in the size of the tooth row from front to back (i.e., larger to smaller, respectively) is less marked than in other caenolestids. No incisors, canines, premolars, or first molars of this species are known. In the M_2, the trigonid is much shorter and somewhat narrower than the talonid. The anterobasal cingulum is short and narrow. The protoconid is large, occupying almost the whole labial half of the trigonid, but much lower than the metaconid. The protoconid and the metaconid are aligned almost transversely to the dental axis, though the metaconid apex is slightly anterior to that of the protoconid. The paraconid is a very small cusp. It is even lower than the protoconid, and it is positioned somewhat labially to the base of the anterior slope of the metaconid, but it is not fused to this cusp. The anterior end of the preprotocristid does not point toward the paraconid; instead, it descends gradually, without forming a notch, until it merges with the most anterior portion of the anterobasal cingulum. In one of the specimens (LACM 140606; Fig. 12), a minute crest (?postparacristid) can be seen extending labially almost to the preprotocristid. Between the paraconid and the anterior edge of the anterobasal cingulum is a small, shallow cavity: the hypoconulid fossa. Because of the peculiar position of the paraconid, the anterior face of the trigonid is more planar than pointed. Behind and lingual to the metaconid is a small, sharp crest connected to the entocristid. Likewise, behind and labial to the protoconid, another crest is present, though less developed. The metacristid is flat and transverse to the talonid basin; its notch is wide and V-shaped in posterior view.

The talonid is broad and elongated, being approximately two-thirds of the total length of the tooth. Its basin is low relative to the trigonid, and labially it is limited by the cristid obliqua, which extends past the labial edge of the talonid to end anteriorly at the posterolabial corner of the protoconid. The hypoconid is broad and low. The entoconid is notably developed, being very high and laterally compressed; consequently, it forms a lingual wall for the entire talonid. Immediately behind and somewhat labial to the entoconid is a minute hypoconulid. The posterior face of the talonid has no postcingulum.

The M_3 is subequal in size to M_2, and it shows several differences with the latter: the trigonid has its labial side somewhat longer than the lingual side; the protoconid and the metaconid are subequal in height; the paraconid is even more reduced than in M_2, and it is positioned more lingually; the anterobasal cingulum is more vertical; the notch at the metacristid is more open, and the crest is not so perpendicular to the talonid plane but, instead, forms a gentle slope at its union with the talonid; the crest behind the metaconid is proportionally more developed; the talonid is proportionally shorter than in M_2, and the difference in height between its basin and that of the talonid is less; the entoconid and metaconid are more anteriorly placed, with the latter being positioned more medially than the protoconid; and the posterior face of the tooth is not flat but, instead, is more convex than in M_2.

The M_4 is clearly smaller than M_{2-3}. The talonid has the same proportions as in M_3, with the following differences: the cristid obliqua is not parallel to the dental axis but ends anteriorly at the middle point of the base of the protoconid, the entoconid is more styliform in outline, and the hypoconulid is relatively larger.

The upper molars, which decrease in size from M^1 to M^4, are subtrapezoidal in outline, with the labial side longer than the lingual side and with the anterior face straighter than the posterior, which is more rounded. Relative to other Paucituberculata, the most distinctive feature of the upper molars is the persistence, at least in M^{1-2}, of a vestigial paracone (Figs. 11A–B), which is very low and attached to the lingual slope of StB. The paracone, though very small, is clearly present in M^1, whereas in M^2, it seems to be even more fused to the base of StB. The paracone is present in M^3, but it is small and partially fused to StB, almost to the tip. Finally, in the M^4, the paracone is either absent or completely fused to StB (Figs. 11C–D). In turn, the metacone

Table 2 Measurements of upper and lower molars of *Perulestes cardichi* and *P. fraileyi* gen. et spp. nov. L = length, W = width.

	Measurement (mm)							
	M^1		M^2		M^3		M^4	
	L	W	L	W	L	W	L	W
Perulestes cardichi								
Upper molars								
LACM 140649	2.36	2.20						
LACM 140650	2.20	2.00						
LACM 149363			1.85	2.00				
LACM 140703			1.70	2.10				
LACM 140613							1.52	1.88
LACM 140618								1.68
Lower molars								
LACM 140606			1.80	1.12				
LACM 140604			2.20	1.60				
LACM 149364			1.60	1.20				
LACM 140652					1.96	1.32		
LACM 140605					1.96	1.20		
LACM 140603						1.20		0.92
Perulestes fraileyi								
Upper molars								
LACM 140651		2.92						
Lower molars								
LACM 140653		1.36						
LACM 140600		1.28						
LACM 140622		1.36						

is present in every molar and ends posteriorly in a small, though visible, postmetacrista directed toward the metastylar corner. The metacone is subequal in height to the StD and faces this cusp in the M^1; in $M^{2–3}$ it is placed slightly behind it, whereas in M^4 it is positioned even more posteriorly.

The M^1 shows a short, wide anterior cingulum that ends labially in a small StA. Labial to this cusp, on the labial side of the tooth is an enamel thickening directed back and downward, surrounding StB labially. StB is larger and taller than StD; sharp crests join both cusps. Below and labial to these crests there is a short labial cingulum. There is no StC. StD develops a short posterior crest that joins the postmetacrista at the metastylar corner of the tooth. The metacone is slightly lower and subequal in size to StD. On the anterolingual side of this cusp, a rounded edge runs lingually toward the metaconule. The protocone is low, but wide, and limits lingually the small trigon fossa. Anteriorly and labially, it develops a preprotocrista connected to the paracone. Posteriorly, the postprotocrista connects with a hypertrophied metaconule, the "hypocone," that forms a major part of the posterolingual corner of the tooth. The metaconule is somewhat smaller, but taller, than the protocone. It develops a postmetaconular crest that extends along the posterior side of the tooth and ends basally near the metastylar corner. LACM 140650 is an almost complete, although worn, tooth recognized as a right M^1.

LACM 149363, LACM 140686, and LACM 140703 are identified as probable M^2s. The second specimen is only a fragment of the parastylar corner of a left molar, and the last is worn down to the very base of its cusps. Major differences of LACM 149363 with the first molar are its smaller size, a larger anterobasal cingulum, and a less developed paracone. The M^4 has the anterior face much longer than the posterior face, a consequence of the more labial position of the metaconule. The metacone is subequal and very close to StD; it is positioned more posteriorly than in M^3. StB is larger than StD. There is no paracone, or, if present, it is completely fused to StB. The anterior cingulum of the tooth is straight and does not end labially as a differentiated StA. The metaconule and the protocone are subequal in height. Below and lingual to the metaconule is an enamel thickening that shapes a narrow cingulum. The metacone and the metaconule are linked by the respective facing edges of each cusp. StD has no posterior crest; consequently, only the postmetacrista reaches the metastylar corner of the tooth.

COMMENTS. Of the two species of *Perulestes* recognized here, *P. cardichi* is better represented, including remains referable to almost the entire upper and lower molar series. Only specimens of M_1

are missing, although they are represented in *P. fraileyi* sp. nov., (see below). Several derived features present in *Perulestes* warrant its placement in the Paucituberculata. In the upper molars, StB and StD are very large and labiolingually compressed. The paracone is reduced and fused basally to StB, thus indicating an early stage of the trend seen in other paucituberculatans where the paracone is completely fused to StB. In the lower molars, the paraconid is reduced, the paracristid lacks a notch, and the entoconid is laterally compressed (Fig. 12). Compared with the various lineages of paucituberculatans, it is evident that *Perulestes* lacks several derived features diagnostic of the Palaeothentidae and Abderitidae, including an extreme reduction or absence of metacone, hypertrophy of M_1, and absence of paraconid in M_{2-4}. *Perulestes* also lacks several derived features diagnostic of Caenolestinae caenolestids, including upper molars with low metaconule, or "hypocone," which more resembles a posterolingual cingulum than a cusp, and lower molars with a dorsoventral compression of the hypoconulid and with hypoconid high and salient.

Perulestes differs from caenolestids of the subfamily Pichipilinae in having reduced paraconids, the preprotocristid parallel to the dental axis and not connected to the paraconid, and the anterior face of the trigonid flat and transverse to the dental axis. Interestingly, all of these features are suggestive of those already present in the Palaeothentidae and Abderitidae. Another generalized feature of *Perulestes,* compared with the genera of Pichipilinae, is the placement of the metaconid with respect to the protoconid: both are aligned transverse to the dental axis, although the metaconid is slightly anterior. On the other hand, in *Pichipilus* Ameghino, 1890, and *Phonocdromus* Ameghino, 1894, the anterior location of the metaconid is much more marked. Finally, the paraconid of *Perulestes* is not paired with the metaconid but is notably reduced in size and somewhat medially placed in the trigonid. In *Pichipilus* and *Phonocdromus,* as in *Quirogalestes almagaucha* Goin and Candela, 1998, a primitive species of Pichipilinae from the lower Eocene of Patagonia, the paraconid is clearly paired with the metaconid, so that in the worn molars it is difficult to recognize both cusps independently. On the other hand, as occurs in *Pichipilus* and *Phonocdromus,* in *Perulestes fraileyi,* the paraconid and the metaconid of the M_1 are normally separated from each other, so that the trigonid shows a normal prefossid (i.e., trigonid basin). Also, the protocristid of this molar shows a deep notch, as in the pichipilines.

In short, it is difficult to precisely assign *Perulestes* to one of the known subfamilies, or even families, of Paucituberculata, mainly because most features present in *Perulestes,* especially in the upper molars, seem to be generalized for the whole order, and in several features, especially in the lower molars, *Perulestes* is intermediate or transitional between Caenolestinae + Pichipilinae caenolestids on the one hand and Palaeothentidae + Abderitidae on the other (see "Discussion"). In overall features, however, *Perulestes* seems to constitute a generalized, but peculiar, genus of the family Caenolestidae, probably closer to pichipilines than to caenolestines.

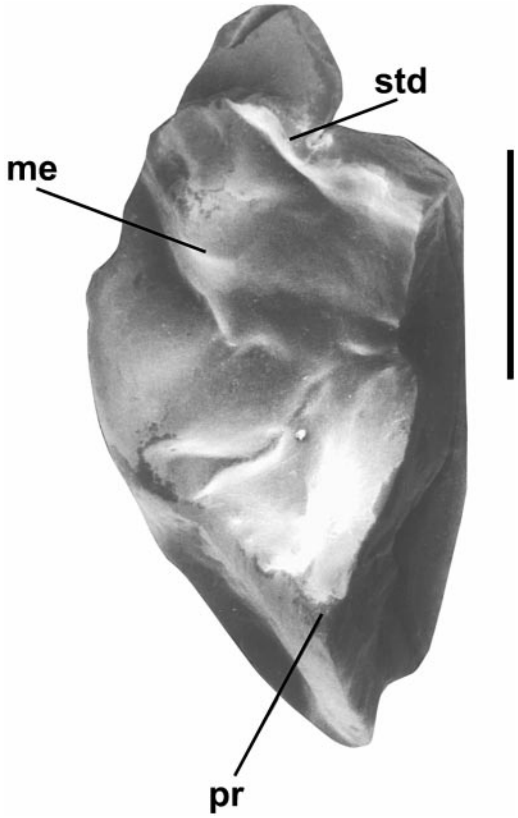


Figure 13 *Perulestes fraileyi* gen. et sp. nov. LACM 140651 (holotype), incomplete right M^4, occlusal view. **Abbreviations:** me, metaconid; pr, protoconid; std, stylar cusp D. Scale = 1 mm.

Perulestes fraileyi sp. nov.

Figures 13, 14

HOLOTYPE. LACM 140651, an incomplete right M^4, without its anterior half and part of the stylar shelf (Fig. 13).

HYPODIGM. The holotype; LACM 140622, right M_1 without talonid (Fig. 14A); LACM 140600, right M_1 without the talonid; LACM 140653, right $M_{?1}$ without the trigonid (Fig. 14B); LACM 144511, isolated left M_3; and LACM 144514, isolated right M^1.

DIAGNOSIS. *Perulestes fraileyi* sp. nov. differs from the type species of the genus by its larger size, and in having lower molars with hypoconulid better developed and more prominent posteriorly, and

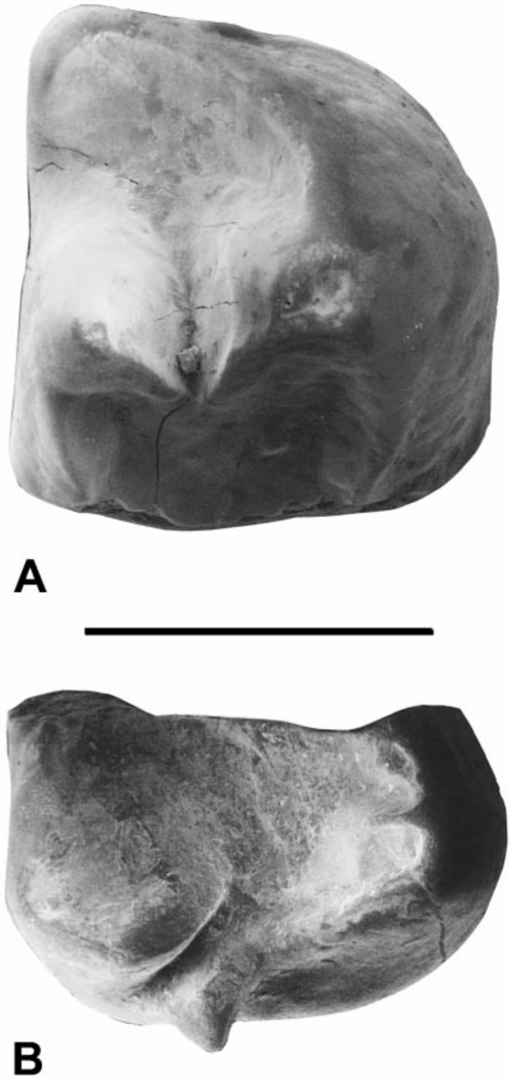


Figure 14 *Perulestes fraileyi* gen. et sp. nov. LACM 140622, right M_1 lacking the talonid: **A,** occlusal view. LACM 140653, right $M_{?1}$ lacking the trigonid: **B,** occlusal view. Scale = 1 mm.

upper molars with metacone positioned more posteriorly with respect to StD.

MEASUREMENTS. See Table 2.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. Honoring Carl D. Frailey, codiscoverer of the Santa Rosa local fauna of eastern Perú; in recognition of his paleontological work in tropical South America.

DESCRIPTION. Only two trigonids are known for the M_1: LACM 140622 and LACM 140600. Both trigonids are identical in size and morphology, although LACM 140622 (Fig. 14A) is less worn and forms the basis for the following description. The protoconid is the largest and tallest cusp of the tooth. Together with the paracristid, it represents two-thirds of the total width of the trigonid. The paracristid is well developed, lacks a notch and, in occlusal view, is not straight but describes a slightly descending curve toward its contact with the paraconid. The paraconid is very small and lingually oriented. The trigonid fossa is open lingually, and the slopes of the three cusps merge on it. The metaconid is intermediate in size and height between those of the paraconid (lower) and the protoconid (taller). The metacristid notch is deep. Behind both the metaconid and the protoconid is a small sharp crest; the one behind the protoconid is more developed. The anterobasal cingulum is vestigial.

The only preserved talonid assignable to this species, LACM 140653, also seems to be an M_1 on the basis of its size and proportions (Fig. 14B). In comparison with the $M_{2–4}$ of the type species of the genus, this specimen has less of a height difference between the entoconid and the hypoconid; the hypoconulid is stronger, more projected backward, and positioned more labially. In turn, the entoconid does not seem to have developed a sharp entocristid. As in the type species of the genus, there is no postcingulum on the posterior side of the talonid of this specimen.

The isolated left M_3 differs from the M_3 of *Perulestes cardichi* in that the posterior face of the trigonid is more vertical, with the protocristid and paraconid comparatively larger. The paraconid is more "normally" positioned on the lingual side of the trigonid. The paracristid is not straight but, instead, forms an almost right angle at the meeting of the preprotocristid and the postparacristid

The only upper molar assignable to this species is the holotype (LACM 140651; Fig. 13), which, judging from the preserved portion, has the same overall proportions and structure as the M^4 of *P. cardichi.* Aside from its much larger size, the greatest differences with the M^4 of the holotypical species of the genus are the following: the metacone is more posteriorly placed; StD seems to have a posterior crest moderately developed; there is a narrow cingulum lingual to the protocone; the metacone is less twinned to StD; the metaconule is lower than the protocone; the premetacrista is still present; and the tooth has a thicker enamel cover, forming superficial "wrinkles" in some places, such as the union between the protocone and the metaconule and the space between StD and the metacone. As in *P. cardichi,* a small lingual crest, the premetaconular crest, connects the metacone with the metaconule.

COMMENTS. *Perulestes fraileyi* is twice the size of the holotypical species of the genus, *P. cardichi.* Unfortunately, the only element preserved for both species is the M^4. The differences, other than size,

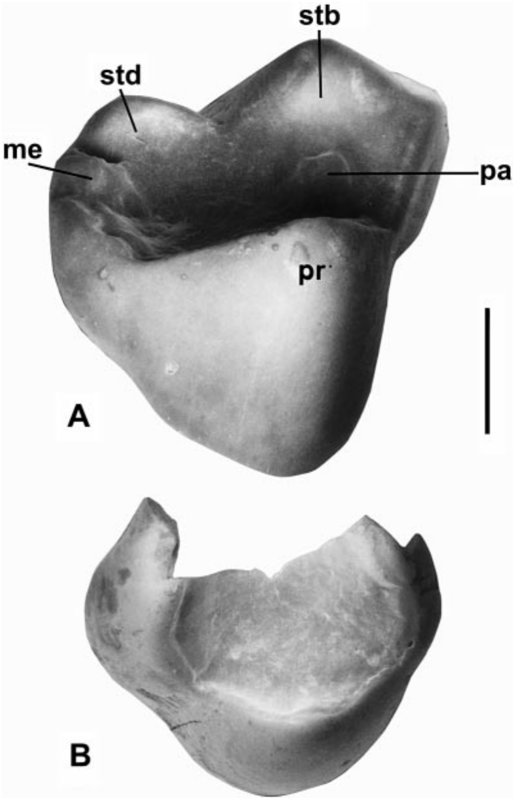


Figure 15 *Sasawatsu mahaynaq* gen. et sp. nov. LACM 140668 (holotype), isolated right M^3: **A,** lingual view. LACM 140647, upper molar ($M^{?4}$): **B,** occlusal view. **Abbreviations:** me, metaconid; pa, paraconid; pr, protoconid; stb, stylar cusp B; std, stylar cusp D. Scale = 1 mm.

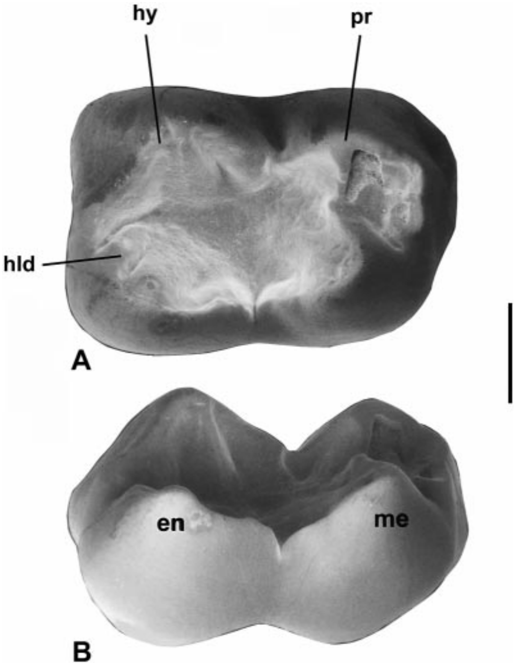


Figure 16 *Sasawatsu mahaynaq* gen. et sp. nov. LACM 140611, isolated left M_2: **A,** occlusal view; **B,** lingual view. **Abbreviations:** en, entoconid; me, metaconid; hld, hypoconulid; hy, hypoconid; pr, protoconid. Scale = 1 mm.

between the M^4 of both species are relatively minor and strengthen their assignment to a single genus.

cf. Family Palaeothentidae Sinclair, 1906

Sasawatsu gen. nov.

TYPE SPECIES. *Sasawatsu mahaynaq* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. From the Quechua *sasa,* "difficult," and *watsu,* "root"; in reference to its problematic, inferred ancestry.

Sasawatsu mahaynaq sp. nov.

Figures 15, 16

HOLOTYPE. LACM 140668, a complete, isolated right M^3 (Fig. 15A).

HYPODIGM. The holotype; LACM 149366, isolated right M^3; LACM 140695, distal portion of lower right incisor (I_2); LACM 140607, fragment of horizontal ramus with intra-alveolar portion of hypertrophied incisor, M_2 complete, and alveoli of P_2–M_1 and M_{3-4}; LACM 140611, complete, isolated left M_2 (Fig. 16); LACM 140646, partial right $M_{?2}$ without posterior half of talonid; LACM 144509, isolated right M_4; LACM 140647, upper ?right molar ($M^{?4}$), lingual half only (Fig. 15B).

TENTATIVELY REFERRED SPECIMEN. LACM 149365, right $M_{?2}$ (see "Comments").

DIAGNOSIS. *Sasawatsu mahaynaq* differs from the remaining species of Paucituberculata in the following combination of features: molars large and low-crowned; M_1 only moderately larger than M_2; lower molars with distinct, although very reduced, paraconid, which is lingual and close to, but not fused with, metaconid; upper molars with paracone and metacone very close to StB and StD, respectively, and much smaller than the latter; stylar cusps not labiolingually compressed.

MEASUREMENTS. See Table 3.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. From the Quechua *mahaynaq,* "unique, unmatched."

DESCRIPTION. LACM 140607 preserves most of the horizontal mandibular ramus. This bone is robust and fusiform, reaching its greatest height below the M_3. In lateral view, the alveolar plane is straight until about the anterior root of the M_3. The posterior root of the M_3 and both roots of the M_4

Table 3 Measurements of upper and lower molars of *Sasawatsu mahaynaq* gen. et sp. nov. L = length, W = width.

	Measurement (mm)					
	M^2		M^3		M^4	
	L	W	L	W	L	W
Upper molars						
LACM 140668			3.28	4.20		
LACM 140647					2.92	
LACM 149366			3.10	4.05		
Lower molars						
LACM 140661	3.80	2.40				
LACM 140607	3.88	2.60				
LACM 140646		2.40				
LACM 149365	4.10	2.90				

are placed on an ascending plane that follows the origin of the masseteric crest. This crest begins behind M_4, as in most Palaeothentidae and unlike in the Abderitidae, in which the ascending ramus arises labial to M_4. In occlusal view, the alveolar row is not straight but curved, being outwardly convex. The horizontal ramus has a flat or slightly concave lingual side and a convex labial side. There are three mental foramina in the labial side. The largest is below the P_3, and two other very small foramina, one below the M_1 and the other below the anterior root of the M_2, are found more posteriorly. On the lingual side of the horizontal ramus the symphysis extends posteriad to a point below the posterior edge of P_3.

Only two teeth are preserved in this ramus, a proximal portion of the hypertrophied incisor (I_2) and the M_2. Anterior to the M_2 are the alveoli of the M_1 and, anterior to those, another four alveoli that decrease in size anteriad. Although the mandible is broken anteriorly, it can be seen that anterior to the latter alveoli is a bony space that, as a diastema, separated them from the hypertrophied incisor. Finally, between the diastema and this incisor, part of the alveolus of a small, single-rooted and somewhat procumbent tooth can be seen. This alveolus probably belonged to the second, which was probably the last, incisor of the series. It is difficult to specify the homologies of the teeth anterior to the M_2 because of the poor preservation of their alveoli. The two alveoli immediately anterior to M_2 correspond to those of the M_1, whereas the most anterior alveolus after the diastema may belong to the canine and the next to three single-rooted premolars or, more probably, to one single-rooted premolar and one two-rooted premolar. Consequently, we think that the most probable lower dental formula was: I/2, C/1, P/2, M/4.

The root of the incisor, LACM 140695, is suboval in cross section. In its distal portion, the incisor is relatively short, robust, and somewhat spatulate, with its larger diameter in the vertical plane and with the enamel coat covering the labial and ventral sides. In LACM 140695, there is a small horizontal wear facet on the tip.

No lower premolars or M_1s are known. Judging from the alveoli of the M_1, it was moderately larger than M_2.

The M_2 is robust, with the labial side considerably higher than the lingual side, and the trigonid, which is anteroposteriorly short, being longer on its labial side than on its lingual side. The protoconid is robust, although lower than the metaconid. The paraconid is very small and positioned at the base of the anterolingual slope of the metaconid, to which it is much closer than to the protoconid. The paracristid forms a right angle in its distal portion, such that the distal third of it, which connects with the paraconid, is perpendicular to the dental axis. The metaconid develops a crest posteriorly that connects with the entocristid. The talonid is as wide as the trigonid, though clearly longer. The entoconid is tall, is subequal in height to the metaconid, and expands anteriorly as a crest that forms a lingual border to the talonid. Two vertical grooves, one anterior and the other posterior to the entoconid cusp, can be observed on its internal face. The hypoconulid is short and occupies a more lingual position than in most Palaeothentidae and Abderitidae.

The M_3, in comparison with the M_2 (Fig. 16), is slightly smaller. It has a difference in height between the labial and lingual sides of the tooth; a hypoconulid that is less distinct and more centrally positioned; the paracristid shorter; the paraconid more mesial and closer to the main axis of the paracristid, being equidistant from the protoconid and the metaconid; the vertical grooves on the internal face of the entoconid deeper; and the anterobasal cingulum better developed.

The M_4 is much smaller than the M_3, but similar in general shape. The paracristid is not straight but, instead, forms in occlusal view an almost right angle at the union between the postparacristid and the preprotocristid. The protoconid is positioned slightly anteriorly compared with the metaconid, and both the entoconid and the hypoconid have noticeable grooves on the slopes that face the talonid basin. The talonid basin of the M_4 is comparatively smaller than that of the M_3, and on its posterior face, the hypoconulid is positioned more centrally and ventrally.

Only three upper molars have been identified: the holotype (LACM 140668; Fig. 15A); LACM 149366, which is essentially identical to the holotype; and LACM 140647 (Fig. 15B), a very fragmented specimen, probably an M^4. The holotype is an M^3, with its anterior side much longer than the posterior side and with a large central basin. The protocone is robust and occupies almost all the lingual side of the tooth. StB is also very large, although low. There is no StC or StA. StD is smaller than StB, and anteriorly, it develops a short crest. The paracone and the metacone are very reduced and tightly paired to StB and StD, respectively. The metaconule is poorly differentiated. There are no sharp cristae.

LACM 140647 ($M^{?4}$) is smaller than the other two upper molars, and it preserves only its lingual half. Only a robust protocone and a poorly developed metaconule bordering lingually a large central basin can be distinguished. No vestiges of the paracone or the metacone can be observed, although this may be because the tooth is broken labially.

COMMENTS. Even though generalized in several features of upper molar morphology, including the persistence of a vestigial paracone and poorly developed metaconules, *Sasawatsu mahaynaq* is a strongly derived species of Paucituberculata. This is a result of its adaptations toward frugivorous feeding habits. All cheek teeth are brachydont, with very low and bunoid cusps, wide basins, and a complete absence of cutting crests. As in *Perulestes,* at least the M^3 preserves a vestige of the paracone, which is almost completely fused to the base of StB. Unlike *Perulestes,* the metacone is notably reduced and attached to the lingual side of StD. In the lower molars, the paraconid occupies a relatively mesial position. In some molars, such as the M_3, it is almost equidistant from the protoconid and the metaconid. The lower dental formula of this peculiar paucituberculatan suggests that it belongs to the Palaeothentidae or Abderitidae. However, judging from the M_1 alveoli, this molar was not much larger than the M_2; in turn, in members of these families, the M_2 is much larger than the M_3. On the other hand, the assemblage of features of upper and lower teeth resembles more those of the Palaeothentidae than those of the Caenolestidae or the Abderitidae.

Sasawatsu is one of the largest (squirrel-sized) and most specialized marsupials of the Santa Rosa local fauna. As with *Perulestes,* persistence of the paracone of the upper molars suggests an early stage in the development of the quadrangular molar of the Paucituberculata.

LACM 149365, an isolated right lower molar, is here regarded as a probable M_2 assignable to this species. It is similar to other M_2s of *S. mahaynaq,* differing only by having a slightly larger size, a higher labial face, the paraconid closer to the metaconid, and a less distinct hypoconulid that is placed higher than in the other M_2s. It could be the case that this molar actually represents a first lower molar. However, its size does not match the size of the alveoli for the first molar in LACM 140607, which indicates a larger tooth. Second, its morphology does not fit with that of any known paucituberculatan first lower molar. Among the Caenolestidae, the trigonid is very open lingually; in the Palaeothentidae, the trigonid is extremely open, and the cristid obliqua meets the metaconid at its anterior end; and in the Abderitidae, the trigonid of the M_1 is comparatively very large and bladelike. None of these features occur in LACM 149365, and given all other sources of evidence, the possibility that this molar might belong to a new, distinct clade of paucituberculatans not recorded up to now seems remote. A more plausible hypothesis is that intraspecific variability (e.g., sexual dimorphism) is responsible for the observed differences between LACM 149365 and other specimens here assigned to M_2s.

Distinct striations occur on the enamel surface of most specimens here assigned to *S. mahaynaq.* They are obvious on the labial surfaces of lower molars and on the lingual surfaces of the upper molars. They seem to be perikamata, which have been described for other mammals (e.g., Moss-Salentijn et al., 1997). Perikamata consist of alternating ridges and grooves on the enamel surface, shaping a banded pattern that is approximately parallel to the dental axis. Perikamata are considered to be the result of differential growth patterns during the early phase of amelogenesis. They are common in primates, including man. To our knowledge, this feature is not present in any other South American fossil or living marsupials.

Order Microbiotheria Ameghino, 1889

Family Microbiotheriidae Ameghino, 1889

Kirutherium gen. nov.

TYPE SPECIES. *Kirutherium paititiensis* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. From the Quechua *kiru,* "tooth" and the Greek *therion,* "beast," a common ending of generic names for microbiotherian marsupials.

Kirutherium paititiensis sp. nov.

Figure 17

HOLOTYPE. LACM 140620, an isolated left M^3, broken at its labial third.

HYPODIGM. The holotype only.

DIAGNOSIS. *Kirutherium paititiensis* differs from other microbiotheriids in the following features: upper molars with vestigial para- and metaconules that are elongate and partially fused with

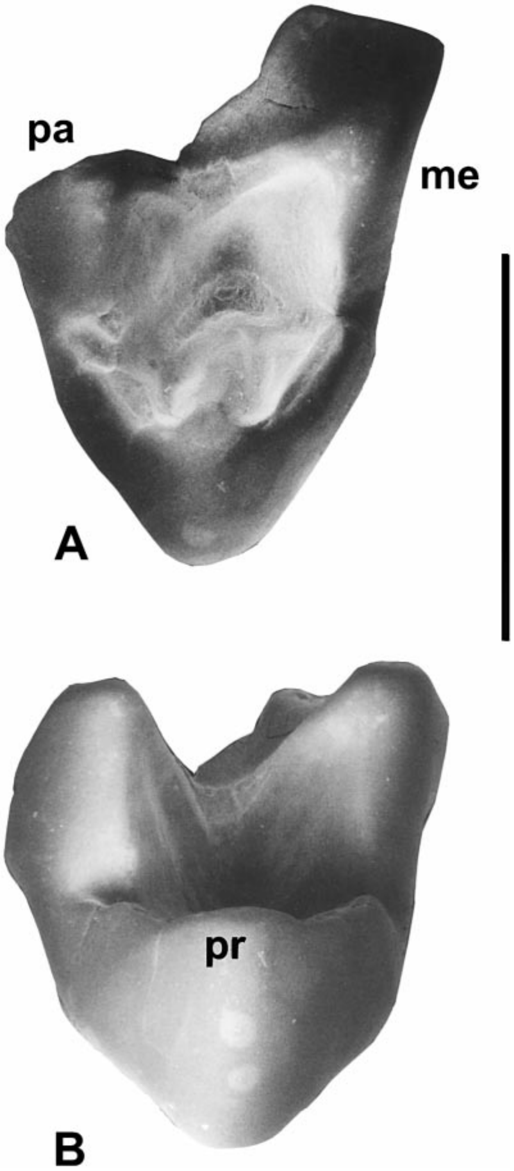


Figure 17 *Kirutherium paititiensis* gen. et sp. nov. LACM 140620 (holotype), isolated left M^3 broken labially: **A,** occlusal view; **B,** lingual view. **Abbreviations:** me, metaconid; pa, paraconid; pr, protoconid. Scale = 1 mm.

pre- and postprotocrista, respectively; trigon basin very deep, having its lingual face divided by two labiolingually oriented grooves; postmetacrista poorly developed.

MEASUREMENTS. LACM 140620: L = 1.23*, W = 1.42; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Paititiensis,* from Paititi, a lost city of the Incas that was probably located in the tropical forests east of the Andean Cordillera.

DESCRIPTION. The holotype, an isolated upper left molar (M^3), is very similar in size to that of the only living microbiotheriid, *Dromiciops gliroides* Thomas, 1894. The labial third is broken in such a way that it lacks almost all of the stylar shelf (Fig. 17A). However, it is evident, judging from the preserved posterolabial corner of the tooth, that the stylar shelf was short, as in *Dromiciops* Thomas, 1894, or *Microbiotherium* Ameghino, 1887. The para- and metacone are subequal in size and height, and they are well separated from each other. Both cusps have their labial sides descending smoothly toward the labial face of the crown. The centrocrista is straight and forms a wide valley at the contact between the postparacrista and the premetacrista. The postmetacrista is only partially preserved, although, judging from its overall proportions, it was relatively short. Neither the preparacrista nor stylar cusps were preserved. The posterior third of the stylar shelf, which is preserved in the holotype, shows no stylar cusps, thus suggesting that, as in other species of the family Microbiotheriidae, stylar cusps were extremely reduced or absent. The protocone is wide, and the trigon basin very deep. On the lingual face of the trigon basin are a couple of peculiar, shallow grooves that border the protocone at its lingual base (Fig. 17A). The protocone is slightly eccentric in that it is oriented anteriorly. Both the para- and metaconule are vestigial, elongate, and partially fused with the labial ends of the pre- and postprotocrista, respectively (Fig. 17B). There are no anterior or posterior cingula in the preserved portion of the tooth.

COMMENTS. Most of the features of *Kirutherium paititiensis* constitute a combination of primitive and derived characters unequivocally diagnostic of the Microbiotheriidae: large protocone, wide and deep trigon basin, straight centrocrista, very narrow stylar shelf with vestigial or absent stylar cusps, relatively short postmetacrista, para- and metacone subequal in size and height, and vestigial para- and metaconule. The overall proportions of the tooth, including the relatively short postmetacrista, agree with those of the M^3 of other microbiotheriids with known upper dentitions. *Kirutherium* seems to be close to *Microbiotherium* and *Dromiciops* in having a wide protocone and deep trigon basin. *Khasia cordillerensis* Marshall and Muizon, 1988, from lower Paleocene (Tiupampian SALMA) levels at Tiupampa, Bolivia, has its protocone more anteroposteriorly compressed and a very reduced stylar shelf without cusps or crests.

Order and Family Indeterminate

Wirunodon gen. nov.

TYPE SPECIES. *Wirunodon chanku* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

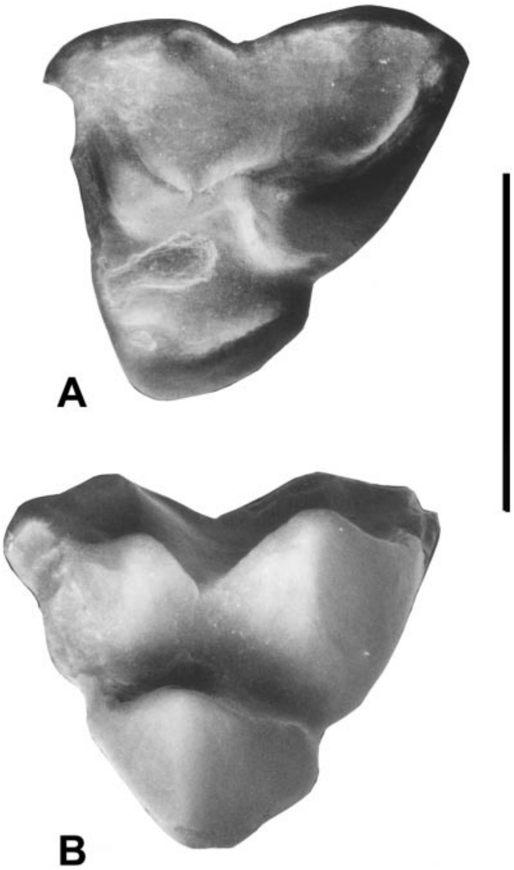


Figure 18 *Wirunodon chanku* gen. et sp. nov. LACM 140621 (holotype), isolated upper left molar ($M^{?3}$): **A,** occlusal view; **B,** lingual view. Scale = 1 mm.

ETYMOLOGY. From the Quechua *wiruna,* "small mallet," and the Greek *odontos,* "tooth," in reference to the relatively small protocone and trigon basin of the holotype of the type species.

Wirunodon chanku sp. nov.

Figures 18, 19

HOLOTYPE. LACM 140621, an isolated upper left $M^{?3}$ (Fig. 18).

HYPODIGM. The holotype and LACM 140677, an isolated right trigonid (Fig. 19).

DIAGNOSIS. Upper molars with almost straight centrocrista; both protocone and trigon basin reduced; stylar shelf wide; postmetacrista well developed; preparacrista connects with stylar cusp A; stylar cusps B and D reduced and labiolingually compressed; paracone very reduced relative to metacone, suboval in section, and with its long axis peculiarly oriented with an anterolabial–posterolingual axis; para- and metaconules absent.

MEASUREMENTS. LACM 140621: L = 1.27, W = 1.12; LACM 140677: L (trigonid) = 0.74, W (trigonid) = 0.78; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. From the Quechua *chanku,* "opossum."

DESCRIPTION. The holotype is very small, comparable in size to an M^3 of the smallest living marmosines. The protocone is eccentric, almost aligned in an axis with StB and the paracone. The paracone is much lower and reduced with respect to the metacone, and the centrocrista is almost straight. The anterior cingulum is wide and extends lingually in the preprotocrista. There is no para- or metaconule. The stylar shelf is wide, and both StB and StD are positioned very labially. StD is more labiolingually compressed than StB. Both StC and StE are absent. The postmetacrista is well developed; the preparacrista apparently connects with a small StA. The paracone and metacone have flat labial surfaces (Fig. 18A), thus both cusps are suboval in section, rather than conical, with their longer axes parallel to the dental row. The paracone, however, is slightly twisted on an anterolabial–posterolingual axis. For this reason the postparacrista is not completely straight, but forms instead, in occlusal view, a minute notch at its contact with the premetacrista (Fig. 18A). The relative width of the stylar shelf and the development of the postmetacrista agree with the pattern seen in the M^3 of other "opossum-like" marsupials.

LACM 140677 is an isolated right trigonid of a lower molar. The anterobasal cingulum is narrow, and it extends basally almost to the paracristid. This crest is well developed as a consequence of the considerable height of the protoconid. The paraconid is well developed, although it is slightly lower than the metaconid (Fig. 19B). The paracristid notch is deep. Even though the talonid is broken away, it can be observed that its basin was very shallow. The anterior end of the cristid obliqua meets the metacristid at a point below the notch, thus suggesting that this specimen is an M_4.

COMMENTS. This enigmatic marsupial is difficult to assign to any known marsupial order. On the one hand, the persistence of an almost straight centrocrista suggests that it belongs to the Peradectia or the Microbiotheria. However, a relationship to the latter can be rejected on the basis of almost all the remaining available characters: the trigon basin is reduced (very wide in Microbiotheriidae); the protocone is not wide, but rather narrow (wide in Microbiotheriidae); the stylar shelf is wide (very reduced in Microbiotheriidae); and the metacone is much larger and taller than the paracone (paracone and metacone subequal in Microbiotheriidae). This last feature also differentiates *Wirunodon* from the Peradectia, as do the smaller protocone, StB, and StD; the great development of the postmetacrista; the absence of para- and metaconules; and the pre-

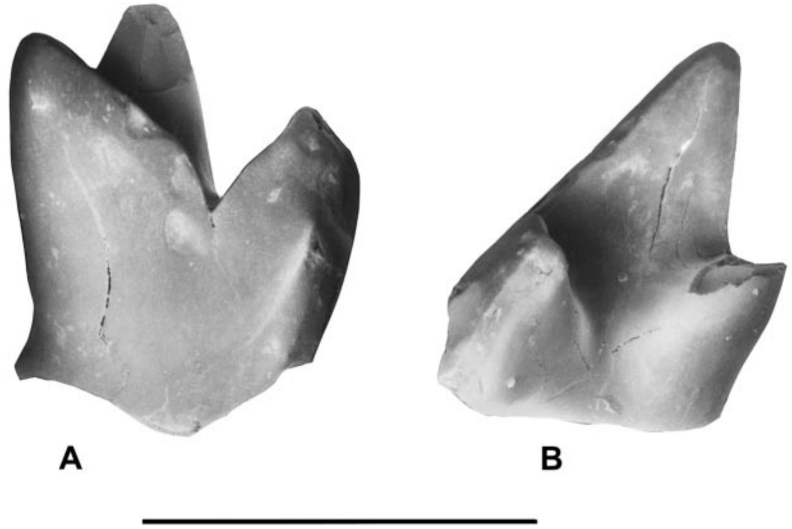


Figure 19 *Wirunodon chanku* gen. et sp. nov. LACM 140677, right trigonid: **A,** labial view; **B,** lingual view. Scale = 1 mm.

paracrista connected with StA. In fact, most derived features of *Wirunodon* are consistent with its assignment to the Didelphimorphia, among which are forms with a well-developed postmetacrista, a clear difference in height between para- and metacone, StB and StD relatively reduced and labiolingually compressed, and para- and metaconule reduced or absent. However, in all known Didelphimorphia the centrocrista is V-shaped, although with variations (Goin, 1997). Finally, sparassodont affinities of *Wirunodon* can be ruled out on the basis of its wide stylar shelf, shallow ectoflexus, and moderately separated, rather than close, paracone and metacone.

The existence of South American peradectians strongly specialized toward frugivorous habits, such as the Caroloameghiniidae (Goin et al., 1998a), suggests that on this continent other peradectian lineages may have differentiated toward faunivorous or even carnivorous habits. On the other hand, it is also reasonable to suppose that the almost straight centrocrista of *Wirunodon* is secondarily derived from a more typical didelphimorphian condition. Regarding the lower molars of *Wirunodon,* the trigonid structure in specimen LACM 140677 is highly generalized, although it shows a long and deep paracristid, along with a well-developed postmetacrista of the holotype. The connection of the cristid obliqua to a point below the notch of the paracristid anteriorly is a primitive feature that is present in all peradectids and in numerous Paleogene didelphimorphians.

The only marsupial known to us that resembles *W. chanku,* with its unique combination of plesiomorphic, apomorphic, and autapomorphic features, is *Kasserinotherium tunisiense* Crochet, 1986, from the lower Eocene of Tunisia (Africa), which is regarded as a peradectid. In particular, one of the specimens assigned to this species (EY 12; see Crochet, 1986:924, figs. 2a–c), referred to as an M^1 or M^2, closely resembles the holotype of *W. chanku* in having a very small size, straight centrocrista, conules absent, reduced protocone and trigon fossa, reduced and labiolingually compressed stylar cusps, wide stylar shelf, and well-developed postmetacrista. The fact that the preparacrista ends labially at the anterolabial corner of the tooth (StA?) may be another feature in common between *Wirunodon* and *Kasserinotherium.* Even though the preparacrista of the M^3 of *K. tunisiense* seems to connect with StB, this may not be the case in more anterior molars (see Crochet, 1986:fig. 2a). In fact, Crochet (1986:924) notes that, in specimen EY 12, “L’angle formé par la centrocrète et la paracrète est plus ouvert qu’il en l’est habituellement pour une dent de ce rang chez les marsupiaux primitifs.”

Kiruwamaq gen. nov.

TYPE SPECIES. *Kiruwamaq chisu* sp. nov.

DIAGNOSIS. As for the type, and only known, species.

ETYMOLOGY. From the Quechua *kiru,* “tooth,” and *wamaq,* “strange, odd.”

Kiruwamaq chisu sp. nov.

Figure 20

HOLOTYPE. LACM 140619, an almost complete, isolated left $M^{2?3}$.

HYPODIGM. The holotype only.

DIAGNOSIS. *Kiruwamaq chisu* differs from all

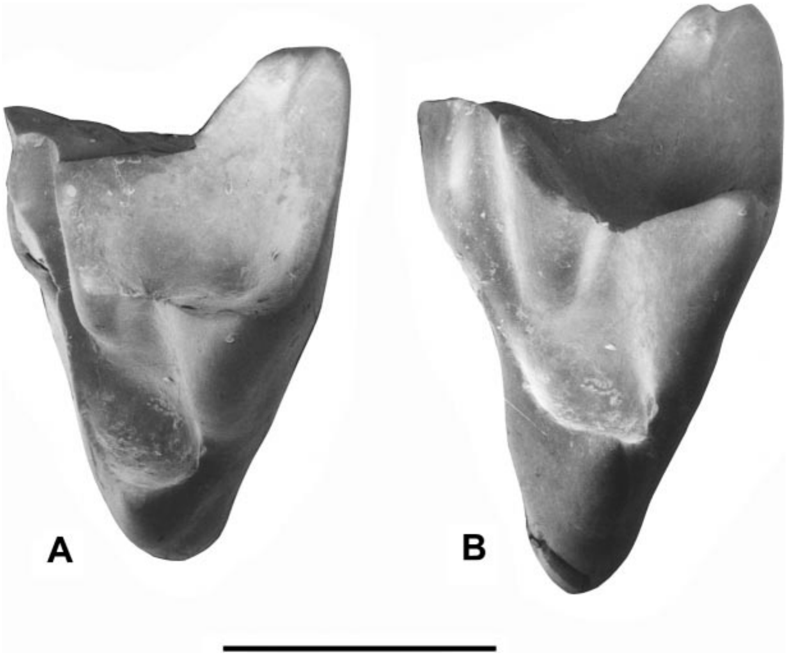


Figure 20 *Kiruwamaq chisu* gen. et sp. nov. LACM 140619 (holotype), isolated upper left molar ($M^{?3}$): **A,** occlusal view; **B,** lingual view. Scale = 1 mm.

other known South American "opossum-like" marsupials in the following combination of characters: very small size; reduced protocone; paracone much smaller, more labially oriented, and very close to the metacone; straight centrocrista; postmetacrista well developed; stylar shelf very wide only in its anterior half; StD very small, labially oriented and labiolingually compressed; preprotocrista connects continuously with anterior cingulum of tooth.

MEASUREMENTS. L = 0.85, W = 1.19; mm.

TYPE LOCALITY. Santa Rosa, Perú. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. From the Quechua *chisu,* "very small."

DESCRIPTION. The holotype is broken at its anterolabial end, including the area of StB and the anterolabial end of the preparacrista (Fig. 20A). It is a very wide and short tooth, with all its crests sharp and with the crown much higher at the postmetacrista than at the preparacrista. The protocone is notably reduced and low; consequently, the trigon basin is vestigial. The preprotocrista does not end at the paracone base; instead, it runs anterior to it and continues to the anterior cingulum. The postprotocrista is, in contrast, very short and ends at the base of the metacone. These features, together with the labial retraction of the paracone, give a peculiar, asymmetric shape to the whole tooth. The paracone is much smaller and lower than the metacone. It, with the metacone, does not form an axis parallel to the dental axis; instead, it is positioned more labially and very close to the metacone. The centrocrista is straight. The preparacrista and the postmetacrista are sharp. The anterior faces of the paracone and the metacone are, as in *Wirunodon chanku,* extremely flat and perpendicular to the plane of the stylar shelf. The preparacrista is broken at its labial end; thus, its eventual connection with any anterior stylar cusp cannot be observed. However, it can be seen that the preparacrista was long, although shorter than the postmetacrista. The ectoflexus was apparently deep. The postmetacrista is notably developed, and, in occlusal view, it is perpendicular to the dental axis. The stylar shelf is very wide for its anterior half. Both the preparacrista and the postmetacrista form gradual slopes on the anterior and posterior limits of the stylar shelf; consequently, the stylar shelf is basin-shaped instead of flat. The great relative development of the postmetacrista suggests that this tooth corresponds to an M^3.

COMMENTS. *Kiruwamaq chisu* is an unusual South American mammal, the affinities of which are a mystery. The possession of a straight centrocrista is a generalized feature present in the Peradectia and Microbiotheria and in some Sparassodonta. However, most remaining derived features of *K. chisu* exclude it from these groups. This species could also be thought to belong to the Didelphimorphia. In fact, some lineages of this order, such as the Sparassocynidae, have also developed large postmetacristae, a strongly reduced protocone and paracone, and a paracone close to the metacone. However, the peculiar shape of the protocone in this species, just as with the width and form of the stylar shelf, is not seen in any known Didelphimorphia.

The strong reduction of the protocone and the paracone, the proximity of the latter to the metacone, and the large development of the postmetacrista are derived characters diagnostic of the Sparassodonta. But, the width of the stylar shelf makes it unlikely that it belongs to this order. Some features of *K. chisu,* however, suggest possible affinities with the most primitive sparassodont, *Allqokirus australis,* from the lower Paleocene (Tiupampian SALMA) of Bolivia. This species also has its paracone somewhat labially oriented relative to the metacone, a preprotocrista that continues labially in the anterior cingulum of the tooth, a preprotocrista and postmetacrista that are well developed, and a labially compressed StD with an elongated anterior crest. *Kiruwamaq chisu* differs from *A. australis* primarily by lacking para- and metaconules and in having a larger reduction of the protocone and a larger relative development of the postmetacrista. All of these features suggest a more derived condition for *K. chisu.* Thus, it could be argued, though the evidence is still scarce, that, on the basis of its small size and the relatively large development of all shearing crests, the Amazonian species belongs to a lineage derived from minute-sized hathliacynid sparassodonts of insectivorous–faunivorous habits.

Finally, some other features of *Kiruwamaq* might suggest different affinities. For example, the remarkable width of the holotype, relative to the total length of the tooth, makes it typically triangular, with the labial face much shorter than the other two. A similar outline, even more prominent than in *Kiruwamaq,* can be seen in the enigmatic ?marsupials of the family Necrolestidae. Known only from Miocene levels (Santacruzian SALMA) of Patagonia, these were probably fossorial forms whose affinities with marsupials are still doubtful. The extreme simplification of the molar pattern in necrolestids hampers more precise comparisons.

DISCUSSION

A NOVEL PALEOGENE MARSUPIAL FAUNA FROM TROPICAL SOUTH AMERICA

The new taxa described herein (Table 4) constitute one of the most outstanding marsupial assemblages discovered in recent years. They add significant knowledge about the Paleogene marsupial diversity in tropical South America, and, most notably, provide evidence regarding the early phases in the evolution of “pseudodiprotodont” (*sensu* Ride, 1962) marsupial lineages.

Table 4 List of marsupial taxa from the Santa Rosa local fauna.

Order Didelphimorphia Gill, 1872
  cf. Family Herpetotheriidae Gray, 1821
    Rumiodon inti gen. et sp. nov.
Order Sparassodonta Ameghino, 1894
  Family Hathliacynidae Ameghino, 1894
    Patene campbelli sp. nov.
Order Microbiotheria Ameghino, 1889
  Family Microbiotheriidae Ameghino, 1889
    Kirutherium paititiensis gen. et sp. nov.
Order Polydolopimorphia Ameghino, 1897
  Family Prepidolopidae Pascual, 1980
    Incadolops ucayali sp. nov.
  Family indeterminate
    Wamradolops tsullodon gen. et sp. nov.
    Hondonadia pittmanae sp. nov.
Order Paucituberculata Ameghino, 1894
  Family Caenolestidae Trouessart, 1898
    Perulestes cardichi gen. et sp. nov.
    Perulestes fraileyi gen. et sp. nov.
  cf. Family Palaeothentidae Sinclair, 1906
    Sasawatsu mahaynaq gen. et sp. nov.
Order and Family indeterminate
    Wirunodon chanku gen. et sp. nov.
    Kiruwamaq chisu gen. et sp. nov.

Size

Almost all specimens recovered at this new locality are small to very small. The largest species represented is the carnivore *Patene campbelli,* which was about the size of a domestic cat, followed by the rat- or squirrel-sized paucituberculatans *Perulestes fraileyi* and *Sasawatsu mahaynaq*. All of the others are of the size of small mice, probably not exceeding the weight of the living microbiotheriid *Dromiciops gliroides* (20–50 g; Hershkovitz, 1999:33).

Feeding Habits

The large proportion of small frugivorous or frugivorous–insectivorous taxa among the Santa Rosa marsupials is striking. Their size and inferred diet are suggestive of arboreal locomotion; however, no cranial or postcranial remains that could test this hypothesis have been recovered so far.

The very fragmentary preserved holotype of *Hondonadia pittmanae* has a morphological pattern seen in other generalized polydolopimorphians with inferred insectivorous–frugivorous diets (e.g., *Rosendolops*). The paucituberculatans *Perulestes cardichi* and *P. fraileyi,* though different in size, also show features suggesting frugivorous feeding habits, such as poorly developed cristae and wide protocones and talonids. *Sasawatsu mahaynaq* seems more strictly adapted to a frugivorous diet, with very low crowned molars; a complete absence of shearing cristae; and wide trigon basins, protocones, and talonids. The microbiotheriid *Kiruther-*

ium paititiensis is reminiscent, in upper molar morphology, of the insectivorous–frugivorous *Dromiciops gliroides,* the only living microbiotheriid marsupial. *Wirunodon chanku* is so small that its probable feeding habits are difficult to interpret. This taxon has reduced protocones, well-developed postmetacristae and paracristids, and reduced stylar cusps, all features that characterize many fossil and living opossums of, at least partially, carnivorous feeding habits. But, because of the minute size of *W. chanku,* it seems more likely that its diet consisted of small insects or worms, rather than of small vertebrates. Another tiny ?opossum recovered from Santa Rosa, *K. chisu,* seems to have been adapted to feed on small insects. The small protocone, and large postmetacrista and paracristid of *Rumiodon inti* suggest partially faunivorous feeding habits.

Wamradolops tsullodon is, by far, the most abundant marsupial of the Santa Rosa local fauna. Almost half of all marsupial specimens from the Santa Rosa fauna are assignable to this species. Several of the most characteristic features of this taxon are probably adaptations related to the breaking down of relatively hard items, such as seeds, small nutlike structures, or bark, or the shearing of fleshy food into smaller pieces. These features include deep and strong mandibles; very large upper and lower premolars with shearing blades; molars with low cusps and, especially in the anterior lower molars, unilateral hypsodonty; a thick enamel layer on all teeth; and a reduction of shearing cristae in upper and lower molars. All of these features, plus its very small size, suggest mainly frugivorous feeding habits. Among South American marsupials, the ?early Oligocene (Divisaderan SALMA) Groeberiidae constitute the group most extremely specialized toward these inferred feeding habits. To Simpson (1970), the diet of groeberiids possibly included bark, wood-burrowing insects, or fruits with hard shells. Several extant mammals, such as the primate *Daubentonia* E. Geoffroy, 1795, from Madagascar, or the marsupial *Dactylopsila* Gray, 1858, also share these feeding habits from New Guinea and Australia (Pascual et al., 1994). Groeberiids show a unique set of cranial and dental adaptations that include short, very high horizontal rami that are ventrally fused; a very deep palate, which, together with the curved edge of the fused mandibles, suggests the existence of a strong, large (parrot-like?) tongue (Pascual et al., 1994); upper and lower incisors very large and strong; teeth markedly heterodont, that is, comprising different morphofunctional units that have a thick enamel layer; a skull with a relatively enormous, tardigrade-like ventral projection of the masseteric process of the zygoma, which suggests a strong horizontal component of the masseteric muscles, etc. Even though no cranial remains of *Wamradolops* are known, several of its most derived dental features are also present in groeberiids: for example, heterodont cheek-teeth with a thick enamel layer; upper molars with a posterolabially "displaced" protocone, resulting in the enlarged metaconule being the most lingual cusp of these molars; and lower molars with an anteriorly displaced entoconid.

Negative Evidence

An additional aspect of the Santa Rosa marsupial association comes from negative evidence, that is, the complete absence of polydolopines (Polydolopimorphia, Polydolopidae). Polydolopines are among the best represented taxa in Paleogene levels of Patagonia, but they have never been recorded at northern latitudes. Even though we are cautious with this negative evidence, it is consistent with what has been found from Paleogene levels north of Patagonia; for example, the Lumbrera Formation (?lower Eocene) and Antofagasta de la Sierra fauna (late Eocene), both from northwestern Argentina, and the Itaboraí Formation (Itaboraian SALMA) of eastern Brazil all lack polydolopines. Regarding the middle upper Paleocene Itaboraí Formation, it is interesting to note that, although no polydolopines are among the extremely rich marsupial fauna recovered from it (see, e.g., Marshall, 1987), the epidolopine *Epidolops ameghinoi* Paula Couto, 1952b, is extremely well represented, comprising about 40 percent of all marsupial specimens from this locality. On the other hand, half of the several hundred marsupial specimens collected at a contemporary (Itaboraian SALMA) locality in the Las Flores Formation in central Patagonia are assignable to epidolopines and polydolopines (the latter forms including half a dozen new, still unnamed, species; Goin et al., 1997). Polydolopines are the most abundant mammal remains known to date from middle Eocene levels of the La Meseta Formation in the Antarctic Peninsula. The youngest polydolopine known, *Polydolops abanicoi* Flynn and Wyss, 1999, also comes from southern South America: the Termas del Flaco region in central Chile, from 34°59′ S. Its age has been estimated as early Oligocene ("Tinguirirican" age; Flynn and Wyss, 1999, and references cited therein; Kay et al., 1999). There seems to be a relationship, probably trophic, between the multituberculate-like polydolopines and southern South American and Antarctic forests where *Nothofagus* sp. (the Southern Beech) is dominant and podocarps and araucarian conifers are common (Case, 1988). In turn, *Nothofagus* Blume, 1850, is considered an indicator of cool, humid climatic conditions. Case (1988) correlates one lower Eocene locality in Seymour Island (RV-8425, "TELM 2"), which is dominated by a large-leafed species of *Nothofagus,* with cooling conditions.

SIGNIFICANCE OF THE SANTA ROSA MARSUPIALS

"Opossum-like" Marsupials

Rumiodon inti may be, if its precise affinities are confirmed (see "Systematic Paleontology"), one of the first records of a South American didelphimorphian of the family Herpetotheriidae (see also Oliveira, 1998). Interestingly, this would not be the only herpetotheriid record for this continent. Work in progress by Goin and Forasiepi on the middle late Paleocene marsupials of the Las Flores Formation of central Patagonia (Goin et al., 1997), suggests that several of the recognized taxa from there belong to this group of didelphimorphians. A review of several taxa from the Itaboraí Formation leads to similar conclusions (Goin, 1991; Oliveira, 1998; Oliveira and Goin, in press). All of these forms share a combination of generalized and derived features that are not present in the Neogene opossums of the family Didelphidae, including well-developed paraconules, metaconules, or both; a narrow stylar shelf; centrocrista ending very labially on the stylar shelf; a well-developed StC that is clearly separate from StB and StD; and unreduced hypoconulids and entoconids.

Reig (1981) recognized the subfamily Herpetotheriinae, including the genera *Herpetotherium* Cope, 1873; *Peratherium*; and *Amphiperatherium* that were known from lower Tertiary levels of North America, Europe, and northern Africa. Reig (1981:56) regarded herpetotheriids as closely related to peradectids (his "Peradectinae") rather than the didelphids, a conclusion also shared by Reig et al. (1987; but see the proposed classification of "didelphimorphs" by these authors in the same work, pp. 81–82, and Marshall, 1987). Previously, Crochet (e.g., 1980) reviewed the European genera *Peratherium* and *Amphiperatherium,* including them in his tribe Didelphini. It should be noted that Crochet's (1980) concept of Didelphidae, Didelphinae, and even of Didelphini was extremely wide. To him, didelphids comprise five subfamilies: Didelphinae, Sparassocyninae, Microbiotheriinae, Glasbiinae, and Caroloameghiniinae, some of which (i.e., his Glasbiinae, Microbiotheriinae, and Caroloameghiniinae) are presently placed in different families or orders (see, e.g., Marshall et al., 1990). In turn, the Didelphinae included the tribes "Didelphini" (Didelphimorphia) and "Peradectini" (currently referred to the order Peradectia). Finally, his "Didelphini" included an extremely wide variety of opossums, several of which are presently allocated in different families and orders (e.g., *Mirandatherium* Paula Couto, 1952c). Perhaps because of his broad approach to the group, his diagnosis of the tribe "Didelphini" stressed features currently regarded as diagnostic of all didelphimorphians (Crochet, 1980:58; Goin, 1991). However, Crochet had already realized the different nature of the South American early Tertiary didelphimorphian radiation with respect to that of the Neogene, finding inconclusive affinities between several South American Paleogene opossums and European herpetotheriids. Regarding the possible origin of his "Didelphini," he noted: "La présence à Sao José de Itaborai et dans l'Eocène européen de Didelphini présentant une dilambdodontie talpidienne peut également étayer la notion de liens entre les faunnes didelphidiennes néotropicale du Paléocène et holarctique de l'Eocène. Mais ce phénomène peut aussi être la consequence d'une convergence hétérochrone. L'absence de ce type morphologique de molaire supérieure dans la documentation nord-américaine disponible n'est pas un obstacle à l'une ou l'autre de ces hypothèses . . . *les genres actuels d'origine essentiellement sud-américaine s'individualisent au cours d'une seconde radiation adaptative,* dont l'âge ne peut encore être précisé par manque de donnés concertant les périodes Eocène et Oligocène." (Crochet, 1980:225; italics ours). A review of South American Neogene opossums by one of us (Goin, 1991, 1994, 1995) led to the same conclusions: Neogene didelphids are derived in different ways than Paleogene didelphids. To the set of molar features mentioned above that separate herpetotheriids from didelphids, all of which are verifiable in the Peruvian *R. inti,* are several other characters that deserve further consideration.

1. The horizontal ramus in didelphines is anteriorly shortened with respect to that of herpetotheriids, with the symphysis reaching posteriad to a point below the posterior edge of P_2. In the herpetotheriid specimens, the mandible is more elongated anteriorly, and the symphysis ends posteriorly just below the P_2. In herpetotheriids with known rostral, or anterior, portions of the mandibles, the entire rostrum seems to have been more elongate, as shown in *Amphiperatherium lamandini* (Filhol, 1876); *A. fontense* Crochet, 1979; *A. ambiguum* Filhol, 1877; *A. exile* Gervais, 1848–1852; *Peratherium elegans* (Aymard, 1846); and *P. caluxi* Filhol, 1877 (see Crochet, 1980:figs. 102a–c, 123, 130, 140, 207, 235a–c). In all of these taxa the horizontal ramus is very elongate, with the symphysis ending posteriorly below the P_2 and the mental foramina much larger than that of didelphines.
2. In didelphids, the P_2 is subequal or larger than the P_3; in herpetotheriids, the P_3 is usually larger than the P_2.
3. Lower incisors are, in most didelphids, subequal in size. In herpetotheriids with preserved anterior dentitions, the second lower incisor (homologous to I_3 of Hershkovitz, 1982) is larger than the rest. This derived character is preserved in several specimens belonging to different species reviewed by Crochet (1980), including *A. minutum, A. ambiguum,* and *Peratherium perrierense* Crochet, 1979 (see Crochet, 1980:figs. 87a–b, 129, 217, 232). Curiously, differences in the relative sizes of the lower incisors among South American didelphids have only been recorded in Paleogene opossums such as the Itaboraian *Derorhynchus* (Paula Couto, 1962; Marshall, 1987) and *Eobrasilia* Simpson, 1947 (Marshall, 1984). Herpetotheriid affinities of *Derorhynchus* and several other opossums were discussed by Goin (1991).

4. Where known, upper incisors of herpetotheriids differ in relative sizes when compared with those of South American Neogene opossums: I^2 is much smaller than I^1 or I^3 (see Crochet, 1980: fig. 119). Among South American Neogene opossums, only the first (I^1) or last (I^5) upper incisors have differences in relative sizes (Takahashi, 1974). All of these features, plus those mentioned previously for the molar teeth, constitute a heterobathmic (*sensu* Hennig, 1968) distribution of generalized and derived features for each clade (i.e., Didelphidae and Herpetotheriidae), thus suggesting that they are sister groups. Until a thorough review of all Paleogene South American opossum taxa is completed, it is not possible to be more precise as to their probable relationships. Goin (1991, 1995) suggested that the concept of Didelphoidea should be restricted exclusively to Neogene and Recent South American opossums. In his systematic proposal, these include the Didelphidae (*s.s.*), Caluromyidae, and Sparassocynidae. On the other hand, herpetotheriines (excluded from the Didelphidae) and several other taxa known exclusively from South American Paleogene levels, such as the Derorhynchidae, Eobrasiliinae, and Protodidelphidae, may be the sister group of the Didelphoidea.

The above considerations have important consequences in paleobiogeographic hypotheses regarding vicariance, dispersal, or both, as events in the early history of didelphimorphian opossums. Particularly debated have been the biogeographic relationships of didelphimorphian and peradectian opossums between South America, North America, Europe, and Africa (see, e.g., Marshall, 1987; Reig et al., 1987; Marshall and Muizon, 1988; Marshall et al., 1990; Marshall and Sempere, 1993; Peters and Storch, 1993). In discussing the origin of the Messel (middle Eocene of Germany) birds and mammals, Peters and Storch (1993) suggested that European *Amphiperatherium* and *Peradectes* Matthew and Granger, 1921, may have used quite different routes and time periods to reach Europe. “North or South America provided the earliest evidence of *Peradectes* (earliest Paleocene), while Europe is third (Early Eocene). . . . This suggests a dispersal of *Peradectes* from North America to Europe via northern North Atlantic bridges during the Early Eocene. Didelphines, on the other hand, appeared about contemporaneously in the early Eocene on the European and North American continent. . . . The fossil records of marsupials from South America, on the other side, includes the earliest known didelphines, coming from the latest Cretaceous or early Paleocene of Bolivia and Peru . . . , and Crochet and Sigé (1983) correspondingly hypothesized didelphine dispersal from South America into Europe via Africa” (Peters and Storch, 1993:264). The record of South American ?herpetotheriid opossums, as we suggest here for *R. inti* and as is argued elsewhere (Oliveira and Goin, in press), makes the hypothesis of Crochet and Sigé (1983) even more plausible. Regarding the alleged North American origins of European herpetotheriids, it should be mentioned that South American and European members of this family are closer to each other than either of them is to *Herpetotherium* and allies (*sensu* Korth, 1994), and the molar pattern of the former is plesiomorphic with respect to that of the latter.

The other “opossum-like” marsupial in the Santa Rosa local fauna is the enigmatic *Wirunodon chanku,* the familial or ordinal assignation of which is very speculative on the basis of available material. Its almost straight centrocrista suggests affinities with the Peradectia, but nearly all the remaining characters are derived for both the Peradectia and the Microbiotheria. Many of these characters are present in several lineages of South American didelphimorphians. To us, the only marsupial comparable to *W. chanku* is *Kasserinotherium tunisiense,* a ?peradectian from the lower Eocene of Tunisia (Africa). If their affinities are confirmed, this would be another piece of evidence supporting South American and African biogeographic relationships during the early Paleogene (see above). However, on the basis of available material, it is very difficult to precisely assign this peculiar Amazonian marsupial to any known family or order. Both hypotheses here presented, that is, either peradectian or didelphimorphian affinities, are admissible. Regarding the first, it is interesting to note Crochet’s (1986:926) suggestion that peradectids, in their present concept, may constitute a paraphyletic taxon.

“Pseudodiprotodont” Marsupials

Three unquestionable species of polydolopimorphian marsupials occur in the Santa Rosa fauna: *Incadolops ucayali, Hondonadia pittmanae,* and *Wirunodon tsullodon.* All three taxa bear significant information concerning the evolutionary history of the order, on which we comment below.

Incadolops ucayali is the most generalized prepidolopid known to date. Its upper molar structure sheds light on how the pairing of the paracone and metacone with StB and StD was achieved. The centrocrista is still generalized for polydolopimorphians, although already open. The stylar shelf is notably reduced, and a large trigon basin, typical of other prepidolopids, is already present. Its tendency toward bunodonty accounts for many secondarily derived features present in representatives of this order. The generalized features of *Incadolops,* compared with other prepidolopids, create doubts as to the inclusion of *Rosendolops primigenium* in this family (see “Systematic Paleontology”).

Hondonadia pittmanae is one of two marsupials of the Santa Rosa local fauna related at the generic level with other marsupials from southern South America (the other being *Patene campbelli*). Com-

Table 5 Suprageneric classification of microbiotherians and polydolopimorphians (in its current concept; see text for explanations). The inclusion of these two lineages in a higher category ("taxon unnamed") implies that both of them (plus the ?Diprotodontia; see Discussion section) belong to a natural group.

- Taxon unnamed
  - Order Microbiotheria
    - Family Microbiotheriidae
  - Order Polydolopimorphia
    - Plesion Glasbiidae
    - Suborder Bonapartheriiformes, new rank
      - Superfamily Bonapartherioidea, new rank
        - Family Prepidolopidae
        - Family Bonapartheriidae
          - Subfamily Bonapartheriinae, new rank
          - Subfamily Epidolopinae
        - Family Gashterniidae
        - Family indeterminate
          - *Hondonadia, Rosendolops*
      - Superfamily Argyrolagoidea
        - Family Groeberiidae
        - Family Patagoniidae
        - Family Argyrolagidae
      - Bonapartheriiformes indeterminate
        - *Wamradolops*
    - Suborder Polydolopiformes
      - Plesion *Roberthoffstetteria*
      - Family Polydolopidae
  - ?Order Diprotodontia

menting on the type species of the genus, *H. feruglioi,* we noted that "... the acquisition of the polydolopimorphian molar pattern had already happened by Paleocene times, for example, *Epidolops, Gashternia* (Candela et al., 1995), or, at the most, by the early Eocene, for example, Prepidolopidae, Bonapartheriidae (Pascual, 1980a, 1980b, 1983). *Hondonadia* represents the second known case of the persistence of this same basic pattern in its most generalized state well into the Paleogene. The first known case was that of *Rosendolops primigenium* [Goin and Candela, 1996]. . . . *Hondonadia* is more primitive than *Rosendolops* in having stylar cusps B and D not so closely twinned with the paracone and metacone, respectively, in that the stylar cusps are less compressed labio-lingually and in the persistence of a preprotoconal cingulum near the anterolingual face of the crown" (Goin and Candela, 1998:83; Spanish in the original). However, in at least one feature, *Hondonadia* is more derived than *Rosendolops*: in the even more labial position of the metacone relative to the paracone. This last feature, probably unique among metatherians, reinforces our previous argument that *Rosendolops* and *Hondonadia* are closely related. Both genera are here referred to as belonging to an undetermined family of the new taxon Bonapartherioidea (see below and Table 5).

Wamradolops tsullodon is enigmatic in that it shares a number of derived features with several different lineages of polydolopimorphians (see "Systematic Paleontology" and below). Several striking molar similarities between *Wamradolops* and *Groeberia* have already been noted. Other dental elements, such as the incisors, have not yet been recovered for the Peruvian marsupial. Some conspicuous, derived features of *Wamradolops,* such as the enlarged, plagiaulacoid-like upper and lower last premolars, are not present in *Groeberia.* Finally, though strong and relatively deep, the horizontal ramus in *Wamradolops* is not as deep or extensively inflected as in *Groeberia,* resembling more the ramus of bonapartheriids. *Wamradolops* also resembles the early Paleocene *Roberthoffstetteria nationalgeographica* in the lingual "displacement" of stylar cusps B, ?C, and D in the M^{1-3}. Taking into account the overall similarities between *Wamradolops,* the prepidolopids, and, especially, the bonapartheriids (see "Systematic Paleontology"), it could be argued that groeberiids may represent an extremely specialized, later version of this original stock. An alternative hypothesis is that *Wamradolops* belongs to a different polydolopimorphian lineage than that including prepidolopids and bonapartheriids. This hypothetical lineage might be related to groeberiids, for which it represents a plesiomorphic sister taxon, but at the same time, it might be convergent on them to some extent.

Paucituberculatan marsupials from Santa Rosa are also crucial for interpreting the early stages in the evolution of the order. *Perulestes* and *Sasawatsu* are important taxa for the interpretation of the evolution of the paucituberculatan molar pattern and adaptations. They demonstrate that the acquisition of the quadrangular upper molar pattern in both major lineages of South American "pseudodiprotodont" marsupials, that is, the Paucituberculata and the Polydolopimorphia, followed quite different pathways.

In his review of South American paucituberculatans, Marshall (1980) named as the "intermediate cuspule" the vestigial cusp that can be seen on the lingual side of the enlarged StD in upper molars of generalized caenolestids, such as *Stilotherium* Ameghino, 1887, and *Caenolestes* Thomas, 1895. In later works (e.g., Marshall, 1987) he recognized that this cusp is homologous to the metacone, which becomes minute and almost fuses with the StD in these caenolestids. The Peruvian paucituberculatans described here, especially *P. cardichi,* show an early stage in the reduction of the metacone, thus confirming the homologies of this cusp. In the upper teeth of this species, the metacone of M^{1-3} is only moderately reduced, although clearly paired with StD, showing for this character the most plesiomorphic condition known for the order. The most interesting feature in the upper molars of *Perulestes* is, undoubtedly, the persistence of the paracone, at least in M^{1-2}. Although this cusp is obviously paired with StB in *P. cardichi,* this taxon reveals an early stage in the gradual reduction and movement of the paracone toward StB, and the final "absorption" of the paracone by StB can be seen.

The Santa Rosa marsupials are very useful for revealing differences between the upper molar pattern of the Paucituberculata and that of the Polydolopimorphia. In the latter, there is an even pairing of the para- and metacone with StB and StD, respectively. In the Prepidolopidae, as in the Bonapartheriidae and Gashterniidae, the resulting pairing did not result in the disappearance of the para- or the metacone but, instead, gave a fusion of both cusps with the stylar cusps. All of these cusps are subequal in size and height, and their pairing implied a notable reduction of the labial half of the upper molars, that is, of the stylar shelf. As in paucituberculatans, the metaconule is strongly developed, forming a hypocone-like structure. But this cusp is crestless and level with the protocone, which is quite different from the paucituberculatan metaconule. Both the paracone and metacone are, in most polydolopimorphians, positioned very labially. In short, the quadrangular upper molar of polydolopimorphians is formed by the "paracone + StB" in the parastylar corner, the "metacone + StD" in the metastylar corner, the metaconule in the posterolingual corner, and the protocone on the anterolingual face.

The acquisition of a quadrangular molar pattern in the Paucituberculata followed a different evolutionary pathway. Here, the paracone was notably reduced and, finally, it fused with StB to form a single cusp, whereas the metacone persisted as an independent cusp, even though reduced to the point of being vestigial in even the most generalized groups (e.g., Caenolestinae). StB and StD are not reduced or equal in height to the paracone and metacone; instead, they are relatively enormous, occupying most of the width of an unreduced stylar shelf. Also, the metaconule, even though it evolved as a "hypocone," persisted as a cusp, including the pre- and postmetaconular cristae. The tip of the metaconule is invariably higher than that of the protocone, and it is placed lingual to it. The morphology of the upper molars of *P. cardichi* shows how this process unfolded (see "Systematic Paleontology"). Thus, *Perulestes* represents an early version of an evolutionary process experienced uniquely by the Paucituberculata among South American "pseudodiprotodont" marsupials. A similar case is represented by *Sasawatsu mahaynaq,* the second genus of paucituberculatan marsupials recognized here. It is difficult, however, to allocate *Sasawatsu* to one of the recognized families of the order (see "Systematic Paleontology"), even though the available evidence suggests that *Sasawatsu* is not a caenolestid but a more advanced paucituberculatan, probably a palaeothentid. If this is the case, it may be concluded that the "absorption" of the paracone by StB and the reduction and pairing of the metacone and StD were acquired independently via convergence in different lineages of this order.

THE SANTA ROSA FAUNA AND ITS SIGNIFICANCE FOR UNDERSTANDING THE POLYDOLOPIMORPHIAN RADIATION

In this section, we briefly discuss and integrate recent research on the evolution of the Polydolopimorphia (Goin and Candela, 1998; Goin et al., 1998a; Goin, 2003; Goin et al., 2003) with the new evidence offered by the Peruvian taxa. On this basis, a formal classification of the Polydolopimorphia is proposed (Table 5).

1. It has already been argued that "pseudodiprotodont" marsupials, that is, the Pseudiprotodontia of Kirsch et al. (1997) that includes the Paucituberculata and the Polydolopimorphia, do not form a natural group. Instead, the early phases of their respective evolutionary histories, as revealed by the paucituberculatans *Perulestes* and *Sasawatsu,* on the one hand, and by *Wamradolops* plus other early polydolopimorphians on the other, suggest the different origins, homologies, and evolutionary processes experienced by each lineage. Upper and lower molar synapomorphies of the Polydolopimorphia are the following: upper molars show a great reduction of the stylar shelf; the paracone and the metacone are paired with StB and StD, respectively; all these cusps are subequal in size and height; the metaconule is large, "hypocone-like," equal in height to the protocone, and, in most lineages, positioned on the lingual face of the tooth; lower molars have short talonids; the hypoconid is not labially salient; and the cristid obliqua is parallel to the dental axis. It is clear to us that both the tempo and mode of evolution of polydolopimorphian molar patterns, as well as of the gliriform incisors and the plagiaulacoid-like cheek teeth (see, e.g., Marshall, 1980, 1982), are indicative of separate origins for the lineages. As discussed below and elsewhere (Goin and Candela, 1998; Goin et al., 1998a; Goin, 2003), polydolopimorphian origins are related to the microbiotherian radiation, whereas the paucituberculatan origins are related to those of the didelphimorphians.
2. Several groups regarded as polydolopimorphians since Marshall's (1987) review of the "opossum-like marsupials" from the middle Paleocene Itaborai fauna of Brazil can be excluded from this order. Neither the Caroloameghiniidae nor the Protodidelphidae show the set of derived features that characterize the Polydolopimorphia in its present concept. Goin et al. (1998b, 1998c) have already argued for the peradectian affinities of the Caroloameghiniidae and for the placement of the Protodidelphidae within the Didelphimorphia. In our opinion, the Protodidelphidae include only the following genera: *Carolocoutoia* Goin et al., 1998c; *Robertbutler-*

ia Marshall, 1987; *Protodidelphis* Paula Couto, 1952a; and, probably, *Guggenheimia* Paula Couto, 1952a.

3. *Palangania brandmayri* Goin et al., 1998a, from the upper Paleocene of Patagonia, sheds considerable light on the origins of the Polydolopimorphia. *Palangania* shares several derived features with the Microbiotheriidae, including low trigonid cusps, posterolingually displaced metaconid relative to the protoconid, and paraconid clearly smaller than the metaconid (although subequal in height in *Palangania*), anterobasal cingulum very reduced or absent, reduced hypoconulid, and large protocone. On the other hand, it also displays derived features characteristic of the most primitive polydolopimorphians. It shows an incipient pairing of StB and StD with the paracone and metacone, respectively; there is some reduction in width of the stylar shelf; and the preparacrista points to StA, the postmetacrista is moderately developed, the centrocrista is vestigial, and the metaconule is well developed (Goin et. al., 1998a). Most notably, *Palangania* shows, in most of these synapomorphies, a molar pattern quite similar to that of *Glasbius* Clemens, 1966, from the Upper Cretaceous of North America, usually regarded as a peradectian. Goin et al. (1998a) suggested that the difficulties in recognizing whether *P. brandmayri* is a Microbiotheria or a Polydolopimorphia are a result of both lineages belonging to a natural group. In this paper, we formally propose these previous suggestions and consider that: (1) microbiotherians and polydolopimorphians (and diprotodonts?, see below) belong to a natural group and (2) glasbiids (including *Palangania,* and probably *Chulpasia* Crochet and Sigé, 1993, from the lower Paleocene of Perú) constitute the plesiomorphic sister group of all other polydolopimorphians (Plesion Glasbiidae; see Table 5).

   Upper and lower molar morphology of the better known Neogene microbiotherians seems to be too derived to be considered ancestral for known polydolopimorphians. Most microbiotheriid specimens are known from Miocene levels in Patagonia (e.g., *Microbiotherium*), as well as from the living *Dromiciops gliroides*. The Santa Rosa microbiotheriid *Kirutherium paititiensis* does not shed light on this topic, as it shares closer affinities with *Microbiotherium* and *Dromiciops* than with any other member of the order. If *Khasia cordillerensis,* from the lower Paleocene of Bolivia, is a microbiothere (and not a pediomyid peradectian, as also could be argued), it also is too derived to be regarded as a model of the generalized microbiothere molar pattern. Nonetheless, Goin et al. (1998a) reported the discovery of upper molars referable to the microbiotheriid *Mirandatherium* from the middle upper Paleocene Las Flores Formation in central Patagonia that have a morphology quite different from the upper molars referred to the same genus by Marshall (1987). These upper molars seem to represent the plesiomorphic pattern for the Microbiotheria. Interestingly, the upper molars of *Mirandatherium* show derived features that, although incipiently developed, are suggestive of those observable in polydolopimorphians (e.g., reduced stylar shelves; distinct stylar cusps StB and StD, which are incipiently paired with the paracone and metacone, respectively; and an enlarged metaconule, but not paraconule). *Mirandatherium* seems to be only one step behind glasbiids, the latter regarded here as generalized polydolopimorphians.

4. A basic dichotomy can be recognized within the Polydolopimorphia. On the one hand is the suborder Polydolopiformes (see Table 5), which includes *Roberthoffstetteria nationalgeographica* plus the polydolopines *s.s* (i.e., *Polydolops* Ameghino, 1897, and allies). On the other hand, the remaining members of the order are placed in the suborder Bonapartheriiformes (new rank). Goin et al. (2003) mention several derived features exclusive of the former: the alignment of the paraconule, protocone, and metaconule in a lingual row; well-expanded anterior and posterior cingula, which are level with the trigon basin; variable occurrence of accessory cuspules on the labial face of the upper molars; and labially placed paraconid with respect to the metaconid in the lower molars. In turn, derived features of the Bonapartheriiformes include a larger metaconule, the absence of StC and StE, and reduction of the paraconid.

   The long-accepted sister group relationship between epidolopines and polydolopines, which composed the Polydolopidae of traditional literature, was challenged by Goin and Candela (1995). *Epidolops* shares with prepidolopids, bonapartheriids, *Gashternia,* and *Wamradolops* the basic set of derived features leading to the acquisition of the quadrangular molar pattern, while lacking the more advanced features that relate the groeberiids, argyrolagids, and patagoniids in a group of their own (see below). The affinities between *Epidolops* and *Gashternia* were suggested by Candela et al. (1995). In our present state of knowledge, we think that the inclusion of *Epidolops* in the Bonapartheriidae, in its own subfamily, the Epidolopinae Marshall 1982 (see Table 5), is the best systematic hypothesis at hand.

5. Three groups usually regarded as paucituberculatans (i.e., the groeberiids, argyrolagids, and patagoniids) should be recognized as part of the Polydolopimorphia (suborder Bonapartheriiformes) in a group of their own: the Argyrolagoidea (Table 5). *Klohnia charrieri,* from lower Oligocene levels of central Chile, was considered by Flynn and Wyss (1999) to be the closest known relative of *Patagonia* Pascual and Carlini, 1987 (Patagoniidae), and they regarded both

taxa as the nearest outgroup to the Groeberiidae. Although originally described as a paucituberculatan, we find that *Klohnia* is, on the contrary, a very interesting polydolopimorphian. *Klohnia* is derived in many features, including the possession of an enlarged, gliriform lower incisor, loss of one molar (M^4/M_4?), a significant diastema between $I_{?1}$ and P_3, and upper and lower cheek teeth with a thick enamel layer. The loss of the last molar is uncommon among marsupials. This feature is present only in a few polydolopimorphians, such as the polydolopines and the prepidolopid *Punadolops alonsoi* Goin et al., 1998b, even though the reduction of the M^4/M_4 is already noticeable in several other members of this order, including *Bonapartherium, Prepidolops, Epidolops,* and *Wamradolops.* The enlarged, anteriorly shifted entoconid of *Klohnia* (the "isolated lingual 'talonid' cusp" of Flynn and Wyss, 1999:358) is also characteristic of *Groeberia* and *Proargyrolagus* Wolff, 1984. This feature is already, although incipiently, developed in *Wamradolops.* In the upper molars, the polydolopimorphian pairing of the paracone and metacone with StB and StD, together with the enlargement of the metaconule forming the posterolingual corner of the teeth, is also present in *Klohnia* (see Flynn and Wyss, 1999:fig. 2G). Finally, a thick enamel layer is present in the cheek teeth of *Bonapartherium, Prepidolops, Wamradolops, Gashternia,* and *Epidolops. Klohnia* is even closer to groeberiids, patagoniids, and argyrolagids in its great enlargement of the first upper and lower incisors, the latter having an intra-alveolar extension that is lingual to the cheek teeth series, and in that the last upper and lower premolars are not hypertrophied, but of normal size relative to the molars. On the other hand, the labial "shifting" of the protocones in the upper molars (see above) relates *Wamradolops* more closely to groeberiids (and argyrolagids). In short, and pending a phylogenetic analysis of these taxa, we find that the molar morphologies of both *Wamradolops* and *Klohnia* represent an incipient stage in the evolution of the more derived Groeberiidae, Argyrolagidae, and Patagoniidae. Within the Argyrolagoidea, Koenigswald and Goin (2000) agree with Flynn and Wyss (1999), in that groeberiids and patagoniids are more closely related to each other than either is to the Argyrolagidae.

6. Within the Bonapartheriiformes we recognize a basic dichotomy. The Bonapartherioidea (new rank) include the Prepidolopidae, Bonapartheriidae, Gashterniidae, *Rosendolops,* and *Hondonadia*; and the Argyrolagoidea include the Groeberiidae, Patagoniidae, Argyrolagidae, and *Klohnia.* Derived features of the Bonapartherioidea include very large, plagiaulacoid-like last premolars. Derived features of the Argyrolagoidea include the great enlargement of the first lower incisor, reduction of the P^3/P_3, metaconule larger than the protocone, enlarged parastylar area, and lower molars with the paraconid anteriorly displaced. Upper and lower molars are hypsodont in some lineages (e.g., the Patagoniidae and most members of the Argyrolagidae).
7. The placement of microbiotherians and polydolopimorphians within a natural group may give a new insight on the evolution of at least some of the Australian marsupial lineages. As stated by Archer et al. (1999:7): "Although there is general consensus, following studies of tarsal anatomy by Szalay (1982), that microbiotherians share a special relationship with Australian marsupials, there are arguments about the precise nature of their placement within Australidelphia, some concluding a special relationship with dasyuromorphians and peramelemorphians . . . , others a sister taxon relationship with dasyuromorphians . . . , dasyuromorphians and notoryctids . . . , diprotodontians . . . , and still others with the whole of the Australian marsupial radiation . . . , or the Australian radiation plus the early South American genus *Andinodelphys*. . ."

Unfortunately, there is no information available for polydolopimorphians on molecular, cranial, or postcranial evidence in order to test these earlier hypotheses because all members of this order are extinct and most are represented by fragmentary jaws, teeth, or the association of both. A few cranial remains are known for *Epidolops* and *Bonapartherium* (Paula Couto, 1952b; Pascual, 1980a), but they are quite fragmentary and, in the case of *Bonapartherium,* very badly preserved.

Ride (1993) argued for the derivation of the macropodid molar pattern from a microbiotherian morphotype (see also Kirsch et al., 1997, and references cited in pp. 252–254). Ride's arguments were based on the molar morphology of *Dromiciops.* As is the case for polydolopimorphians, the pattern seen in both *Dromiciops* and *Microbiotherium* is already too derived to regard it as ancestral for the Diprotodontia. Earlier microbiotheriids, to the contrary, show an upper and lower molar pattern much more suitable for inferring diprotodont origins. Paleocene microbiotherians, such as *Mirandatherium* and other, still undescribed taxa from the middle upper Paleocene Las Flores Formation, show a combination of generalized and derived features quite suggestive of a pattern ancestral to diprotodonts. Even some generalized polydolopimorphians, such as the prepidolopid *Incadolops,* bear derived features that could be interpreted as diprotodontian synapomorphies. The characteristic W-shaped diprotodontian "ectoloph" (preparacrista + postparacrista + premetacrista + postmetacrista), for instance, is already present in *Incadolops.* In turn, the molar pattern of both prepidolopids and *Mirandatherium* sp.

would seem to exclude any possible derivation from them of dasyuromorphians, peramelemorphians, or allied taxa.

COMMENTS ON THE AGE OF THE SANTA ROSA MARSUPIALS

Tropical faunas, both extant and extinct, frequently include taxa that have plesiomorphic features relative to contemporary, closely related taxa from higher latitudes (Goin, 1997). This is true, for example, in living didelphids. *Lestodelphys halli* (Thomas, 1921), by far the most specialized taxon of the clade composed of *Thylamys* Gray, 1843, *Gracilinanus* Gardner and Creighton, 1989, and *Lestodelphys* Tate, 1934, is presently distributed almost exclusively in Patagonia, ranging from southern Mendoza Province in western Argentina to eastern Santa Cruz Province in southernmost Argentina. *Gracilinanus,* in turn, has most of its species distributed in middle latitudes, whereas the more generalized genera *Marmosa* Gray, 1821, and *Micoureus* Lesson, 1842, have most of their species distributed in low, intertropical latitudes. Goin (1997) suggested a similar case for middle Miocene (Laventan SALMA) marsupials of La Venta, Colombia. Among the La Venta marsupials, the persistence of *Pachybiotherium* Ameghino, 1902, a genus not present in the Patagonian fossil record after Colhuehuapian (early Miocene) time is noteworthy. Also, two thylacosmilid sparassodonts from La Venta (*Anachlysictis gracilis* Goin, 1997, and a specimen belonging to a still unnamed genus and species) represent successive "stages of evolution," or morphotypes, leading to the extremely specialized craniodental pattern seen in late Miocene thylacosmilids from southern South America. The Santa Rosa marsupials might represent a similar case. It appears that at least some marsupial taxa represent the persistence of generalized types in stratigraphic levels younger than those deposits of southern South America that include closely related taxa.

It is also difficult to constrain the age of the sediments bearing this Amazonian marsupial fauna on the basis of the recognized taxa because all are new species, and the overwhelming majority are new at higher taxonomic levels. Of the eleven species recognized in this study, eight are assignable to new genera, and only two (*Patene campbelli* and *Hondonadia pittmanae*) can be assigned to previously known genera. In addition, two of the Amazonian species, *Wirunodon chanku* and *Kiruwamaq chisu,* cannot be assigned even at ordinal level. Below, each taxon is discussed in detail.

The genus *Patene* is known from three species: *P. colhuapiensis,* from upper Eocene (Casamayoran SALMA) levels of Patagonia; *P. simpsoni,* whose biochron ranges from the middle upper Paleocene (Itaboraian SALMA) of Patagonia and Brazil to the Casamayoran SALMA of northwestern Argentina (Goin et al., 1986; Bond et al., 1995); and the new species from Santa Rosa, *P. campbelli.* The Amazonian species shares more similarities with *P. simpsoni,* which is, in turn, the most generalized of the genus.

The available material of *K. chisu* (an $M^{?3}$) does not permit a secure assignment to any of the families or orders of Metatheria currently recognized. A better knowledge of this species, however, may establish its relationship to the generalized sparassodonts of the family Hathliacynidae (see "Systematic Paleontology"). But, *Kiruwamaq* is so uniquely derived that its affinities, beyond its possible assignment to this family, cannot be established. Of all the hathliacynids compared with *Kiruwamaq,* the species that appeared to be the closest was the oldest and most generalized of the family: *Allqokirus australis* Marshall and Muizon, 1988, from the lower Paleocene (Tiupampian SALMA) of Bolivia.

Alternative hypotheses on the peradectian or didelphimorphian affinities of *W. chanku* are mentioned above. One hypothesis is that *Wirunodon* is an early didelphimorphian, derived in some characters but not in others, such as the persistence of a predilambdodont centrocrista. The dilambdodont, or V-shaped, centrocrista appears as early as the early Paleocene (Tiupampian SALMA) in several South American opossums (Marshall et al., 1995, and references cited therein). However, in dental terms, dilambdodonty is the main derived feature diagnostic of early didelphimorphians. A second hypothesis is that *Wirunodon* is, in fact, a very derived peradectian specialized toward faunivorous feeding habits. The known biochron of peradectians in South America ranges from the lower Paleocene of Laguna Umayo and Tiupampa, where the most generalized forms are recorded (Sigé, 1972; Muizon, 1991), to the last record of the specialized Caroloameghiniidae in the late Eocene (Casamayoran SALMA). We suggested above that *Wirunodon* might be related to *Kasserinotherium tunisiense,* which is known only from the lower Eocene of Chambi, in northern Africa (Crochet, 1986).

The microbiotheriid *Kirutherium paititiensis* shares closer affinities with the Oligocene–Miocene *Microbiotherium* and the living *Dromiciops* than with the oldest microbiotheriids hitherto recognized [i.e., *Khasia cordillerensis* from the lower Paleocene of Bolivia, or *Mirandatherium,* from the middle upper Paleocene (Itaboraian SALMA) of Argentina and Brazil]. However, the upper dentitions of several Paleogene and Neogene microbiotheriids, which could be even closer to *Kirutherium* than the genera mentioned above, are unknown. These include the Casamayoran SALMA *Eomicrobiotherium gaudryi* and *Pachybiotherium acclinum* Ameghino, 1902, from the lower Miocene (Colhuehuapian SALMA) of Patagonia.

Rumiodon inti is a ?herpetotheriid didelphimorphian with several features in common with Paleogene species of marsupials of Europe. Among the European forms, *R. inti* is comparable to *Amphiperatheium minutum* (Aymard, 1846), whose biochron ranges from the late Eocene to the middle Oligocene, and with two Eocene species of *Peratherium*: *P. monspeliense* Crochet, 1979, and *P. matronense* Crochet, 1979 (Crochet, 1980). Likewise, *R. inti* has several features in common with still unnamed species of herpetotheriines from the middle upper Paleocene (Itaboraian SALMA) of Patagonia and Brazil (Oliveira, 1998; Goin and Forasiepi, unpublished data).

Hondonadia pittmanae is recognized on the basis of a very fragmentary upper molar. The type species of the genus comes from Gran Hondonada (uppermost Eocene, Mustersan SALMA; Goin and Candela, 1998) in central Patagonia. Several specimens coming from ?post-Mustersan to ?pre-"Tinguirirican" levels at the classic southern cliffs of Lake Colhué Huapi may also be referred to this genus (Goin, unpublished data).

Incadolops ucayali is slightly more generalized than other known prepidolopids (e.g., species of *Prepidolops* and *Punadolops*) known from Casamayoran and Mustersan levels of northwestern Argentina.

Wamradolops tsullodon is intermediate in several, but not all, features between prepidolopids and bonapartheriids. Both groups are simultaneously recorded in different, upper Eocene (Casamayoran and Mustersan SALMAs) sites in northwestern Argentina. Some derived features also suggest that *Wamradolops* may represent an ancestral lineage of the ?early Oligocene (Divisaderan SALMA) groeberiids from western Argentina, as well as of a basal argyrolagoid, *Klohnia charrieri,* from the lowermost Oligocene ("Tinguiririca" age) of central Chile.

Both *Perulestes* and *Sasawatsu* are, in their generalized features, comparable only to a new, still undescribed caenolestid recovered from "Tinguirirican" age (lower Oligocene) levels at the southern cliffs of Lake Colhué Huapi in central Patagonia (Goin, unpublished data). The new Patagonian caenolestid is represented by no less than a dozen tiny, upper and lower molars. Interestingly, the upper molars have their paracone even less reduced than that of *Perulestes* and *Sasawatsu,* their "hypocone" is well developed in M^1 but vestigial in M^3, and there is some posterior displacement of the metacone relative to StD. In these last features, the Patagonian taxon is very similar to *P. cardichi.*

In summary, two of the Peruvian taxa show affinities with genera of the Casamayoran SALMA. A third taxon related at the generic level with other South American marsupials is *Patene campbelli,* which seems more closely related to a middle late Paleocene species (*P. simpsoni*). Other taxa (e.g., *Wirunodon* and *Rumiodon*) seem to be pre-Casamayoran, whereas the remaining ones provide no confident age-related information. Although it is evident that this fauna is middle Paleogene in age, it is impossible to assign it to any of the recognized SALMAs of the South American biostratigraphic scheme. Taking into account all these considerations, the most likely hypothesis is that the Santa Rosa mammal-bearing levels are middle to upper Eocene in age, although a lower Oligocene age, while improbable, cannot be discarded.

SUMARIO EN ESPAÑOL

Existe un marcado sesgo en nuestro conocimiento de los mamíferos sudamericanos paleógenos debido a dos factores principales: en primer lugar, la mayor parte de las localidades fosilíferas se localizan en el extremo austral de este continente (esto es, en la Patagonia; véase la Fig. 1); en segundo lugar, buena parte de los mamíferos exhumados hasta ahora es de moderado a gran tamaño. En parte, esto refleja tanto la historia de la paleomastozoología sudamericana, comenzando con los trabajos pioneros de Ameghino en la Argentina central y del sur, como también las técnicas tradicionales de recolección (búsqueda de fósiles a ojo desnudo). En lo que respecta a los marsupiales sudamericanos, este sesgo es particularmente importante dado que la mayor parte de los marsupiales sudamericanos vivientes es de distribución intertropical y que estos mamíferos son, y muy probablemente lo han sido también en el pasado, formas de muy pequeño a mediano tamaño. Esto no está siendo reflejado actualmente en el registro paleógeno de los marsupiales. La utilización, en años recientes, de técnicas de lavado y tamizado sedimentario para la prospección fosilífera ha cambiado nuestra percepción sobre la diversidad de estos mamíferos.

El segundo aspecto que oscurece un mejor conocimiento sobre la radiación temprana de los marsupiales sudamericanos es la ausencia de niveles mamalíferos paleógenos de ubicación intertropical. Al respecto, en este trabajo analizamos una nueva fauna de marsupiales procedente de niveles paleógenos de la localidad de Santa Rosa, en la Amazonia peruana. La asociación estudiada incluye 79 especímenes, en su mayor parte molares superiores e inferiores aislados, muy pequeños, representativos de once nuevas especies referibles a todos los linajes mayores (órdenes) de marsupiales sudamericanos. La localidad fosilífera de Santa Rosa (latitud 9°29′39″ S, longitud 72°45′48″ W) se ubica 2 km al norte del pueblo de Santa Rosa (Provincia Atalaya, Departamento de Ucayali, Perú), sobre el margen oeste del Río Yurúa, cerca de su confluencia con el Río Beu. Los fósiles proceden de depósitos de canal expuestos en dicho margen. Campbell et al. (2004) sugieren que estos depósitos pertenecen a la Fm. Yahuarango, también conocida como Fm. Huayabamba, Capas Rojas inferiores, Puca inferior, o Fm. Huchpayacu, de posible edad Paleoceno-Eoceno. Los niveles fosilíferos corresponden a depósitos de canal de tipo calcáreo, mayormente rellenos con concreciones calcáreas, huesos, dientes, conchillas y material vegetal.

Los nuevos taxones aquí descriptos (Tabla 4; Resumen) constituyen una de las más notables asociaciones de marsupiales descubiertas en los últimos años. Su estudio agrega información significativa sobre la diversidad paleógena de estos mamíferos y, especialmente, proporciona nuevas evidencias sobre las fases tempranas de la evolución de los marsupiales "pseudodiprotodontes" (*sensu* Ride, 1962), esto es, los Polydolopimorphia y los Paucituberculata. *Rumiodon inti* gen. et sp. nov. (Didelphimorphia, ?Herpetotheriidae) presenta sus molares superiores mucho más largos que anchos, con los protoconos reducidos y postmetacristas bien desarrolladas. *Patene campbelli* sp. nov. (Sparassodonta, Hathliacynidae) difiere de las otras especies del género por su menor tamaño y por el desarrollo intermedio del metacono y del cíngulo anterobasal en el M^4. *Incadolops ucayali* gen. et sp. nov. (Polydolopimorphia, Prepidolopidae) muestra rasgos generalizados en relación con otros prepidolópidos (metacónulo más desarrollado, menor diferencia de altura entre el protocono, por un lado, y el paracono y el metacono por el otro). *Wamradolops tsullodon* gen. et sp. nov. (Polydolopimorphia, fam. indet.) es intermedio en varios rasgos (pero no todos) entre los prepidolópidos y los bonapartéridos. Los molares superiores de *Hondonadia pittmanae* sp. nov. (Polydolopimorphia) tienen el metacono mayor que el paracono y mucho más labialmente ubicado. *Perulestes cardichi* y *P. fraileyi* gen. et spp. nov. (Paucituberculata, Caenolestidae) son generalizados para todo el Orden Paucituberculata al presentar el protocónido del M_1 mucho más alto que el metacónido y, en los molares superiores, el paracono aún presente, si bien ya muy reducido y fusionado basalmente a la cúspide estilar B en los M_{1-2}. *Sasawatsu mahaynaq* gen. et sp. nov. (Paucituberculata, cf. Palaeothentidae) presenta una combinación de rasgos primitivos y derivados: molares bunoides, sin crestas, con la persistencia del paracono y metacono como cúspides individuales. *Kirutherium paititiensis* gen. et sp. nov. (Microbiotheria, Microbiotheriidae) difiere de otros microbiotéridos en que en los molares superiores persisten paracónulos y metacónulos vestigiales y elongados, parcialmente fusionados con la pre- y la postprotocrista; la cuenca del trígono es muy profunda y la postmetacrista está aparentemente poco desarrollada. *Wirunodon chanku* gen. et sp. nov. (orden y familia indet.) es una minúscula, enigmática "comadreja" que muestra caracteres tanto primitivos (e.g., molares superiores con la centrocrista casi recta) como derivados (e.g., protocono y cuenca del trígono reducidos, amplia plataforma estilar, postmetacrista bien desarrollada, preparacrista conectando con la cúspide estilar A). *Kiruwamaq chisu* gen. et sp. nov. (orden y familia indet.) difiere del resto de los marsupiales sudamericanos en que los molares superiores tienen el protocono muy reducido, el paracono cercano al metacono, mucho más pequeño que este último y más labialmente orientado, la centrocrista recta, la postmetacrista bien desarrollada y la plataforma estilar muy amplia.

Casi todos los ejemplares recuperados en Santa Rosa son de tamaño pequeño a muy pequeño. *Patene campbelli,* del tamaño de un gato, es el más grande hasta ahora registrado. Le siguen los Paucituberculata *Perulestes fraileyi* y *S. mahaynaq,* del tamaño de una ardilla. El resto es una serie de formas similares a pequeños ratones, las que probablemente no excedían en peso a aquel del marsupial viviente *Dromiciops gliroides* (entre 20 y 50 gramos). En relación con sus hábitos alimentarios, es llamativa la gran proporción de formas cuya morfología dentaria implica dietas frugívoras o frugívoro–insectívoras. Su tamaño y hábitos inferidos sugieren que buena parte de ellas pudo haber tenido un estilo de vida arborícola. Un aspecto adicional de la asociación de Santa Rosa procede de la evidencia negativa: no se registra un solo marsupial polidolopino (Polydolopimorphia, Polydolopidae). Estos últimos, cuya dentadura es similar a la de los extintos multituberculados, son muy abundantes en niveles paleógenos de la Patagonia, pero no aparecen nunca en latitudes más bajas. Parece existir cierta relación, probablemente trófica, entre los polidolopinos y las floras australes subantárticas dominadas por especies del género *Nothofagus,* junto con podocarpáceas y araucarias.

El análisis de los marsupiales Polydolopimorphia y Paucituberculata exhumados en Santa Rosa es crucial para interpretar la evolución temprana de los representantes de ambos grupos sudamericanos de "pseudodiprotodontes," los que, a la luz de estos resultados, no conforman un grupo natural. El patrón cuadrangular de los molares superiores en ambos grupos es similar, aunque el camino evolutivo que siguió cada uno de ellos es diferente. En los Polydolopimorphia se aprecia el apareamiento del paracono y el metacono con las cúspides estilares B y D, respectivamente. En las formas basales de este grupo, dicho apareamiento no produjo la desaparición del para- ni del metacono, sino en cambio la fusión en la base de estas cúspides con las estilares. Todas estas cúspides son subiguales en tamaño y altura, y su apareamiento implicó una notable reducción de la región labial (i.e., la plataforma estilar) de los molares superiores. Al igual que en los Paucituberculata, el metacónulo está muy bien desarrollado, formando una estructura similar a un hipocono. Sin embargo, a diferencia de los Paucituberculata, su metacónulo no tiene crestas y está nivelado con el protocono; ambas cúspides están ubicadas al mismo nivel sobre la cara lingual del diente. En suma, el patrón cuadrangular del molar superior de los polidolopimorfios está compuesto por el paracono y la StB en la esquina parastilar, el metacono y la StD en la metastilar, el metacónulo agrandado en la esquina posterolingual y el protocono en la anterolingual. La adquisición de un molar superior cuadrangular en los Paucituberculata siguió una distinta vía evolutiva. En éstos, el paracono se redujo notablemente, hasta fusionarse con la StB en una única cúspide, mientras que el metacono persistió como cúspide independiente, si bien se redujo al punto de quedar vestigial, incluso en los grupos más generalizados (i.e., Caenolestidae) sobre la ladera lingual de la StD. Por su parte, las cúspides estilares B y D no se redujeron o nivelaron en altura con el paracono y el metacono, sino que son de tamaño muy grande y ocupan la mayor parte de la (no reducida) plataforma estilar. El metacónulo, que también evolucionó a modo de "hipocono," persistió como cúspide, incluyendo sus crestas pre- y postmetaconulares. Su cúspide es invariablemente más alta que aquélla del protocono y se ubica más lingualmente que este último.

El estudio de los marsupiales polidolopimorfios de Santa Rosa permite incrementar notablemente nuestro conocimiento sobre las relaciones intergenéricas e incluso interfamiliares de este grupo (Tabla 5). Nuestras conclusiones son las siguientes.

1. Los Microbiotheria, Polydolopimorphia y, posiblemente, los Diprotodontia de Australasia conforman un grupo natural (el "Taxón innominado" de la Tabla 5).
2. Los Glasbiidae (representados en el Cretácico tardío norteamericano por el género *Glasbius,* en el Paleoceno de la Patagonia por *Palangania* y, probablemente, en el Paleoceno temprano de Perú por *Chulpasia*) constituyen el grupo hermano plesiomorfo de todos los restantes polidolopimorfios.
3. Los representantes de este Orden muestran la siguiente serie de sinapomorfías: molares superiores con la plataforma estilar reducida, paracono y metacono apareados con las cúspides estilares B y D, respectivamente, todas estas cúspides son subiguales en tamaño y altura; metacónulo agrandado y a la misma altura que el protocono y, en casi todos los linajes, ocupando toda la esquina posterolingual del diente; molares inferiores con los talónidos cortos, el hipocónido poco saliente labialmente y con la crístida obliqua paralela al eje dentario.
4. Varios grupos que habían sido incluidos en este Orden desde la revisión de Marshall (1987) deberían ser excluidos del mismo. Por ejemplo, ni los Caroloameghiniidae ni los Protodidelphidae muestran la serie de rasgos derivados que caracteriza a los Polydolopimorphia en su concepción actual.
5. Se reconoce una dicotomía básica entre los representantes de este Orden: por un lado, *Roberthoffstetteria nationalgeographica* más los polidolopinos *s.s.* (i.e., *Polydolops* y formas afines), los que se agrupan aquí en el Suborden Polydolopiformes; sinapomorfías de este grupo son, en los molares superiores, el alineamiento del paracónulo, protocono y metacónulo en una hilera lingual, el desarrollo de amplios cíngulos anterior y posterior, nivelados con la cuenca del trígono y una variable existencia de cúspulas estilares accesorias; en los molares inferiores, la ubicación labial del paracónido con respecto al metacónido. En segundo lugar, los restantes miembros del Orden componen el nuevo Suborden Bonapartheriiformes, cuyos rasgos derivados diagnósticos incluyen un metacónulo muy agrandado, ausencia de las cúspides estilares C y E y la reducción del paracónido.
6. Tres familias generalmente asignadas a los Paucituberculata son aquí incluidas entre los Bonapartheriiformes: Groeberiidae, Argyrolagidae y Patagoniidae. Estas familias comprenden la Superfamilia Argyrolagoidea, cuyos rasgos derivados incluyen el agrandamiento del primer incisivo inferior, la reducción de los últimos premolares superiores e inferiores, la presencia de un metacónulo mayor que el protocono, un área parastilar agrandada y el desplazamiento anterior del paracónido en los molares inferiores. El resto de los Bonapartheriiformes (los Prepidolopidae, Bonapartheriidae, Gashterniidae, *Rosendolops* y *Hondonadia*) se incluyen en la Superfamilia Bonapartherioidea, cuyos rasgos derivados incluyen la posesión de últimos premolares muy grandes, de tipo "plagiaulacoideo."

La estimación de la edad de los sedimentos fosilíferos de Santa Rosa es problemática. Por un lado, es evidente que la fauna de Santa Rosa representa un Paleógeno medial; por el otro, sin embargo, no es posible referirla con certeza a ninguna de las edades-mamífero sudamericanas (SALMAs) reconocidas para el Paleógeno de este continente. Dos de los taxones de Santa Rosa muestran afinidades a nivel genérico con formas de la SALMA Casamayorense. Un tercer taxón, la nueva especie *Patene campbelli,* remite a formas afines del Paleoceno medial (*P. simpsoni*). Otros taxones (e.g., *Wirunodon, Rumiodon*) parecen ser pre-Casamayorenses, mientras que los restantes no proveen información significativa en torno a la posible edad de esta fauna. Teniendo en cuenta estos datos, como así también resultados recientes sobre la datación absoluta de la Subedad Barranquense de la SALMA Casamayorense, nuestra hipótesis más plausible es que los sedimentos de Santa Rosa fueron depositados durante el Eoceno medio o tardío aunque una edad Oligoceno temprano no debería descartarse por completo.

ACKNOWLEDGMENTS

We thank Kenneth E. Campbell and Carl D. Frailey for making available to us the marsupial specimens from Santa Rosa for study and for many helpful comments. Patricia Sarmiento and Rafael Urréjola helped us make the SEM photos. Augusto Cardich kindly helped us with Quechua vocabulary, which we used in the naming of the new taxa. Discussions with Marcelo Reguero and Mariano Bond, from the Museo de La Plata, regarding the age of Santa Rosa mammal fauna, were enlightening. Finally, we thank Christian de Muizon and an anonymous reviewer for their useful comments and criticisms on the manuscript.

LITERATURE CITED

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1:1–26.

———. 1890. Los plagiaulacídeos argentinos y sus relaciones zoológicas, geológicas y geográficas. *Boletín del Instituto Geológico Argentino* 11:143–201.

———. 1894. Enumération synoptique des espécies de mammiféres fosiles des formations éocènes de Patagonie. *Boletín de la Academia de Ciencias de Córdoba* 13:259–452.

———. 1897. Mammifères crétacés de l'Argentine (Deuxième contribution á la connaissance de la faune mammalogique des Couches á Pirotherium). *Boletín del Instituto Geológico Argentino* 18:406–521.

———. 1902. Première contribution à la connaissance de la faune mammalogique des couches à Colpodon. *Boletín de la Academia de Ciencias de Córdoba* 17: 71–141.

———. 1904. Nuevas especies de mamíferos cretácicos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* 56:193–208 (1903); 57:162–175, 327–341 (1904); 58:35–71, 182–192, 225–291 (1904).

Archer, M., R. Arena, M. Bassarova, K. Black, J. Brammall, B. Cooke, P. Creaser, K. Crosby, A. Gillespie, H. Godhelp, M. Gott, S. Hand, B. Kear, A. Krikmann, B. Mackness, J. Muirhead, A. Musser, T. Myers, N. Pledge, Y. Wang, and S. Wroe. 1999. The evolutionary history and diversity of Australian mammals. *Australian Mammalogy* 21:1–45.

Aymard, A. 1846. Essai monographique sur un genre nouveau de mammifère fossile trouvé dans la Haute-Loire et nommé *Entelodon. Annales des Societé Agricole du Puy* 12:227–267.

———. 1850. Compte rendu de la séance du 13 avril 1849, réponse à M. Robert. *Annales des Societé Agricole du Puy* 14:80–86.

Blume, K.L. 1850. Lugduno-Batavum sive stirpium exoticarum, novarum vel minus cognitarum ex vivis aut siccis brevis expositio et descriptio. *Museum Botanicum Leiden* 1(15):225–240.

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 concomitance in a Paleocene succession from Central Patagonia. *VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, Actas*: 47–58.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Candela, A.M., F.J. Goin, and R. Pascual. 1995. Los Polydolopimorphia (Mammalia, Marsupialia) de la Formación Las Flores (Paleoceno medio, Patagonia central, Argentina). *Acta Geológica Lilloana* 18(1): 149.

Case, J.A. 1988. Paleogene floras from Seymour Island, Antarctic Peninsula. *Geological Society of America, Memoir* 169:505–521.

Clemens, W.A. 1966. Fossil mammals of the Type Lance Formation, Wyoming. Part II: Marsupialia. *University of California Publications in Geological Sciences* 62:1–122.

Cope, E.D. 1873. Third notice of extinct vertebrata from the Tertiary of the plains. *Paleontological Bulletin* 16:1–8.

Crochet, J.-Y. 1979. Les marsupiaux fossiles d'Europe. 7° *Réunion Annuelle des Sciences de la Terre, Lyon,* p. 137.

———. 1980. *Les Marsupiaux du Tertiaire d'Europe*. Paris: Editions de la Fondation Singer-Polignac, 279 pp.

———. 1986. *Kasserinotherium tunisiense* nov. gen., nov. sp., troisième marsupial decouvert en Afrique (Eocene inferieur de Tunisie). *Comptes Rendus de l'Académie des Sciences, Paris* 302(14):923–926.

Crochet, J.-Y., and B. Sigé. 1983. Les mammiferes Montiens de Hainin (Paleocene moyen de Belgique) Part III: Marsupiaux. *Palaeovertebrata* 13(3):51–64.

———. 1993. Les mammifères de Chulpas (formation Umayo, transition Crétacé-Tertiaire, Pérou): données préliminaires. *Documents du Laboratoire de Géologie* 125:97–107.

Filhol, H. 1876. Mammifères fossiles nouveaux provenant des dépôts de phosphate de Chaux du Quercy. *Comptes Rendus de l'Académie des Sciences, Paris* 82:289.

———. 1877. Recherche sur les Phosphorites du Quercy. *Annales de la Societé Géologique* 7:1–220; 8(1):1–340.

———. 1879. Etude des mammifères fossiles de St-Gérand-le-Puy. *Bibliotéque Ecole des Hautes Etudes* 10: 1–253.

Flynn, J.J., and A.R. Wyss. 1999. New Marsupials from the Eocene–Oligocene transition of the Andean Main Range, Chile. *Journal of Vertebrate Paleontology* 19(3):533–549.

Gardner, A.L., and G.K. Creighton. 1989. A new generic name for Tate's (1933) *microtarsus* group of South American mouse opossums (Marsupialia, Didelphidae). *Proceedings of the Biological Society of Washington* 102(1):3–7.

Geoffroy Saint-Hilaire, E. 1795. Untitled. *La Décade Philosophique, Litteraire et Politique: Par une Société des Republicains* 4(28):195.

Gervais, P. 1848–1852. *Zoologie e Paléontologie Francaises (animaux vertebrés) ou nouvelles recherches sur les animaux vivantes et fossiles de la France,* vol. 1, 1st ed. Paris: Arthus Bertrand, 271 pp.

Goin, F.J. 1991. *Los Didelphoidea (Mammalia, Marsupialia, Didelphimorphia) del Cenozoico tardío de la Región Pampeana*. Unpublished thesis, Universidad Nacional de La Plata, 327 pp.

———. 1994. Living South American opossums are *not* living fossils. *VI International Theriological Congress (Univ. Of South Wales, Kensington), Sydney, Abstracts,* p. 112.

———. 1995. Los Marsupiales. In *Evolucion biológica y climática de la Región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental,* ed. M.A. Alberdi, G. Leone, and E.P. Tonni, 165–179. Madrid: Museo Nacional de Ciencias Naturales/CSIC.

———. 1997. New clues for understanding Neogene marsupial radiations. In *A history of the Neotropical fauna. Vertebrate paleobiology of the Miocene in Colombia,* ed. R.F. Kay, R.H. Madden, R.L. Cifelli, and J. Flynn, 185–204. Washington, D.C.: Smithsonian Institution Press.

———. 2003. Early marsupial radiations in South America. In *Predators with pouches: The biology of carnivorous marsupials,* ed. M. Jones, C. Dickman, and

M. Archer, 30–42. Colingwood: CSIRO (Commonwealth Scientific and Industrial Research Organization).

Goin, F.J., and A.M. Candela. 1995. Una nueva especie de *Epidolops* Paula Couto, 1952 (Marsupialia, Polydolopimorphia, Polydolopidae). Consideraciones sobre el patrón molar inferior de los Epidolopidae. *VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, Actas,* pp. 143–148.

———. 1996. A new Early Eocene polydolopimorphian (Mammalia, Marsupialia) from Patagonia. *Journal of Vertebrate Paleontology* 16(2):292–296.

———. 1997. New Patagonian marsupials from Ameghino's "Astraponotèen Plus Supèrieur" (post-Mustersan–pre-Deseadan age). *Journal of Vertebrate Paleontology* 17(3)(Suppl.):2.

———. 1998. Dos nuevos marsupiales "Pseudodiprotodontes" del Paleógeno de Patagonia. In *Paleógeno de América del Sur y de la Península Antártica.* Asociación Paleontológica Argentina, Buenos Aires, Publicación Epecial, 5:79–84.

Goin, F.J., A.M. Candela, M. Bond, R. Pascual, and V. Escribano. 1998a. Una nueva "comadreja" (Mammalia, Marsupialia, ?Polydolopimorphia) del Paleoceno de Patagonia, Argentina. In *Paleógeno de América del Sur y de la Península Antártica.* Asociación Paleontológica Argentina, Buenos Aires, Publicación Especial, 5:71–78.

Goin, F.J., A.M. Candela, and C. de Muizon. 2003. The affinities of *Roberthoffstetteria nationalgeographica* (Marsupialia) and the origin of the polydolopine molar pattern. *Journal of Vertebrate Paleontology* 23(4):869–876.

Goin, F.J., A.M. Candela, and A. Forasiepi. 1997. New, middle Paleocene marsupials from central Patagonia. *Journal of Vertebrate Paleontology* 17(3 Suppl.): 49A.

Goin, F.J., A.M. Candela, and G. López. 1998b. Middle Miocene marsupials from Antofagasta de la Sierra, northwestern Argentina. *Geobios* 31(1):75–85.

Goin, F.J., E.V. Oliveira, and A.M. Candela. 1998c. *Carolocoutoia ferigoloi* n. gen. et sp. (Protodidelphidae), a new Paleocene "opossum-like" marsupial from Brazil. *Palaeovertebrata* 27(3–4):145–154.

Goin, F.J., R.M. Palma, R. Pascual, and J. Powell. 1986. Persistencia de un primitivo Borhyaenidae (Mammalia, Marsupialia) en el Eoceno temprano de Salta. Aspectos geológicos y paleoambientales relacionados. *Ameghiniana* 23(1–2):47–56.

Goin, F.J., M. Woodburne, J. Case, S.F. Vizcaíno, and M. Reguero. 1999. New discoveries of "opossum-like" marsupials from Antarctica (Seymour Island, Middle Eocene). *Journal of Mammalian Evolution* 6(4):335–365.

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository* 15(1):296–310.

———. 1843. *List of the specimens of Mammalia in the collection of the British Museum.* London: British Museum of Natural History, 266 pp.

———. 1858. List of species of Mammalia sent from the Aru Islands by Mr. A.R. Wallace to the British Museum. *Proceedings of the Zoological Society of London* 1858:106.

Hennig, W. 1968. *Elementos de una sistemática filogenética.* Buenos Aires: Eudeba, 353 pp.

Hershkovitz, P. 1982. The staggered marsupial lower third incisor (I_3). *Geobios,* mémoire spécial 6:191–200.

———. 1999. *Dromiciops gliroides* Thomas, 1894, last of the Microbiotheria (Marsupialia), with a review of the Family Microbiotheriidae. *Fieldiana Zoology (New Series)* 93:1–60.

Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G.H. Re, M. Heizler, and H. Sandeman. 1999. Revised age of the Casamayoran South American Land Mammal "Age"—Climatic and biotic implications. *Proceedings of the National Academy of Sciences, Washington* 96(23):13235–13240.

Kirsch, J.A.W., F.-J. Lapointe, and M. Springer. 1997. DNA-hybridization studies of marsupials and their implications for metatherian classification. *Australian Journal of Zoology* 45:211–280.

Koenigswald, W.v., and F.J. Goin. 2000. Enamel differentiation in South American marsupials and a comparison of placental and marsupial enamel. *Palaeontographica* A255:129–168.

Korth, W.W. 1994. Middle Tertiary marsupials (Mammalia) from North America. *Journal of Paleontology* 68:376–396.

Lesson, R.P. 1842. *Nouveau tableau du règne animal. Mammifères.* Paris: Arthus Bertrand, 204 pp.

Loomis, F.B. 1914. *The Deseadan Formation of Patagonia.* Concord, New Haven: The Rumford Press, 232 pp.

Marshall, L.G. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana Geology (New Series)* 5:1–145.

———. 1982. Systematics of the extinct South American marsupial family Polydolopidae. *Fieldiana Geology (New Series)* 12:1–109.

———. 1984. The lower jaw of *Eobrasilia coutoi* Simpson, 1947, a unique Didelphoid (not Borhyaenoid) marsupial from the Paleocene of Brasil. *Journal of Paleontology* 58:173–177.

———. 1987. Systematics of Itaboraian (middle Paleocene) age "opossum-like" marsupials from the limestone quarry at São José de Itaborai, Brasil. In *Possums and opossums: Studies in evolution,* vol. 1., ed. M. Archer, 91–160. Sydney: Surrey Beatty & Sons Pty Limited and The Royal Zoological Society of New South Wales.

Marshall, L.G., J.A. Case, and M.O. Woodburne. 1990. Phylogenetic relationships of the families of marsupials. In *Current mammalogy,* vol. 2, ed. H. Genoways, 433–505. New York: Plenum Press.

Marshall, L.G., and C. de Muizon. 1988. The dawn of the age of mammals in South America. *National Geographic Research* 4(1):23–55.

Marshall, L.G., C. de Muizon, and B. Sigé. 1983. Late Cretaceous mammals (Marsupialia) from Bolivia. *Geobios* 16:739–745.

Marshall, L.G., C. de Muizon, and D. Sigogneau-Russell. 1995. *Pucadelphys andinus* (Marsupialia, Mammalia), from the early Paleocene of Bolivia. *Mémoires du Muséum National d'Histoire Naturelle* 165:1–164.

Marshall, L.G., R. Hoffstetter, and R. Pascual. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata,* Memoire Extraordinaire 1983:1–93.

Marshall, L.G., and R. Pascual. 1977. Nuevos marsupiales Caenolestidae del "Piso Notohippidense" (SW de Santa Cruz, Patagonia) de Ameghino. Sus aportaciones a la cronología y evolución de las comunidades de mamíferos sudamericanos. *Publicación del Museo Municipal de Ciencias Naturales de Mar del Plata (Lorenzo Scaglia)* 2(4):91–122.

Marshall, L.G., and T. Sempere. 1993. Evolution of the Neotropical Cenozoic land mammal fauna in its geochronologic, stratigraphic, and tectonic context. In *Biological relationships between Africa and South America,* ed. P. Goldblatt, 328–392. New Haven, Connecticut, and London: Yale University Press.

Matthew, W.D., and W. Granger. 1921. New genera of Paleocene mammals. *American Museum Novitates* 13:1–7.

Moss-Salentijn, L., M.L. Moss-Salentijn, and M. Sheng-Tien Yuan. 1997. The ontogeny of mammalian enamel. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sanders, 5–30. Rotterdam: A.A. Balkema.

Muizon, C. de. 1991. La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucia), Bolivia. In *Fósiles y Facies de Bolivia.* Vol. 1. *Vertebrados,* ed. R. Suarez-Soruco. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, 12(3–4): 575–624.

———. 1994. A new carnivorous marsupial from the Paleocene of Bolivia and the problem of marsupial monophyly. *Nature* 370:208–211.

Oliveira, E.V. 1998. *Taxonomia, Filogenia e Paleobiogeografia de marsupiais "Poliprotodontes" do Mesopaleoceno da Bacia de Itaborai, Rio de Janeiro, Brasil.* Unpublished thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, 327 pp.

Oliveira, E.V., and F.J. Goin. In press. Marsupiais fósseis do Paleoceno de Itaboraí: Origem, Irradiação e História Biogeografica. In *Marsupiais do Brasil,* ed. N.C. Caceres. Rio de Janeiro: Universidade Federal do Rio de Janeiro.

Pascual, R. 1980a. Nuevos y singulares tipos ecológicos de marsupiales extinguidos de América del Sur (Paleoceno Tardío o Eoceno Temprano) del Noroeste Argentino. II *Congreso Argentino de Paleontología y Bioestratigrafía, Buenos Aires, Actas* 2:151–173.

———. 1980b. Prepidolopidae, Nueva Familia de Marsupialia Didelphoidea del Eoceno Sudamericano. *Ameghiniana* 17(3):216–242.

———. 1983. Novedosos marsupiales paleógenos de la Formacion Pozuelos (Grupo Pastos Grandes) de la Puna, Salta, Argentina. *Ameghiniana* 20(3–4):265–280.

Pascual, R., and A. A. Carlini. 1987. A new superfamily in the extensive radiation of South American Paleogene marsupials. *Studies in Neotropical Mammalogy: Essays in Honor of Philip Hershkovitz. Fieldiana Zoology* 39:99–110.

Pascual, R., F.J. Goin, and A.A. Carlini. 1994. New data on the Groeberiidae: Unique late Eocene–early Oligocene South American marsupials. *Journal of Vertebrate Paleontology* 14(2):247–259.

Pascual, R., E. Ortiz Jaureguizar, and J.L. Prado. 1996. Land mammals: Paradigm for Cenozoic South American geobiotic evolution. *Munchner Geowissenschaftlich Abhandlungen* (*A*) 30:265–319.

Patterson, B. 1952. Un nuevo y extraordinario marsupial deseadiano. *Revista del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata* 1:39–44.

Paula Couto, C. de. 1952a. Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Didelphidae. *American Museum Novitates* 1567:1–26.

———. 1952b. Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. *American Museum Novitates* 1559: 1–27.

———. 1952c. A new name for *Mirandaia riberoi* Paula Couto 1952. *Journal of Mammalogy* 33(4):503.

———. 1962. Didelfídeos fósiles del Paleoceno de Brasil. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Zoología* 8(12):137–166.

Peters, D.S., and G. Storch. 1993. South American relationships of Messel birds and mammals. *Kaupia* 3: 263–269.

Reig, O.A. 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. *Monographiae Naturae* 1:1–162.

Reig, O.A., J.A.W. Kirsch, and L.G. Marshall. 1987. Systematic relationships of the living and Neocenozoic American "opossum-like" marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In *Possums and opossums: Studies in evolution,* vol. 1, ed. M. Archer, 1–89. Sydney: Surrey Beatty & Sons and the Royal Zoological Society of New South Wales.

Ride, W.D.L. 1962. On the evolution of Australian marsupials. In *The evolution of living organisms,* ed. G.W. Leeper, 281–386. Melbourne: Melbourne University Press.

———. 1993. *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. *Association of Australasian Palaeontologists Memoir* 15:441–459.

Sigé, B. 1972. La faunule de Mammifères du Crètace Supèrieur de Laguna Umayo (Andes Peruviènnes). *Bulletin du Muséum National d'Histoire Naturelle,* 3º ser., 99, *Sciénces du Terre* 19:375–409.

Simpson, G.G. 1935. Descriptions of the oldest known South American mammals, from the Río Chico Formation. *American Museum Novitates* 793:1–25.

———. 1938. A new marsupial from the Eocene of Patagonia. *American Museum Novitates* 989:1–5.

———. 1947. A new Eocene marsupial from Brazil. *American Museum Novitates* 1357:1–7.

———. 1964. Los mamíferos Casamayorenses de la Colección Tournouër. *Revista del Museo Argentino de Ciencias Naturales, Paleontología* 1:1–21.

———. 1970. Addition to the knowledge of *Groeberia* (Mammalia, Marsupialia) from the mid-Cenozoic of Argentina. *Breviora* 362:1–17.

Szalay, F.S. 1982. A new appraisal of marsupial phylogeny and classification. In *Carnivorous marsupials,* vol. 2, ed. M. Archer, 621–640. Mosman, New South Wales: Royal Zoological Society of New South Wales.

Takahashi, F. 1974. Variaçao morfologica de incisives em Didelfideos (Marsupialia, Didelphinae). *Anais da Académia Brasileira de Ciências* 46(3–4):413–416.

Tate, G.H.H. 1934. New generic names for two South American marsupials. *Journal of Mammalogy* 15: 154.

Thomas, O. 1894. On *Micoureus griseus,* Desm., with the description of a new genus and species of Didelphidae. *Annals and Magazine of Natural History* (Series 6) 14:184–188.

———. 1895. Descriptions of four small mammals from South America. Including one belonging to the peculiar marsupial genus "*Hyracodon*" Thomes. *Annals and Magazine of Natural History* (Series 6) 16: 367–370.

———. 1921. A new genus of opossum from southern Patagonia. *Annals and Magazine of Natural History* (9ª Series 8) 1921:136–139.

Wolff, R.G. 1984. New early Oligocene Argyrolagidae (Mammalia, Marsupialia) from Salla, Bolivia. *Journal of Vertebrate Paleontology* 1:108–113.

Received 2 July 2003; accepted 29 December 2003.

Paleogene Notoungulates from the Amazon Basin of Peru

Bruce J. Shockey,[1] Ralph Hitz,[2] and Mariano Bond[3]

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 "Tinguiririca̲n" *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 "Tinguiririca̲n" 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.

RESUMEN. Se describen y documentan notoungulados (Orden Notoungulata) de grado paleógeno procedentes de la fauna local de Santa Rosa, en el este de Perú. Los especímenes incluyen al menos dos especies de notoungulados toxodóntidos (Suborden Toxodontia) y el primer registro de un interatérido (Suborden Typotheria) de la Cuenca Amazónica. Los materiales de toxodóntidos incluyen dientes aislados de un animal del tamaño de una oveja, así como también un diente de, tal vez, el más pequeño toxodóntido conocido. Los especímenes asignables al toxodóntido de mayor tamaño incluyen un molar superior con crestas distintivas, abiertas y múltiples, un premolar superior de tipo leontínido y un molar inferior cuya morfología coincide con la de los toxodóntidos, leontínidos y notohípidos deseadenses o más tardíos. El ejemplar de interatérido consiste en una mandíbula inferior cuyos molares son parecidos a los de *Eopachyrucos plicifera,* del "Tinguiririquense", y a los de un pequeño y aún innominado interatérido de Salla, Bolivia (SALMA Deseadense). Los especímenes de toxodóntidos, así como el de interatérido, son comparables a los notoungulados que se registran entre el "Tinguiririquense" al Deseadense (31.5–24 Ma). Estos materiales ofrecen pistas muy interesantes en relación con la fauna de notoungulados de la Cuenca Amazónica, y sugieren una región a explorar a los efectos de encontrar las huellas de la rápida radiación de notoungulados avanzados ocurrida a fines del Paleógeno y comienzos del Neógeno.

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

---

[1] Department of Zoology, University of Florida, 223 Bartram, Gainesville, Florida 32611. Email: BShockey@excite.com

[2] Tacoma Community College, 6501 South 19th Street, Tacoma, Washington 98466. Email: rhitz@tcc.tacoma.ctc.edu

[3] Departamento Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. Email: palvert@museo.fcnym.unlp.edu.ar

Science Series, Number 40, pp. 61–69
Natural History Museum of Los Angeles County, 2004

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, is 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 "Astraponotéen plus supérieur" (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 Río Yurúa near its confluence with the Río 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.

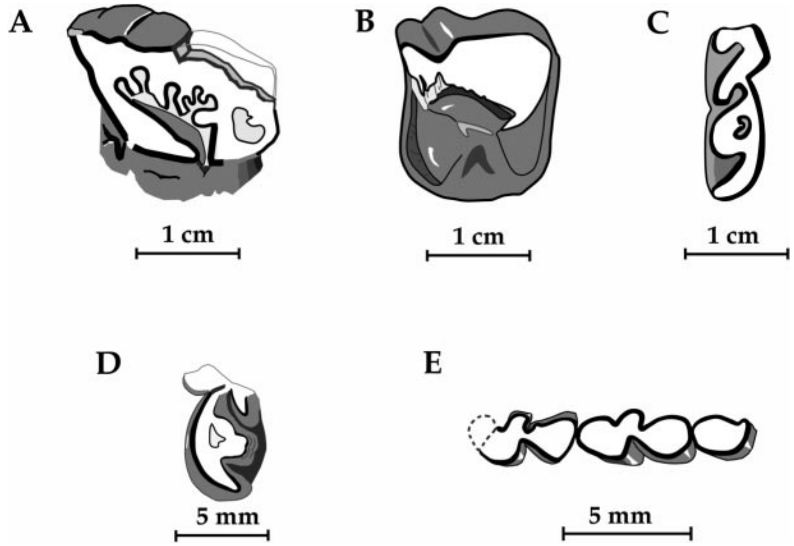


Figure 1 Occlusal views of notoungulate teeth from Santa Rosa, Peru. **A,** LACM 140569, left M^1 or M^2; **B,** LACM 144304, left P^4; **C,** LACM 144305, right M$_{?1}$, illustrating the 7/9 morphology discussed in the text; **D,** LACM 140570, left lower molar of small ?notohippid; **E,** LACM 140571, interatheriid molars of partial mandible, M$_1$–trigonid of M$_3$.

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 M^1 or M^2; LACM 144304, left upper premolar; LACM 144305, right M$_1$ or M$_2$; LACM 144307, left M$_1$ or M$_2$ (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 (M^1 or M^2) is distinctive in having multiple and open cristae. It is mesodont and has an oblique protoloph that is significantly longer than the transversely oriented metaloph. 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 fossette, suggesting that the tooth is minimally worn. Another millimeter or so of wear would have isolated this infolding as the major fossette. The short posterior cingulum forms an oval-shaped fossette that is partially bisected by a posterior enamel projection, giving the fossette 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 cuspule. 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 each other medially. Although the tendency to develop cuspules adjacent to the ectoloph is pronounced in notoungulates (Patterson, 1934), such cuspules 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, 1985; *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, *Acoelohyrax* Ameghino, 1902 (this synonymy and use of the generic name *Acoelohyrax* 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 *Puelia 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 parastyle 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 parastyle 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 (posterolabial 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 canquelnesis* Simpson, 1934, but its anteroposterior dimension is within the size range of P^3s and in the lower end of the size range of P^4s of *Ancylocoelus frequens* Ameghino, 1895. It is almost as large as the P^4 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 $M_{?1}$, 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" (Cifelli, 1993). The molar at hand is smaller than those of most leontiniids, and it is most comparable in size to those of nesodontine 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 M_1 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 P^3s of the smallest leontiniids and within the lower end of the size range of the P^4s (e.g., *Ancylocoelus* Ameghino, 1895, and a small species of an unnamed genus at Salla; Shockey, 1997b). The upper molar (LACM 140569), however, is smaller than the M^1s of the smallest leontiniids. The undulated median surface of the ectoloph of the M^1 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 M_1 or M_2 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 *Plexotemnus*-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 M_{1-3} (only the trigonid of M_3 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 interatheriines, LACM 140571 is very small. The length and width of the M_1 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_3 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_{1-3}. 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 plicifera* 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 interathere taxa, the smallest of which ranges widely in size (MacFadden et al., 1985; Hitz, 1997). The dentition of LACM 140571 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 12-1529), a taxon known from several localities from southern Argentina (Gran Barranca, Chubut; Cañadon Blanco, Chubut; Rocas Bayas, Río Negro). *Eopachyrucos plicifera* was first allocated to the Hegetotheriidae 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 "Astraponotéen plus supérieur" level. Several localities in Argentina have been tentatively correlated to the Astraponotéen plus supérieur level at the Gran Barranca, including Cañadon Blanco and Rocas Bayas (Hitz et al., 2000). Furthermore, the Astraponotéen 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 leontiniids, which tend to have multiple cristae, although they are expressed as labial fossettes or enamel pits. LACM 140569 also differs from leontiniids by having linear dimensions that are only 90 percent of those of the smallest known leontiniids. The upper premolar (LACM 144304) has a morphology (e.g., "leontiniid basin") comparable to leontiniids, 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 leontiniid. The lower molar (LACM 144305) has the general morphology of the "advanced Toxodontia" (*sensu* Cifelli, 1993). Although it is almost identical to the M_1 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 leontiniids. Thus, all three of the larger specimens may have come from a very small and primitive leontiniid.

The diminutive ?notohippid, LACM 140570, is comparable to Deseadan taxa, but it is lower crowned. The interatheriid, LACM 140571, is most comparable to the early Oligocene "Tinguiririცan" *Eopachyrucos plicifera* and an unnamed interathere 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, Pachybiotherium*) 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 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 "Friasian" 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 "Tinguiririican" 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 interathere 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 ("Tinguiririican" 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 Toxodontia," suggesting that they represent taxa near the base of the radiation of leontiniids, Deseadan notohippids, and toxodontids. LACM 140569 presents characters suggestive of an advanced *Plexotemnus*-like toxodont or a primitive leontiniid, 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.

ACKNOWLEDGMENTS

We thank K.E. Campbell for inviting us to examine these interesting specimens. We also appreciate the thoughtful, critical, and thus helpful, reviews of earlier versions of this work by D. Croft and R. Madden. An International Research Fellowship from the National Science Foundation provided support for BJS during the initial phases of this study.

LITERATURE CITED

Ameghino, F. 1895. Premiére contribution la connaissance de la fauna mammalogique de couches à *Pyrotherium. Boletín Instituto Geográfico Argentino* 15:603–660.

———. 1897. Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la fauna mammalogique des couches à *Pyrotherium. Boletín Instituto Geográfico Argentino* 18:406–521.

———. 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 16: 349–429.

———. 1902. Notices preliminaire sur des mammiféres nouveaux des terrain crétaces de Patagonie. *Boletín Academia Nacional de ciencias Córdoba* 17:5–70.

———. 1904. Nuevas especies do mamíferos, cretáceos y terciarios de la República Argentina. *Anales de Sociedad de Ciencias de Argentina, Buenos Aires* 56: 193–208.

Bond, M., and G. Lopez. 1993. El primer Notohippidae (Mammalia, Notoungulata) de la Formación Lumbrera (Grupo Salta) del Noroeste Argentino. Consideraciones sobre la sistematica de la Familia Notohippidae. *Ameghiniana* 30:59–68.

Bond, M., G. Lopez, and M. Reguero. 1996. "Astrapontoéen plus supérieur" of Ameghino: Another interval in the Paleogene record of South America. *Journal of Vertebrate Paleontology* 16(3)(Suppl.):23A.

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard. *Annales Museo Nacional Buenos Aires* 3:95–174.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pitman. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Carlini, A.A., S.R. Vizcaíno, and G.J. Scillato-Yané. 1997. Armored xenarthrans: A unique taxonomic and ecologic assemblage. In *Vertebrate paleontology of the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, J.J. Flynn, and R.L. Cifelli, 213–226. Washington, D.C.: Smithsonian Institution Press.

Cifelli, R.L. 1993. The phylogeny of the native South American ungulates. In *Mammal phylogeny: Placentals,* vol. 2, ed. F.S. Szalay, M.J. Novacek, and M.C. McKenna, 195–216. New York: Springer-Verlag.

Cifelli, R., and J. Guerrero. 1997. Litopterns. In *Vertebrate paleontology of the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, J.J. Flynn, and R.L. Cifelli, 289–302. Washington, D.C.: Smithsonian Institution Press.

Colwell, J. 1965. A new notoungulate of the family Leontiniidae from the Miocene of Colombia. Unpublished Master's thesis, University of California, Berkeley.

Flynn, J.J., J. Guerrero, and C.C. Swisher III. 1997. Geochronology of the Honda Group. In *Vertebrate paleontology of the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, J.J. Flynn, and R.L. Cifelli, 44–59. Washington, D.C.: Smithsonian Institution Press.

Flynn, J.J., and C.C. Swisher III. 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. In *Geochronology time scales and global stratigraphic correlation,* ed. A. Berggren, D.V. Kent, and J. Hardenbol. Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication, 54:317–333.

Frailey, C.D., and K.E. Campbell, Jr. 2004. Paleogene rodents from Amazonian Peru: The Santa Rosa local fauna. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 71–130.

Goin, F.J., and A. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Hitz, R. 1997. *Contributions to South American mammalian paleontology: New Interatheres (Notoungulata) from Chile and Bolivia, Typothere (Notoungulata) phylogeny, and paleosols from the Late Oligocene Salla beds.* Unpublished Ph.D. dissertation, University of California, Santa Barbara.

Hitz, R., M. Reguero, A. Wyss, and J.J. Flynn. 2000. New interatheriines (Interatheriidae, Notoungulata) from the Paleogene of central Chile and southern Argentina. *Fieldiana, New Series* 42:1–26.

Kay, R.F., R.H. Madden, J.M. Plavcan, R.L. Cifelli, and J. Guerrero Díaz. 1987. *Stirtonia victoriae,* a new species of Miocene Colombian primate. *Journal of Human Evolution* 16:173–196.

Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G.H. 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 Science* 96(23):13235–13240.

MacFadden, B.J., K.E. Campbell, R.L. Cifelli, O. Siles, N.M. Johnson, C.W. Maeser, and P.K. Zeitler. 1985. Magnetic polarity stratigraphy and mammalian fauna of the Deseadan (Late Oligocene–Early Miocene) Salla beds of northern Bolivia. *Journal of Geology* 93(3):223–250.

Madden, R.H., J. Guerrero, R.F. Kay, J.J. Flynn, C.C. Swisher, and A.H. Walton. 1997. The Laventan Stage and Age. In *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, J.J. Flynn, and R.L. Cifelli, 499–519. Washington, D.C.: Smithsonian Institution Press.

McKenna, M., and S. Bell. 1997. *Classification of mammals above the species level.* New York: Columbia University Press, 631 pp.

Pascual R. 1965. Los Toxodontidae de la Formación Arroyo Chásico de la Provincia de Buenos Aires. *Ameghiniana* 19:19–35.

Patterson, B. 1934. Upper premolar–molar structure in the notoungulata with notes on taxonomy. *Geological Series of Field Museum of Natural History* 6: 91–111.

Paula Couto, C. de. 1981. Fossil mammals from the Cenozoic of Acre Brazil. IV—Notoungulata Notohippidae and Toxodontidae Nesodontinae. *Anais do II Congresso Latinoamericano de Paleontologia, Porto Alegre* 2:461–477.

———. 1982a. *Purperia,* a new name for *Megahippus* Paula Couto, 1981. *Iheringia* 7:69–70.

———. 1982b. Fossil mammals from the Cenozoic of Acre Brazil. V—Notoungulata Nesodontinae (II), Toxodontinae and Haplodontheriinae, and Litopterna, Pyrotheria and Astrapotheria (II). *Iheringia* 7:5–43.

Ribeiro, A.M., and M. Bond. 1999. Consideraciones sobre *Purperia cribatidens* (Paula Couto, 1981) (Notoungulata, Toxodontia) del Cenozoico de Acre, Brasil. *Ameghiniana* 36(1):107.

Roth, S. 1902. Notas sobre algunos neuvos mamíferos fósiles. *Anals de Museo La Plata* 10:251–256.

Shockey, B.J. 1997a. Two new notoungulates (Family Notohippidae) from the Salla beds of Bolivia (Deseadan: Late Oligocene): Systematics and functional morphology. *Journal of Vertebrate Paleontology* 17(3):584–599.

———. 1997b. *Toxodontia of Salla, Bolivia (Late Oligocene): Taxonomy, systematics, and functional morphology.* Unpublished Ph.D. dissertation, University of Florida, Gainesville, Florida.

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

———. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85:1–350.

———. 1960. Notes on the measurement of faunal resemblance. *American Journal of Science* 258A:300–311.

———. 1967. The beginning of the age of mammals in South America, part 2. *Bulletin of the American Museum of Natural History* 137:1–259.

Soria, M.F., and H. Alvarenga. 1989. Nuevos restos de mamíferos de la Cuenca de Taubaté, Estado de São Paulo, Brasil. *Anais Académia Brasileira de Ciências* 61:157–175.

Stirton, R.A. 1953. A new genus of interatheres from the Miocene of Colombia. *University of California Publications in Geological Sciences* 29:265–348.

Villarroel, C., and J. Colwell Danis. 1997. A new leontiniid notoungulate. In *Vertebrate paleontology of the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, J.J. Flynn, and R.L.

Cifelli, 303–318. Washington, D.C.: Smithsonian Institution Press.

Villarroel, C., and J. Guerrero. 1985. Un nuevo y singular representante de la familia Leontiniidae? (Notoungulata, Mammalia) en el Mioceno de La Venta, Colombia. *Geología Norandina, Bogotá* 9:35–40.

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.

Received 2 July 2003; accepted 29 December 2003.

Paleogene Rodents from Amazonian Peru: The Santa Rosa Local Fauna

Carl David Frailey[1] and Kenneth E. Campbell, Jr.[2]

ABSTRACT. The first large and diverse sample of ?Eocene rodents from South America consists of forms that are more primitive than those of the Oligocene genera to which they are surely allied. The teeth of these rodents are brachydont, are quadrangular with rounded corners in occlusal outline, and have low crests and four distinct cusps. The clean, scissorslike cutting surface of younger caviomorphs appears to be in its formative stages. All of these early rodent taxa share a basic tetralophodont enamel pattern that illustrates the beginning of patterns seen in the modern rodent families Erethizontidae, Echimyidae, and Agoutidae, and one genus shows consistent and characteristic signs of pentalophodonty. The pentalophodont condition appears to have evolved following the merging of minor cuspules into a distinct crest within the metaflexus, which, with wear, produced the fifth loph, a neoloph. All available mandibular rami are hystricognathous, indicating an early appearance of this character.

New genera include *Eopululo* (Erethizontidae, one new species), *Eoincamys* (Agoutidae, two new species), *Eobranisamys* (Agoutidae, two new species), *Eopicure* (Agoutidae, one new species), *Eosallamys* (Echimyidae, two new species), *Eoespina* (Echimyidae, one new species), *Eosachacui* (Echimyidae, one new species), and *Eodelphomys* (Echimyidae, one new species). Fragmentary or excessively worn specimens of several other indeterminate taxa indicate a greater diversity in the Santa Rosa local fauna than that suggested by the named taxa.

The Santa Rosa local fauna is dated to the ?Eocene (early Mustersan South American Land Mammal Age, SALMA) on the basis of the stage of evolution of the included rodent taxa and that of other mammalian taxa in the fauna. The presence of such a highly diverse rodent fauna at this early date in the South American fossil record requires a reexamination of hypotheses of hystricognath origin and dispersal. Heretofore, hypotheses regarding the origins of the South American hystricognaths have placed their roots in North America or Africa, with dispersal to South America occurring sometime before the Deseadan SALMA or, more recently, the post-Mustersan/pre-Deseadan “Tinguirirican” time. The diverse ?Eocene Santa Rosan rodent fauna increases the possibility that the South American hystricognaths might have originated after vicariant isolation from the ancestral rodent lineage during the breakup of Gondwana. This hypothesis requires a much older date of origination for South American hystricognath rodents than previously suggested by the fossil record.

RESUMEN. La primera muestra de roedores del ?Eoceno de América del Sur consiste en formas más primitivas que aquéllas de los géneros oligocenos con las cuales están seguramente relacionadas. Los dientes de estos roedores son braquidontes, cuadrangulares, con esquinas redondeadas en su perfil oclusal y tienen crestas bajas y cuatro cúspides diferenciadas. Parecen encontrarse en una etapa formativa las superficies netas y cortantes de los caviomorfos de menor edad. Todos estos taxones de roedores tempranos comparten un patrón básico tetralofodonte, ilustrativo de los comienzos de los patrones observables en las familias modernas de roedores Eretizontidae, Echimyidae y Agoutidae; uno de los géneros muestra signos consistentes y característicos de pentalofodoncia. La condición pentalofodonte parece haber evolucionado a partir de la fusión de cúspulas menores en una cresta diferenciada dentro del metaflexo; con el desgaste se produce el quinto lofo, un neolofo. Todas las ramas mandibulares estudiadas son hystricognatas, indicando la temprana aparición de este carácter.

---

[1] Johnson County Community College, Overland Park, Kansas 66210; Museum of Natural History, University of Kansas, Lawrence, Kansas 66045; Research Associate, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: cfrailey@jccc.net

[2] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: kcampbel@nhm.org

Science Series, Number 40, pp. 71–130
Natural History Museum of Los Angeles County, 2004

Los nuevos géneros incluyen a *Eocoendu* (Erethizontidae, una especie nueva), *Eoincamys* (Agoutidae, dos nuevas especies), *Eobranisamys* (Agoutidae, dos nuevas especies), *Eopicure* (Agoutidae, una nueva especie), *Eosallamys* (Echimyidae, dos nuevas especies), *Eoespina* (Echimyidae, una nueva especie), *Eosachacui* (Echimyidae, una nueva especie) y *Eodelphomys* (Echimyidae, una nueva especie). Aparecen también especímenes fragmentarios o excesivamente desgastados pertenecientes a varios otros taxones indeterminados, lo que revela una diversidad aun mayor en la fauna local de Santa Rosa.

La edad de la fauna local de Santa Rosa se postula como ?Eoceno (SALMA Mustersense temprano) sobre la base de el grado evolutivo de los roedores estudiados, así como también de otros taxones de mamíferos presentes en la misma. La presencia de una asociación tan diversa de roedores en esta etapa temprana del registro fósil sudamericano requiere una revisión de las hipótesis sobre el origen y distribución de los histricognatos. Hasta ahora, dichas hipótesis han postulado el origen norteamericano o africano de los histricognatos, con una dispersión hacia América del Sur ocurrida algo antes de la SALMA Deseadense o, más recientemente, hacia los tiempos "Tinguiririquenses" (post-Mustersense/pre-Deseadense). La diversa fauna de roedores de Santa Rosa sugere la posibilidad de que los histricognatos sudamericanos pudieron haberse originado a partir del aislamiento vicariante del linaje ancestral de roedores durante la partición de Gondwana. Esta hipótesis requiere un tiempo de origen de los histricognatos sudamericanos muy anterior al sugerido por el registro fósil.

INTRODUCTION

The presence of rodents in the Eocene record of South America has been hypothesized for many years (for summary discussions, see George, 1993; Lavocat, 1993; Wood, 1993; Vucetich et al., 1999). The great diversity of uniquely South American rodents in the Oligocene (and their total absence in older faunas) suggested an undiscovered Eocene appearance followed by rapid diversification. Rapid diversification, indeed, for among rodents of the Deseadan South American Land Mammal Age (SALMA) are 19 genera within six families of the order Rodentia (following the taxonomic arrangement of McKenna and Bell, 1997). Radiometric dates indicate that the Deseadan SALMA extends from 29.4 Ma to younger than 25.65 Ma in Bolivia (Kay et al., 1998), or from 29 to 27 Ma in Patagonia (Flynn and Swisher, 1995). The sudden, mid-Tertiary appearance of a diverse suite of rodents in a continent that had been isolated from all other continents for the first half of the Tertiary has led to considerable debate as to how and when rodents arrived in South America.

The first look at the rodent fauna of the supposed period of arrival and diversification was the discovery of a rodent in the pre-Deseadan Tinguiririca local fauna of Chile (Wyss et al., 1993), which was dated to 31.5 Ma (early Oligocene) and originally thought to have possibly extended back as far as 37.5 Ma (late Eocene; Wyss et al., 1993, 1994; Flynn and Wyss, 1999). Wyss et al. (1993) left the taxonomic placement of their single specimen as "Dasyproctidae?, unnamed new genus and species" because it was too badly worn to reveal many taxonomic characters. Nonetheless, the mandibular ramus is clearly hystricognathous and dentally allied with later caviid rodents. From this specimen it could be inferred that by "Tinguirirican" time, taxonomic diversification of South American rodents was well underway.

But it is the Santa Rosa local fauna that finally reveals the extent of rodent diversification in the interval surrounding the Eocene–Oligocene transition and that answers many questions about the nature of these earliest caviids. From a small sample of concentrated matrix taken from the Santa Rosa locality (Campbell, 2004) in 1995, about 200 complete, isolated rodent teeth, one intact upper tooth row and partial maxilla, and numerous isolated incisors and tooth fragments resulted from the screenwashing of approximately 400 kg of sediment. This sample was enlarged by a return expedition in 1998. Much of the concentrated matrix collected then, all of which is less than 4 mm diameter, has not yet been sorted, but several partial dentitions recovered in the field and several dozens of additional isolated teeth sorted from a sample of the matrix were a significant addition to the sample. Three families, eight genera, and eleven species are represented by sufficiently diagnostic material to permit identification and description herein (Table 1). The majority of these taxa (the erethizontids being the principal exceptions) appear to be closely allied to taxa from the Deseadan SALMA deposits of Salla, Bolivia, yet consistently demonstrate more primitive dental features. Six additional species, represented by material considered inadequate for description, are also present. These are undoubtedly new to science and could be named if the specimens were more numerous or more complete.

MATERIALS AND METHODS

The taxonomic placement of genera within families of the suborder Hystricognatha in this paper follows McKenna and Bell (1997). The parvorder Caviida Bryant and McKenna, 1995, corresponds to the restricted concept of Caviomorpha, that is,

Table 1 Classification of the Santa Rosan rodents described in this paper.

- Order Rodentia Bowdich, 1821
  - Suborder Hystricognatha Woods, 1976
    - Infraorder Hystricognathi Tullberg, 1899
      - Family Erethizontidae Bonaparte, 1845
        - *Eopululo* new genus
          - *Eopululo wigmorei* new species
    - Parvorder Caviida Bryant and McKenna, 1995
      - Superfamily Cavioidae Fischer de Waldheim, 1817
        - Family Agoutidae Gray, 1821
          - Subfamily Dasyproctinae Gray, 1825
            - *Eoincamys* new genus
              - *Eoincamys pascuali* new species
              - *Eoincamys ameghinoi* new species
            - *Eobranisamys new genus*
              - *Eobranisamys romeropittmanae* new species
              - *Eobranisamys riverai* new species
            - *Eopicure* new genus
              - *Eopicure kraglievichi* new species
            - Genus and species indeterminate A
            - Genus and species indeterminate B
            - Genus and species indeterminate C
    - Superfamily Octodontoidea Waterhouse, 1839
        - Family Echimyidae Gray, 1825
          - Subfamily Heteropsomyinae Anthony, 1917
            - *Eosallamys* new genus
              - *Eosallamys paulacoutoi* new species
              - *Eosallamys simpsoni* new species
            - *Eoespina* new genus
              - *Eoespina woodi* new species
            - *Eosachacui* new genus
              - *Eosachacui lavocati* new species
          - Subfamily Adelphomyinae Patterson and Pascual, 1968
            - *Eodelphomys new genus*
              - *Eodelphomys almeidacomposi* new species
          - Subfamily indeterminate
            - Genus and species indeterminate A
            - Genus and species indeterminate B
            - Genus and species indeterminate C

South American hystricognaths exclusive of the Erethizontidae (Bryant and McKenna, 1995). Dentally, the erethizontids are similar to the other genera of South American rodents, especially so in the Santa Rosa local fauna, but this family is excluded from the Caviida because of other characteristics. Much rich discussion of the evolution, and therefore of the systematic relationships, of these rodents and their appropriate taxonomy exists in the scientific literature. The Santa Rosan rodents bring new evidence to these discussions, as will be presented. However, a discussion of family level rodent systematics, and a detailed defense of the choice of familial designations herein for certain genera, is not the purpose of this paper, and indeed, such is not possible without parts of the skeleton beyond the teeth currently available to us. All comparative analyses are at the generic level and will always mention the particular genus or genera under consideration. Subsequent familial placement of the Santa Rosa genera is with the closest comparable genera of a younger age. Higher level taxonomic reassortment of genera, should it be necessary in the future, should not affect the validity of the generic comparisons presented in this paper.

The choice of names for genera in this paper reflects the similarities to Oligocene and later genera of South American rodents and the probable Eocene age (see "Discussion") for these new rodents. The choice of species names honors people who have contributed to vertebrate paleontology in South America.

A complete classification of the taxa discussed in this paper is presented in Table 1. Measurements of all teeth discussed in the text are given in Appendix 1. Appendix 2 is a photo gallery of the rodent specimens from the Santa Rosa local fauna discussed herein.

All specimens are currently housed in the collections of the Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County (LACM). Unless otherwise specified, specimen numbers refer to this collection. Other acronyms used in this paper: PU, Princeton University; YPM, Yale Peabody Museum.

GENERAL DESCRIPTIVE ODONTOLOGY

In general, the teeth of these early rodents are what would be expected of primitive forms, and they are consistent with the theoretical description for early caviid rodents given by Wood (1981:83). They are squat, or brachydont, and quadrangular with rounded corners when viewed in occlusal outline. Upper teeth display only slight unilateral hypsodonty. In general, lophs and lophids are broad based and taper to narrow crests. Distinct cusps are present in early wear stages, particularly in those taxa that appear to be near *Branisamys* Hoffstetter and Lavocat, 1970, from Salla, Bolivia. Wear stages are seen in which the lophs or lophids have not fused, and in which the wear surface is sloping and may extend onto the side of the tooth. All of the teeth are fundamentally similar, with taxonomic differences found in the size and placement of the lophs and lophids. The basic patterns of the Santa Rosan genera are diagramed in Figure 1. In most instances, and with a little practice, these diagrams are sufficient to make an identification to genus of an unknown tooth.

The species of rodents documented by these teeth represent the earliest known South American members of the Hystricognathi. The presence of recognizable cusps indicates that these teeth are not far removed from bunodonty. The degree of brachydonty is such that minor wrinkles and bumps in the crown surface quickly, with wear, become part of

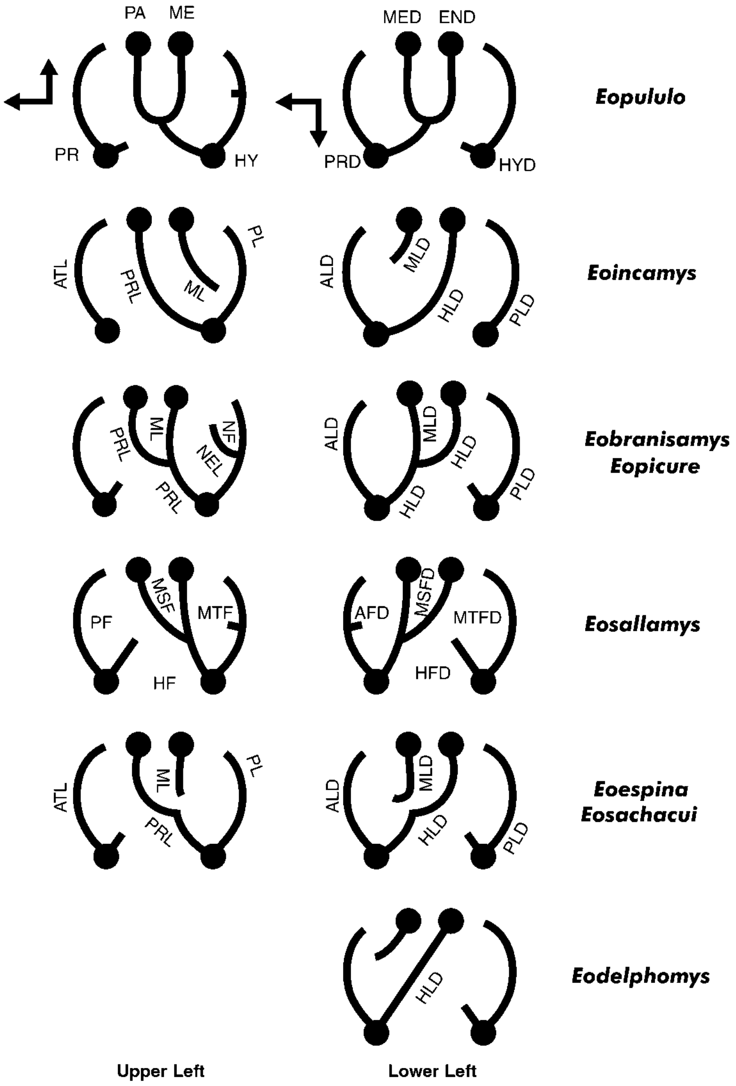


Figure 1 Dental terminology and comparative sketches of the occlusal patterns of the Santa Rosan rodent teeth. Arrows indicate anterior (to left) and labial directions. Dental nomenclature used in this paper is indicated. With wear, a flexus may become a fossette and a flexid may become a fossettid. Lophs shown terminating without connecting with other lophs or cusps indicate lophs that are unconnected initially, but which connect with wear. **Upper teeth.** Cusps: HY, hypocone; PA, paracone; PR, protocone; ME, metacone. Lophs: ATL, anteroloph; ML, metaloph; NEL, neoloph; PL, posteroloph; PRL, protoloph. Flexuses and fossettes: HF, hypoflexus; MSF, mesoflexus; MTF, metaflexus; NF, neoflexus; PF, paraflexus. **Lower teeth.** Cuspids: END, entoconid; HYD, hypoconulid; MED, metaconid; PRD, protoconid. Lophids: ALD, anterolophid; HLD, hypolophid; MLD, metalophid, PLD, posterolophid. Flexids and fossettids: AFD, anteroflexid; HFD, hypoflexid; MSFD, mesoflexid; MTFD, metaflexid.

the occlusal surface. The simple patterns, often subtle distinctions that separate taxa, and the innumerable variations, some exasperatingly intermediate between taxa as defined here, made for great difficulty in the separation and identification of some genera and species.

Deseadan SALMA representatives of the rodent families documented at Santa Rosa have higher crowned teeth (although still low crowned when compared with later genera), nontapering and more distinct lophs and lophids, fusion of lophs and lophids during early wear, and relatively indistinct cusps and cuspids. The occlusal view of wear patterns seen in the Santa Rosan rodents and their younger Deseadan relatives are so similar in some cases that one can mentally see the derivative pat-

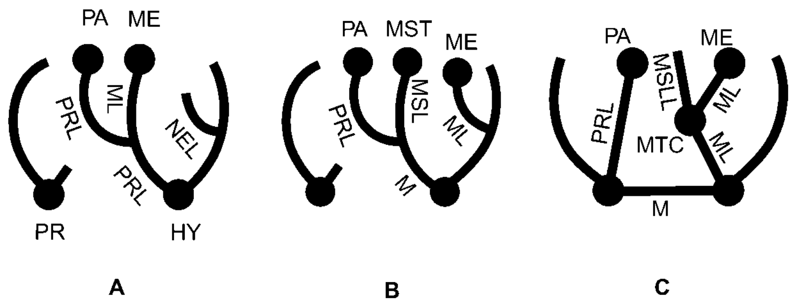


Figure 2 Differing interpretations of dental features of early rodents as displayed in an upper left molar (anterior to left). **A,** From Patterson and Wood (1982) and followed in this paper; **B,** from Lavocat (1976); **C,** from Flynn et al. (1986). HY, hypocone; M, mure; ME, metacone; ML, metaloph; MSL, mesoloph; MSLL, mesolophule; MST, mesostylid; MTC, metaconule; NEL, neoloph; PA, paracone; PR, protocone; PRL, protoloph.

tern created by no more than a slightly increased crown height and the loss of separate identities for the individual cusps, the suppression of a crest or mure, or the stabilization of what, in some Santa Rosan forms, appear to be simple irregularities in the crown surface. Such changes as these are not an insignificant matter, however, and they might only have been achieved over great lengths of time. Currently, the lack of age data prevents us from obtaining, or offering, insights into rates of evolution of early caviid rodents. Nonetheless, it is fair to suggest that the Santa Rosan rodents were moving along the evolutionary path that led to some of the known Oligocene genera of South American rodents.

In that the dental patterns of the rodent teeth in the Santa Rosa local fauna are very similar to those described by Patterson and Wood (1982) for the Deseadan SALMA rodents of Bolivia, for the sake of direct comparison, and consistent with our interpretation of dental homologies, we use their character designations with only slight modification. This terminology is derived from Wood and Wilson (1936) and illustrated in Figures 1 and 2. On upper molars, the protoloph is designated as the crest that connects the paracone and hypocone [the terms loph(s) and crest(s) are used interchangeably in this paper]. This crest is invariably the stronger and the first of the interior crests to form as the crown wears. Such usage is somewhat at odds with standard caviid nomenclature in which the connection between the protoloph and metaloph is identified simply as a mure and the segment of the crest between the hypocone and the junction of the protoloph and metaloph is not further identified other than as part of the hypocone (e.g., Patterson and Wood, 1982). As defined here, the continuous protoloph standardizes the dental nomenclature for all of the Santa Rosan genera, in particular including *Eoincamys* new genus, in which no other crest unites with the protoloph.

The metaloph, as here defined, is a weak crest that decreases in height toward the interior of the crown surface. Its union with the protoloph, which occurs in all genera except *Eoincamys* new genus, is near the midpoint of the protoloph and marked by a deflection in that crest. Among the upper teeth of these genera, the protoloph is frequently, but not consistently, wide at this point and short crests may extend toward both the metaloph and the protocone. These crests then become connecting crests as crown wear progresses. This might be the expression of a mesocone (*sensu* Lavocat, 1981; Vucetich and Verzi, 1990) or metaconule (*sensu* Flynn et al., 1986). If so, this argues against identification of the third loph as a mesoloph or metaconule in the Santa Rosan rodent teeth in that in these genera the third loph does not progress with wear toward the labial margin. Rather, it proceeds internally from a labial cusp, which we identify as the metacone.

Patterson and Wood (1982, and references therein) identify the fourth crest in the upper teeth of caviids as a neoloph and refer to the third crest from the anterior as the metaloph. We find the terminology of Patterson and Wood (1982) more in accord with the crown patterns of the Santa Rosan rodents and in contradiction to the terminology and hypotheses of pattern origin expressed by Lavocat (1976, 1981), Flynn et al. (1986), Vucetich and Verzi (1990), and Candela (1999) (see "Discussion").

On the lower teeth, the patterns are simpler. The preeminent crest that corresponds to the protoloph of the uppers is the hypolophid. In our usage, the hypolophid connects the entoconid and protoconid. Patterson and Wood (1982) use the term hypolophid, but it is not included in their figure 1, and it does not correspond exactly to our usage. The labial, oblique portion of what we call the hypolophid is termed the ectolophid by Patterson and Wood (1982). This crest is not identifiable in *Eoincamys* new genus. In describing the crests of chapattimyid lower teeth, Flynn et al. (1986) identify the second of four crests as a metalophulid II. As with their nomenclature for the upper teeth of these rodents, this designation is probably correct for the rodents that they studied, but unlikely for the Santa Rosan rodents in which the labial terminus of the second lophid is a large cuspid, here termed the metaconid, and the lophid therefore identified as a metalophid. What Flynn et al. (1986) call the metalophid is our anterolophid.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Suborder Hystricognatha Woods, 1976

Family Erethizontidae Bonaparte, 1845

Eopululo new genus

TYPE SPECIES. *Eopululo wigmorei* new species.

INCLUDED SPECIES. Monotypic.

DIAGNOSIS. Teeth brachydont with major, identifiable cusps. Upper molars square with rounded corners in occlusal outline. Protoloph and metaloph parallel to each other and to transverse axis of tooth; approximately equal in length and width. Parafossette, mesofossette, and metafossette large, nearly equal in size, and oval (parafossette) to egg-shaped (metafossette) in outline.

ETYMOLOGY. *Eos,* dawn, Greek; *pululo,* local Peruvian name for a porcupine.

Eopululo wigmorei new species

Figure 12A; Appendix 2

HOLOTYPE. LACM 143269, right M^x.

REFERRED SPECIMENS. M^x: left, 149489; right, 143272. M_x: left, 143410, 149465; right, 143263 (partial), 143268 (partial). All catalogue numbers pertain to LACM collections.

DIAGNOSIS. As for the genus.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. Named in honor of John G. Wigmore, a distinguished former member of the Board of Governors of the Natural History Museum of Los Angeles County, who financially supported the Rio Yurúa expeditions and participated in the Santa Rosa discovery expedition of 1995.

DISCUSSION. This taxon is one of the largest species recovered from Santa Rosa. The three upper teeth assigned to it are fragmental or in an advanced stage of wear. In one, LACM 143272, the dental pattern is almost gone. LACM 143269 is the best of the three specimens, and the following description is taken primarily from that specimen. Complete teeth are rounded squares in occlusal view. As is typical of erethizontid teeth, the two central crests are thin, parallel, and at nearly 90 degrees to the anteroposterior axis of the tooth. They are approximately equal in length and prominence. The protocone is connected to the protoloph by a weak mure. All three labial folds of this tooth have been closed into fossettes, although it is clear that the mesofossette was the last to be encircled and that this was only achieved at the advanced state of wear seen in this particular tooth. All three fossettes are large and subequal in size, with the metafossette only slightly larger than the others. The three labial fossettes are large, which is consistent with the rounded outline of the tooth and the central placement of the protoloph and metaloph. In outline, these three labial fossettes are a curved oval (parafossette, curving around the protoloph), rectangular in form (mesofossette), or ovate (metafossette). The shape of the metafossette is created by the greater width of the posteroloph at its labial end. At this position in teeth of *Protosteiromys* Wood and Patterson, 1959, the posteroloph may be crenulated or even have a neoloph, but no such irregularities are present on the holotype of *Eopululo wigmorei.* The hypoflexus is narrow, but it gives no indication of closure into a fossette. On the heavily worn and damaged specimen, LACM 143272, all fossettes are nearly gone, but because they were flat bottomed, rather than steeply sloped toward their centers, their former extent and the outlines of the crests are still evident. As well as can be determined, the surviving, remnant pattern of that tooth matches the description of the specimen that is better preserved.

LACM 143410 is a nearly complete lower tooth, but LACM 143268 is only a small fragment of what was probably a lower tooth. Both show a large, deep, and roughly rectangular mesoflexid. On the more complete specimen, LACM 143410, it can be seen that only slight wear has caused the labial ends of the anterolophid and metalophid to join; that is, the anterofossettid has formed, and the posterior two crests have nearly encircled the metaflexid.

Another lower tooth, LACM 143263, is missing most of the anterolophid and the labial one-third of the tooth. What survives is very representative of lower teeth found among species of the Erethizontidae. The anterofossettid is on the verge of forming, although wear on the tooth is slight. With additional wear, the metafossettid and then the mesofossettid would form, in that order, with the mesoflexid remaining free until advanced wear. The two central crests (i.e., the metalophid and hypolophid) are nearly parallel to each other and the transverse axis of the tooth. The metalophid is only slightly thinner than the hypolophid. The large and oval anteroflexid and metaflexid are highly characteristic of the elongate lower teeth seen in species of the Erethizontidae.

Parvorder Caviida Bryant and McKenna, 1995

Superfamily Cavioidae Fischer de Waldheim, 1817

Family Agoutidae Gray, 1821

Subfamily Dasyproctinae Gray, 1825

Eoincamys new genus

TYPE SPECIES. *Eoincamys pascuali* new species.

INCLUDED SPECIES. *Eoincamys ameghinoi* new species.

DIAGNOSIS. Enamel pattern similar to that of *Incamys* Hoffstetter and Lavocat, 1970, but differs by having low, rounded lophs and recognizable cusps. Teeth brachydont with four broad upper lophs; major cusps evident in lophs. Protoloph runs diagonally across the tooth. Connections between protoloph and posteroloph incomplete until late wear stage. Metaloph with weak or no connection to posteroloph.

ETYMOLOGY. *Eos,* dawn, Greek; *Incamys,* a genus of Deseadan rodent, indicating similarity to that genus.

DISCUSSION. This is one of the most easily identifiable dental patterns among the generally similar rodent teeth from Santa Rosa. In the upper teeth, the protoloph dominates the occlusal surface, and it is usually unconnected with either the posteroloph or metaloph. The metaloph tends to parallel the curvature of the protoloph and thereby unite with the posteroloph rather than the protoloph. The protoloph never unites with the anteroloph; that is, the paraflexus and hypoflexus are confluent as a single flexus. This is very similar to the condition in the Oligocene genus *Incamys* (Fig. 14), although because of a higher crown height the parafossette of *Incamys* more often opens onto the labial margin.

A comparable loph arrangement exists in lower teeth assigned to this genus, but here the hypolophid is the dominant crest. Like the metaloph, the metalophid is comparatively small and subject to more variation. The metalophid may unite with the hypolophid, may be discontinuous at its middle, or, through miscellaneous enamel spurs, may unite with both the hypolophid and anterolophid.

A small metaloph/metalophid is present in the initial wear stages of upper and lower molars of *Incamys,* and the metaflexus and anteroflexid are discernible. There is an indication in both upper and lower teeth of *Eoincamys* that a three-crested dental pattern typical of *Incamys* is developing through a process whereby the metaloph/metalophid is being eliminated in upper and lower teeth, respectively, by a reduction and union with the posterior crest (upper teeth) or anterior crest (lower teeth).

Eoincamys pascuali new species

Figures 3, 12B, 13A, 14; Appendix 2

HOLOTYPE. LACM 143318, left M^x.

REFERRED SPECIMENS. P^4: left, 143321; right, 143313, 143322. M^3: right, 143324. M^x: left, 143314, 143316, 143319, 149463; right, 143312, 143317, 143323, 149478. dp_4: left, 143335, 143456; right, 143328, 143331. P_4: 143301, 143333, 143334, 143336. M_1: left, 143303. M_3: right, 149445, 149449. M_x: left, 143304, 143306, 143307, 143308, 143309, 149446; right, 143299, 143300, 143305, 143310, 143427, 143434, 143504, 149452, 149453. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. The larger of two species referred to *Eoincamys.* Crown with four crests. Anteroloph, protoloph, and metaloph parallel. Metaloph and posteroloph of same length.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene

ETYMOLOGY. *Pascuali,* in honor of Rosendo Pascual, a friend, colleague, and preeminent mammalian paleontologist of Argentina.

DESCRIPTION. Upper Teeth. The protoloph, hypoloph, and metaloph are approximately parallel, smoothly curved, and run diagonally across the occlusal surface of the tooth. The metaloph and posteroloph are much reduced in length and confined to the posterolateral corner of the tooth. These two crests are almost completely united in the unworn condition at both their lingual and labial margins. The uniting of these crests causes an oval metafossette, rather than a metaflexus, to be a prominent feature of these teeth. In two specimens, LACM 143317 and 143319, a short enamel spur, which we interpret to be spatially equivalent to a neoloph, extends into the small metafossette. This spur is here considered to be a variation in the anterior enamel wall of the posteroloph rather than a neoloph. The labial portion of the anteroloph is closely associated with the paracone, and it is separated from the rest of the anteroloph by a constriction in the crest. The length of the anteroloph that is lingual to the constriction is about the same as that of the metaloph, but much wider.

Lower Teeth. In occlusal outline, the teeth have a flattened anterior margin and a curved posterior margin. The hypolophid is comparatively straight, with only slight deflections of small enamel spurs at the location of potential (i.e., with wear) connections with the metalophid and posterolophid. The hypofossettid and metafossettid are combined throughout most of the wear stages, and they are open at both labial and lingual margins. The metalophid commonly unites with the lingual end of the anterolophid to create a U-shaped curve, opening laterally, that persisted on many specimens until late wear was achieved.

The lower molars of *Eoincamys pascuali* are similar to those of the Deseadan taxon *Incamys bolivianus* Hoffstetter and Lavocat, 1970, in that the dental pattern is dominated by two oblique lophids, the hypolophid and posterolophid. The protoconid is the labial terminus of the hypolophid. The anterolophid and metalophid unite on the lingual border. With moderate wear, the metalophid joins the hypolophid, but a connection between the anterolo-

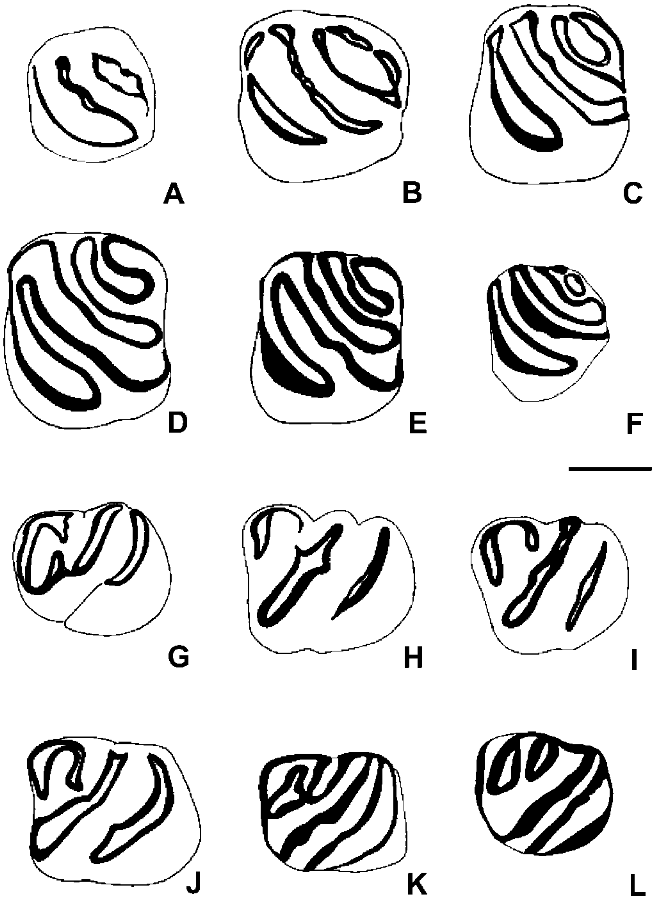


Figure 3 *Eoincamys pascuali.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." P^4: **A,** LACM 143322. M^x: **B,** LACM 143318 (holotype of genus); **C,** LACM 143319; **D,** LACM 143323r; **E,** LACM 143316; **F,** LACM 143324r. P_4: **G,** LACM 143336r. M_x: **H,** LACM 143308; **I,** LACM 143299r; **J,** LACM 143306; **K,** LACM 143305r; **L,** LACM 143434r. Scale = 1 mm.

phid and hypolophid does not occur until late wear. The size and position of the anterolophid and metalophid of *Eoincamys* and *Incamys* are very similar, except that in *Incamys* the metalophid fuses with the anterolophid to create a single crest anterior to the hypolophid. There is no complete mure between the hypolophid and posterolophid; that is, the hypoflexid and metafossettid are fully confluent, although remnants of a partial mure are present in most specimens of *E. pascuali,* and the limits of the hypoflexid and metafossettid are discernible. A complete mure is more likely to form, albeit weakly, in the sister species, *E. ameghinoi* new species.

Eoincamys ameghinoi new species

Figures 4, 12C; Appendix 2

HOLOTYPE. LACM 143339, left M^x.

REFERRED SPECIMENS. Maxilla, partial, with P^4–M^2, 149495. P^4: left, 149473; right, 149430. M^3: left, 143315; right, 143340. M^x: left, 143320, 143338, 143396 (partial), 149470; right, 143279, 143437, 143468, 149450. P_4: left, 143332; right, 143445. M_x: left, 143280, 143435, 149435, 149442; right, 143507, 149444. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. The smaller of two species assigned to this genus. Metaloph short, small, and not connected to posteroloph until advanced wear. Paracone and metacone large and conical.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Ameghinoi,* in honor of Carlos and Florentino Ameghino, pioneering vertebrate paleontologists of Argentina.

DISCUSSION. The teeth of *Eoincamys ameghinoi* appear to be even more brachydont than those

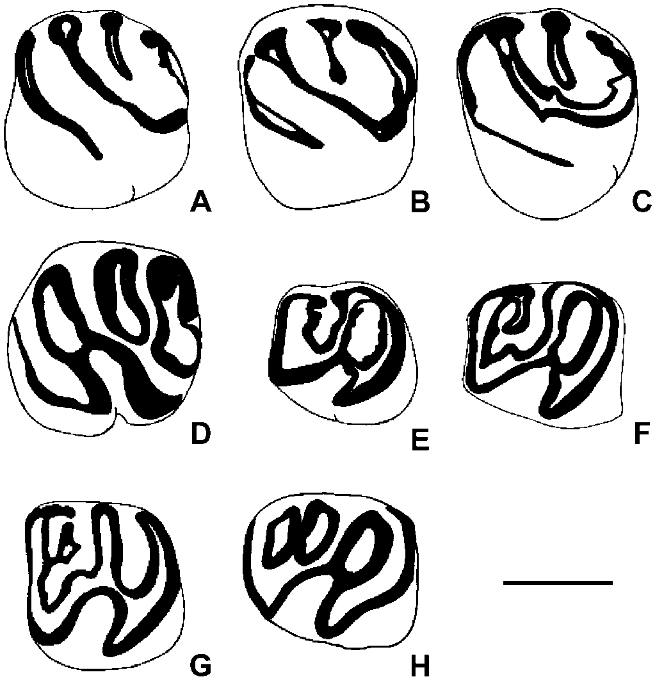


Figure 4 *Eoincamys ameghinoi.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." M^x: **A,** LACM 143339 (holotype); **B,** LACM 143338; **C,** LACM 143340r; **D,** LACM 143279r. P_4: **E,** LACM 143445r. M_x: **F,** LACM 143507r; **G,** LACM 143435; **H,** LACM 143280. Scale = 1 mm.

of *E. pascuali,* although the difference is small and questionable because of variations resulting from wear. The greater brachydonty may explain the more variable patterns seen in teeth of *E. ameghinoi* in that the occlusal surface is more likely to be affected by minor irregularities in the crown surface.

Upper Teeth. This small species is most easily separated from *E. pascuali* by its proportionally smaller metaloph. The effective result is to have a single valley anterior to the protoloph that consists of the paraflexus and hypoflexus, with a V-shaped, combined mesofossette and metafossette posterior to the protoloph. The latter are joined medially. The combined posterior fossette, rather than a flexus, is created by the encircling of the posterior two-thirds of the occlusal surface by a nearly continuous crest composed of the protoloph, posteroloph, and labial margin of the tooth. Only shallow notches exist on the labial margin to indicate the entrances to the three labial valleys.

Lower Teeth. As in the uppers, and as is characteristic of this genus, an incipient three-crested pattern is indicated by the reduction of one crest from the occlusal surface. In this case, the reduced crest is the metalophid. The union of this lophid with the anterolophid at their lingual ends is not so strong as in *E. pascuali,* and the curved, U-shaped metalophid/anterolophid is not nearly so strongly formed. That union is approached in several specimens (LACM 143332 and 143507), but in these specimens there appears to be a typically tetralophodont pattern. However, in these specimens, the metalophid is incomplete at its center. In one specimen (LACM 143445, a P_4), at a wear stage equivalent to the aforementioned specimens, the metalophid has disappeared into a broadly confluent anterolophid/metalophid. It seems that the metalophid is a highly variable part of the dental pattern of this genus, and more so in *E. ameghinoi* than in *E. pascuali.*

Eobranisamys new genus

TYPE SPECIES. *Eobranisamys romeropittmanae* new species.

INCLUDED SPECIES. *Eobranisamys riverai* new species.

DIAGNOSIS. Enamel pattern similar to that of *Branisamys* Hoffstetter and Lavocat, 1970, but differs in having low, rounded crests and identifiable cusps.

ETYMOLOGY. *Eos,* dawn, Greek; *Branisamys,* a genus of Deseadan agoutid, indicating affinity with that genus.

DISCUSSION. Upper Teeth. The specimens referred to this genus are similar to teeth of the monotypic Deseadan genus *Branisamys* in that the upper molars are pentalophodont with the anteroloph completely separate until at least moderate wear is attained. The fifth loph appears to have formed from the alignment of enamel irregularities on the surface of the metaflexus, or from crenulations on the anterior edge of the posteroloph, or both, supporting the conclusion of Patterson and Wood (1982) that the tetralophodont enamel pattern is primitive for the parvorder Caviida. The term "neoloph" is therefore used in this paper for the short loph between the metaloph and the posteroloph. The anteroloph and protoloph, including the hypocone, are strongly curved, producing a quarter-moon shape to the combined paraflexus and hypoflexus. In several specimens, even after moderate wear, the metaloph does not connect with the protoloph. The neoloph and posteroloph are always fused in *Branisamys,* but may or may not be fused in specimens of *Eobranisamys*.

Lower Teeth. The lower teeth of *Eobranisamys* have four strong crests. The four lophids are approximately equal in thickness, with the metalophid being the narrowest. The posterolophid is convexly curved, but the anterolophid is straight. The anterolophid roughly parallels the metalophid and the medial half of the hypolophid, with slight variations that are important in distinguishing species. More so than in any other Santa Rosan genus, after fusion of the metalophid with the hypolophid it is the metalophid that appears to be a continuous, gently curved crest from the lingual surface to the protoconid, to which the lingual half of the hypolophid has joined. The hypolophid turns at the medial extent of the hypoflexid and curves to meet the metalophid. With slight wear, the hypolophid is connected to the posterolophid by a small mure. The posterolophid is continuous with the hypoconulid. The mesoflexid lies on the central labiolingual plane.

The dp_4 of *Eobranisamys* has a modification of the enamel pattern of the lower molars, with the posterior half of the tooth the least altered (Figs. 13B–D). A complete and independent posterolophid, which terminates labially in the hypoconid, occupies the posterior border of the tooth. The hypolophid reaches from the lingual margin, beginning at the entoconid, to the anteroposterior midline of the tooth, as in the molars. Unlike with the molars, the hypolophid of the dp_4 has a weak connection to the protoconid and stands as an abbreviated lophid. As a result, the metalophid, which connects the metaconid and protoconid, extends transversely across the occlusal surface as an isolated lophid. It connects to the hypolophid at the anteroposterior midline only during late wear stages of the tooth. In its unworn state, the anterolophid is composed of two or more unnamed cuspids. With a little wear of the crown, these cuspids fuse to create a lophid that eventually unites with the metalophid at the anteroposterior midline and, anteriorly, with a small cingulate crest. The small, anterior cingulate cuspid and the short anterolophid create the forward elongation and narrowing of the dp_4.

This pattern differs from that of the dp_4 of *Branisamys,* in which the protoconid is equally connected to the hypolophid and to the metaconid. Stated differently, the metalophid of *Branisamys* is more molariform. The anterior cingulate cuspid is variable in size and position in *Eobranisamys,* but in *Branisamys* it appears to be larger and less lophate.

Eobranisamys romeropittmanae new species

Figures 5, 12D, 13B, 14; Appendix 2

HOLOTYPE. LACM 144297, partial maxilla with right M^{1-2}.

REFERRED SPECIMENS. Maxilla, partial, right, with M^2–M^3, 144296; M^3: left, 143354, 143381, 149490; right, 143364, 143365, 149493. M^x: left, 149482; right, 143355, 143356, 143357, 143358, 143359, 143360, 143362. Mandible, partial, right, with dp_4–M_2, 144293; left, with damaged dp_4–M_2, 144292. dp_4: left, 143352, 143423 (partial); 143505 (partial); right, 143419. M_1: left, 149487. M_3: left, 143347. M_x: left, 143341, 143342, 143343, 143346, 149462; right, 143266, 143344, 143345, 149483. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. Larger of two species assigned to *Eobranisamys*. Metaloph short and not fully connected to protoloph, which connects to hypocone; neoloph well established.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Romeropittmanae,* in honor of Lidia Romero-Pittmann, a friend, colleague, and codiscoverer of the Santa Rosa local fauna.

DISCUSSION. Upper Teeth. Of the two species referred to this genus, the upper teeth of *Eobranisamys romeropittmanae* display the greatest separation of the anteroloph from the protoloph. In almost all specimens there is an enamel spur, or a deflection in the curve of the protoloph, to indicate a potential connection with the anteroloph. However, a connection is apparently never achieved, even in advanced wear. In two teeth (LACM 143365 and 143381), the stage of wear is such that the labial ends of the anteroloph and protoloph are united. Even here, there is no mure that connects these lophs. Also, the anteroloph is more strongly curved than in the other species, and it often has completely turned toward the posterior as it reaches the protocone. The protoloph and metaloph are not parallel. Instead, the protoloph is angled toward the anterolabial margin of the tooth and the metaloph approximates the labiolingual plane. The metaloph and neoloph appear to be the last to join the other crests as wear progresses. The neofossette is large, circular to oval in outline, and closes early with wear.

Lower Teeth. The lower teeth are quadrangular

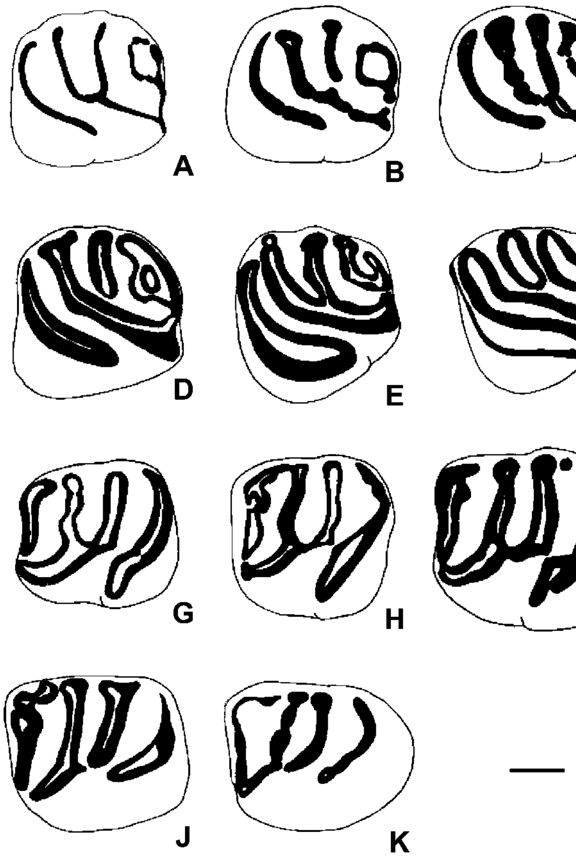


Figure 5 *Eobranisamys romeropittmanae*. Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." M^x: **A,** LACM 143356r; **B,** LACM 143362r; **C,** LACM 143359r; **D,** LACM 143358r. M^3: **E,** LACM 143364r; **F,** LACM 143365r. M_x: **G,** LACM 143345r; **H,** LACM 143343; **I,** LACM 143346; **J,** LACM 143266r. M_3: **K,** LACM 143347. Scale = 1 mm.

in outline. Of the two species referred to this genus, the lower teeth of *E. romeropittmanae* are the more lophate. The metaconid and entoconid are small and obscure. The mesoflexid is nearly as wide as the adjacent flexids, and it curves sharply anteriad at its lateral terminus. The metalophid and hypolophid are oblique to the anteroposterior axis of the tooth, and they approximate the parallel curvature of the posterolophid.

The lower deciduous premolar has a metalophid and an anterolophid that are curved and that rest obliquely on the occlusal surface; they parallel the hypolophid and posterolophid. The anterior cingulate cusp, rather than being centrally located as in *Branisamys* and the other species of *Eobranisamys,* is displaced to the anterolingual corner (Fig. 13B).

Two partial dentitions in fragmentary mandibles are referred to this species (LACM 144292 and 144293; Appendix 2). Both specimens are broken at the mandibular symphysis and the ascending rami are missing. LACM 144293 preserves an excellent dentition from dp_4 to M_2. The teeth are badly damaged on LACM 144292, but from the position of the roots and length of the first tooth (crown broken away), a dp_4 was present. The dental patterns of M_{1-2} cannot be determined, and only the roots of the M_3 are preserved. The allocation of LACM 144292 to *E. romeropittmanae* is based on the resemblance of this mandibular ramus to that of LACM 144293.

Both mandibular rami are short, robust, and fully hystricognathous. The lower incisors extend beneath the tooth rows. The proximal, or posterior, end of the lower incisor is exposed by breakage in LACM 144292. The incisor can be seen posterior to the M_3 only a few millimeters below the posterior alveolar margin of M_3. The masseteric fossa is deep, smoothly concave, and terminates anteriorly as a blunt point that reaches to the posterior margin of dp_4. The diastema is short (approximately 1.5 times the length of dp_4) and shallow. A circular mental foramen is located beneath the posterior third of the diastema and about halfway between

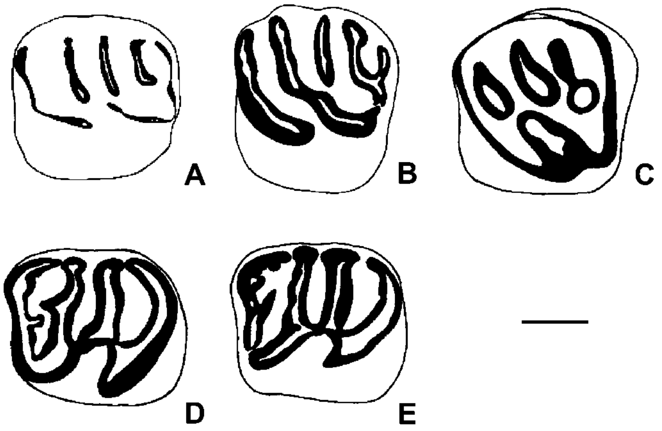


Figure 6 *Eobranisamys riverai.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." M^1: **A,** LACM 143503r (holotype); **B,** LACM 143372; **C,** LACM 143377. M_x: **D,** LACM 143366; **E,** LACM 143367. Scale = 1 mm.

the lateral alveolar ridge and the lower margin of the mandible at the diastema. When viewed with the anterior part of the incisor placed vertically, the tooth row does not tilt toward the midline to the extent seen in modern, or even Deseadan, taxa of the Caviida. Instead of an approximate 30 degree tilt as mentioned by Patterson and Wood (1982) for the rodents from Salla, Bolivia, the tilt is no more than 10 degrees. Similarly, the lateral torsion of the occlusal plane, in which P_4 or dp_4 is more vertical than the inwardly tilting posterior tooth row, is less evident in *Eobranisamys* than in *Branisamys* (Dinomyidae; Patterson and Wood, 1982:438, fig. 25F) or in *Incamys* (Agoutidae, personal observation).

Although the dental patterns of LACM 144292 and 144293 are obscured by wear and breakage, one aspect of these dentitions is especially interesting and pertinent to the evolution of the Caviida. In LACM 144293, all the molars were fully erupted and worn, and yet the dp_4 was present with no replacement tooth in the ramus (see X-ray, Appendix 2). In LACM 144292, the first tooth is broken away, but the size and position of its roots indicate a long, anteriorly tapered dp_4 instead of a quadrangular P_4. Again, there is no evidence of a permanent P_4 in the mandible.

The possibility that dp_4s were retained and not replaced by P_4s resurrects an old discussion about relationship between Old and New World hystricognaths. The retention of the dp_4 was cited as a character in common between Caviida ("Caviomorpha") and the Old World hystricognaths ("Phiomorpha") by Hoffstetter (1975:520, cited by Patterson and Wood, 1982:498). Phiomorpha is treated as a junior synonym of the infraorder Hystricognathi Tullberg, 1899, by McKenna and Bell (1997). In thryonomyids (Old World), deciduous premolars are a permanent part of the tooth row by the early Oligocene (Patterson and Wood, 1982: 498). Normal replacement of the deciduous premolars in the caviids was used by Wood (1981:80, 88) to exclude the African hystricognaths from a position of direct ancestry to the caviids because the African forms retained the dp_4 throughout life, whereas all known Oligocene genera of caviids replaced the dp_4 (Wood and Patterson, 1959:305). This statement was adjusted by Patterson and Wood (1982:391) to say that the Echimyidae retained dp_4 from the Colhuehuapian SALMA (early Miocene) on, but that in the Deseadan SALMA (late Oligocene) replacement was typical. The fossils from Santa Rosa create some questions in this regard. For example, *Branisamys* (Deseadan SALMA; Agoutidae) replaced the dp_4 (Patterson and Wood, 1982). But no replacement, permanent fourth premolars of any species of *Eobranisamys* (Agoutidae) are identified in the sample from Santa Rosa, and the two mandibular fragments attributed to *E. romeropittmanae* retained the dp_4 as a permanent part of the tooth row with no indication of a P_4 underneath. Permanent lower premolars of other species are represented in the collection. Now, with the apparent development of this trait (i.e., retention of the dp_4) in at least one genus of the Santa Rosan rodents, the proposed relationship between South American caviids and the African hystricognaths might be strengthened, but because this feature is not universal among the Santa Rosan rodents, it might represent only a common propensity within species of the Hystricognatha.

Eobranisamys riverai new species

Figures 6, 12E, 13C–D; Appendix 2

HOLOTYPE. LACM 143503, right M^1.

REFERRED SPECIMENS. M^2: right, 143378. M^3: left, 143302; right, 143428. M^x: left, 143372, 143373, 143377, 149474; right, 149464. dp$_4$: left, 143368 (partial), 143369, 143506; right, 143270 (partial), 143371. M$_x$: left, 143366, 143367, 149456, 149461, 149475; right, 149476, 149485. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. Smaller of two species assigned to this genus. Metaloph connected to protoloph; neoloph variable in shape and position, with weak or no connection to the posteroloph medially.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Riverai,* in honor of Hugo Rivera Mantilla, Director Técnico, Instituto Geológico Minero y Metalúrgico (INGEMMET), who has long encouraged and facilitated our research into the prehistory of Amazonian Peru, and without whose support the Santa Rosa local fauna would remain unknown.

DISCUSSION. Upper Teeth. The anteroloph is less curved than in *Eobranisamys romeropittmanae,* and it does not extend posteriad to the labiolingual midline of the tooth. The union between anteroloph and protoloph appears to occur late, and in one specimen (LACM 143373) it might never have occurred as the crown became worn. The protoloph and metaloph diverge, but less so than in *E. romeropittmanae,* and as a result the mesoflexus is smaller. There is a strong deflection in the curvature of the protoloph at the point where it meets the metaloph. When these two crests unite, the protoloph and metaloph appear to be attached to opposite ends of a mure from which the metaloph continues to the hypocone. The neofossette is comparatively smaller than that of *E. romeropittmanae.*

Lower Teeth. Lower teeth tend to be quadrangular, but rectangular in outline rather than square as in *E. romeropittmanae.* The metaconid and entoconid are large cusps, equal to the hypoconid in size, and present as knobs at the medial terminus of their respective lophids. The entoconid exceeds the metaconid in size. An enlarged anteromedial portion of the anterolophid, possibly the anteroconid, is equal to the hypoconid in size and is placed diagonally to the hypoconid, its posterolateral opposite. In one specimen, LACM 143366, the anterofossettid is invaded by enamel projections from both the anterolophid and metalophid, reflecting what is probably individual variation. The mesoflexid is constricted at its medial opening.

Eopicure new genus

TYPE SPECIES. *Eopicure kraglievichi* new species.

INCLUDED SPECIES. Monotypic.

DIAGNOSIS. Upper molars strongly rectangular in occlusal outline. Protocone conical and partially isolated from the other major cusps. Metaflexus occupied either by a small, isolated cusp or enamel spurs from adjoining crests.

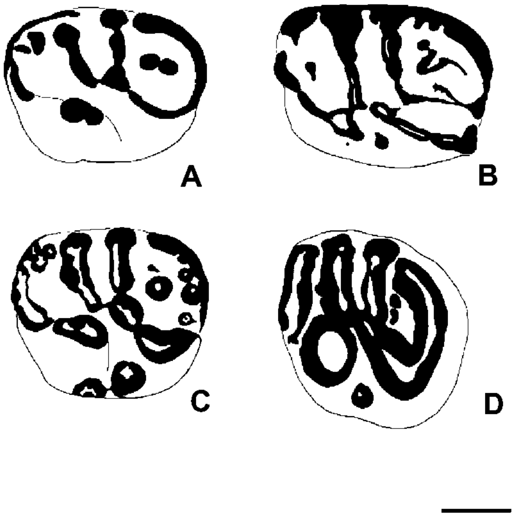


Figure 7 *Eopicure kraglievichi.* Variations in dental and wear patterns in upper teeth. **A,** LACM 143264 (holotype of genus); **B,** LACM 149455; **C,** LACM 143353; **D,** LACM 149479. Scale = 1 mm.

ETYMOLOGY. *Eos,* dawn, Greek; *picure,* local Peruvian name for an agoutid (Agoutidae), indicating affinity with that group.

DISCUSSION. This genus is placed in the Agoutidae, subfamily Dasyproctinae, on the basis of similarities to *Eobranisamys* in the arrangement of the crests and in the multiple enamel extensions into the metaflexus that are suggestive of the neoflexus of *Eobranisamys.*

Eopicure kraglievichi new species

Figures 7, 12F; Appendix 2

HOLOTYPE. LACM 143264, left M^x.

REFERRED SPECIMENS. M^x: left, 143353, 149455; right, 149454, 149466, 149479. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. As for the genus.

ETYMOLOGY. *Kraglievichi,* in honor of Lucas Kraglievich, a prominent vertebrate paleontologist of Argentina in the first one-third of the twentieth century, among whose publications are several pertaining to fossil rodents.

DESCRIPTION. In occlusal outline, these upper teeth have the shape one expects in lower molars, in that the length exceeds the width by an average of 25 percent (range, 17–40 percent). All six teeth have slight unilateral hypsodonty, which is characteristic of upper teeth. Two of the six (LACM 143264 and 149455) are unworn and rootless and may never have fully erupted. One other tooth, LACM 143353, has had the roots broken in such a way as to partially obscure the single medial root expected in an upper tooth, but it appears to be present. Three teeth (LACM 149454, 149466, and 149479) have enough of the roots present to safely say that they are upper teeth, and, by inference, that the others are as well.

Other aspects of the occlusal surfaces of these teeth are highly definitive. Of all the rodent specimens from Santa Rosa, these six teeth display the weakest expression of lophodonty. The poorly formed crests exist more as a series of connected cusps, some elongated to form a portion of a crest and others less so and more suggestive of individual cones. The most obvious expression of this is the isolation of the protocone, which exists more as a separate conical cusp than as the enlarged end of the anteroloph in five of the six specimens. Only in LACM 149455 is the protocone definitely continuous with the anteroloph in a totally unworn condition, and for that reason this specimen is the least confidently assigned to this species. The protoloph and metaloph are close and approximately parallel. The metaloph follows a smooth curve and continues as the medial half of the protoloph to the hypocone. The lateral half of the protoloph curves sharply near the middle of the occlusal surface and meets the metaloph. This part of the enamel pattern is very similar to that of *Eobranisamys.* Innumerable accessory cusps are present on the crowns of these teeth. Most frequently these are found in the metaflexus (all specimens), but variations in the crests are also present in two specimens (LACM 143353 and 149454) in which the paraflexus is invaded by a spur from the small cuspid that marks the lateral terminus of the anteroloph.

In three specimens (LACM 143264, 143353, and 149479), a small isolated cusp is in the center of the metaflexus, whereas in the others, and most dramatically so in the unworn crown of LACM 149455, one to three small enamel spurs enter the metaflexus from the metaloph and posteroloph.

An intriguing feature is the presence of an isolated cusp in the hypoflexus of three specimens (LACM 143353, 149454, and 149479). This cusp is especially large in LACM 149479.

On the most worn of the six specimens, LACM 149479, an unusual pattern of wear has completely removed the protocone. The site is occupied by a circular pit that extends well into the dentine. Even at this advanced and strange degree of wear, the circular margin of the protocone is recognizable. The protocone was separated from nearby crests for most of its circumference.

DISCUSSION. This taxon is represented in the fauna by only six teeth, all part of the upper dentition. Lower teeth of this species may lie unrecognized among unreferred specimens or specimens referred to other species in this fauna, but the unusual features of the upper teeth suggest that comparably diagnostic features should be present in the lower teeth as well, but no such teeth have been found. The more elongate upper molars have an occlusal outline that one would associate with lower molars, but the arrangement of roots and unilateral hypsodonty are typical of upper teeth. Should any of these six teeth eventually prove to be lower teeth, they are sufficiently different from all other lower teeth in the collection to ensure the retention of this taxon.

Indeterminate Specimens

After long consideration, the following four teeth have been isolated as unreferable material. They are placed within the family Agoutidae, subfamily Dasyproctinae because of their general similarities to *Eoincamys* and *Eobranisamys.* Although there are only one or two specimens per unnamed taxon, they are sufficiently distinctive to suggest that they represent real, but very rare, taxa in the fauna. We think this treatment reflects, probably more accurately, the species diversity of the Santa Rosa local fauna. The possibility remains, however, that some of these specimens are no more than curious dental variations of named Santa Rosan species.

Agoutidae, Genus and Species Indeterminate A

Appendix 2

REFERRED SPECIMEN. LACM 144299, right M_x.

DESCRIPTION AND DISCUSSION. A single lower molar represents an unknown taxon that has a dental pattern similar to that of *Eobranisamys.* This tooth has four lophids and a dental pattern in which the metalophid and hypolophid are close together and angle to meet each other before continuing to the protoconid as the hypolophid. The union of the metalophid and hypolophid occurs at the center of the occlusal surface.

The tooth of this species differs from those attributed to species of *Eobranisamys* in that it is much larger and the metalophid is centrally placed. Identification below the family level is not justified for this tooth because of the relatively simple and similar patterns seen in almost all rodent lower teeth in this local fauna. The slight differences from lower teeth of *Eobranisamys* that have been noted may or may not be significant.

Agoutidae, Genus and Species Indeterminate B

Appendix 2

REFERRED SPECIMEN. LACM 143375, right M^x.

DESCRIPTION AND DISCUSSION. This specimen is very similar to teeth that have been assigned to *Eobranisamys riverai,* but it differs in several aspects, one of which might prove to be highly diagnostic. This molar is slightly larger than the upper molars of *E. riverai,* and the union of the metaloph with the protoloph occurs closer to the hypocone. More significantly, however, the neoloph does not curve posteriorly to meet with the posteroloph. Instead, it extends mediad as a long, straight crest that does not meet another crest, and it would not have connected with another crest until very extensive wear of the tooth had occurred. This is so unusual that we cannot place this specimen within the genus *Eobranisamys* at this time. If additional specimens appear in which this condition can be identified as a natural variation on the pattern of *Eobranisamys,* then LACM 143375 might be assigned to *E. riverai.* If the position of the neoloph remains consistent in other specimens found in the future, then this specimen would represent another genus closely related to *Eobranisamys.*

Agoutidae, Genus and Species Indeterminate C

Appendix 2

REFERRED SPECIMENS. LACM 143349 and 143351, left M_x.

DISCUSSION. These specimens are much like those assigned to *Eobranisamys romeropittmanae.* They would, however, be the largest lower molars of that species in the collection. These teeth are typical for this group, in that they have four crests in which the anterior three converge on the protoconid, and in which the connection between the hypolophid and posterolophid is weak. The most unusual element of these teeth is unique among specimens in the fauna. Near the middle of the metalophid are two opposing, but offset, enamel spurs. One faces anteriad and the other posteriad. There is considerable variation in surface dental features among the teeth in this collection that frequently blur taxonomic distinctions, and in most cases, these variations are taken here as evidence of a close relationship among taxa because of the early stage of caviid diversification represented at Santa Rosa. On these specimens, however, the enamel spurs are not just odd variations. They are crisply defined aspects of the grinding surface that extend from the floors of the bordering fossettids. This is so unlike any other lower teeth in the sample that we think it best to recognize them as unique in the present discussion of the local fauna.

Family Echimyidae Gray, 1825

Subfamily Heteropsomyinae Anthony, 1917

Eosallamys new genus

TYPE SPECIES. *Eosallamys paulacoutoi* new species.

INCLUDED SPECIES. *Eosallamys simpsoni* new species.

DIAGNOSIS. Molar teeth brachydont. Enamel pattern similar to that of *Sallamys* Hoffstetter and Lavocat, 1970, but retains four low and rounded lophs with expansive cusps, as opposed to higher crowned pattern of three lophs after only moderate wear and cusps that are less separable from lophs in *Sallamys.*

ETYMOLOGY. *Eos,* dawn, Greek; *Sallamys,* a genus of Deseadan echimyid of South America.

DISCUSSION. On both upper and lower teeth of the two species referred to this genus, the positions of major cusps are indicated by terminal swellings in the crests, which is consistent with brachydonty. These cusps continue to be evident through moderate crown wear and disappear only as the enamel crests become broadly confluent. These species are placed near the Deseadan genus *Sallamys* on the basis of the reduced metaloph (upper teeth) and metalophid (lower teeth) that with wear disappear into union with the posteroloph and anterolophid. In so doing, a three-crested dental pattern very similar to the higher crowned teeth of *Sallamys* is achieved from what was originally a tetralophodont pattern.

The upper teeth of this genus have four principal lophs, of which the diagonal protoloph dominates the occlusal surface. The central two lophs are inclined slightly in the direction of the hypocone. The metaloph is much smaller than the protoloph and variable in its size and point of contact with the protoloph. Frequently, it is doubly curved in a sinuous, flat S-shape that turns anteriad at its contact with the protoloph. In the terminology chosen for this paper, the protoloph is considered to be the crest that extends between the paracone and the hypocone, rather than the shorter portion between the paracone and the site of union between the protoloph and the metaloph. This decision was made because in most of the Santa Rosan rodents, including *Eosallamys,* the metaloph does not connect to the hypocone as early as does the labial half of the protoloph, and a strong crest runs directly from the paracone to the hypocone, with only a slight deflection where it is joined, or is to be joined, by the metaloph. However, in *Eosallamys,* it is the small and initially incomplete metaloph and not the protoloph that extends as a smooth curve from the metacone toward the hypocone. When the crests are fully united, the appearance is that of a metaloph that extends between the metacone and hypocone and to which the protoloph joins near the center of the occlusal surface.

The hypoflexus is deep in *Eosallamys,* being placed at an angle greater than 45 degrees with respect to the labial margin of the tooth, and it appears to terminate at the base of the labial half of the protoloph. In the other genera of Santa Rosan rodents, the hypoflexus appears to be a continuation of the parafossette, with the two fossettes separated only by the connection between the protoloph and anteroloph. Frequently, but not invariably, the metafossette is invaded by spurs or crenulations from the posteroloph and with wear may be divided into labial and lingual halves. Two specimens identified as upper third molars of *E. paulacoutoi* new species (LACM 143363) and *E. simpsoni* new species (LACM 143380) have strangely shaped crests that connect the posteroloph with the metaloph and disrupt the metafossette. This appears to be a variable aspect of the teeth in this genus, and particularly so with regard to M^3s.

The following description is derived mostly from the lower teeth of *E. simpsoni,* for which better material is available. In the lower teeth of *Eosallamys,* four crests are present with the hypolophid as the strong, centrally positioned loph. As in the uppers, the two central lophids incline slightly toward the protoconid, which is in the opposite direction of that seen in the uppers. The metalophid, like the metaloph, is relatively smaller and sinuous (S-shaped) in outline. The belly of the S-shape marks the position of a mure that, with wear, can separate the anterofossettid into labial and lingual subfossettids (as happens with the metafossette in the upper teeth). It is the anterior fossette in the lower teeth, versus the posterior fossette in the upper teeth, in which irregularities in the bordering enamel form partial lophids and spurs that enter the fossettid. The metalophid is not complete in all specimens, and it may curve to meet the anterolophid rather than connecting with the hypolophid (LACM 143311 and 143412), further obscuring the anterofossettid. This condition anticipates the loss of this lophid by its incorporation within a broad anterolophid, as seen in *Sallamys.* The hypoflexid is deep and positioned at an angle greater than 45 degrees with respect to the lingual margin of the tooth. It appears to terminate at the base of the lingual half of the hypolophid rather than exist as an extension of the metalophid.

The four-lophed pattern seen in the lower teeth referred to this genus is in direct contrast to the three-lophed pattern seen in lower cheek teeth of *Sallamys.* The three-lophed pattern in *Sallamys* is formed from the reduction of the labial portion of the metalophid and the fusion of the lingual portion with the anterolophid (Patterson and Wood, 1982: figs. 5C,E). Some lower teeth of *E. simpsoni* new species show the beginning of this process (LACM 143311, 143412, and 143413).

The octodontid affinities of this genus are indicated by the deep hypoflexid that effectively divides the tooth into anterior and posterior halves. The labiolingual transverse midplane of the tooth is marked by the anterior edge of the hypolophid.

In the two species assigned to this genus, the entoconid is present as an enlarged, medial tip of the hypolophid, but the metaconid is small and variable in size, and in some specimens of *E. simpsoni* new species, it cannot be distinguished from the remainder of the metalophid. The anteroflexid is the largest entrant, with the mesoflexid and metaflexid of approximately equal size.

The anterolophid and posterolophid curve lingually to meet the two central lophids. For the two named species, with moderate wear, the anterofossettid forms before the posterofossettid. The mesofossettid is the last of the flexids to close.

Eosallamys paulacoutoi new species

Figures 8, 12G, 13E–F; Appendix 2

HOLOTYPE. LACM 143422, maxilla, partial, right, with P^4–M^3.

REFERRED SPECIMENS. P^4: left, 149460; right 143415, 149480. M^3: right, 143363. M^x: left, 149494; right, 143267, 144302. dp_4: left, 143418 (partial), 143451, 149458 (partial); right, 143370, 143420, 143450. P_4: 149492. M_3: right, 143262. M_x: right, 143265, 143361 (partial), 144524. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. The larger of two species assigned to this genus. Posteroloph thick; metafossette heavily invaded by enamel spurs. Hypoflexus narrow, forming a hypofossette with moderate to heavy wear.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Paulacoutoi,* in honor of Carlos de Paula Couto, a prominent Brazilian vertebrate paleontologist who published many papers on fossil vertebrates of Amazonia.

DISCUSSION. Specimens of this species are uncommon in the Santa Rosa local fauna, but an excellent, complete upper tooth row is included in the collection, and it has been designated as the holotype. It is moderately worn, but the major elements of the dental patterns of the various teeth are evident.

Upper Teeth. In *Eosallamys paulacoutoi,* the metafossette is shallow and partially filled with irregular crenulations of the posteroloph. With wear, the metafossette is the first fossette to close. It then disappears into several small enamel lakes as the metaloph fuses with the posteroloph in a pattern that anticipates the condition of the Oligocene genus *Sallamys* (Patterson and Wood, 1982:fig. 4A). The hypoflexus appears to be unusually narrow. In the holotypical specimen, the hypoflexus has closed into a hypofossettid in the first two teeth of the tooth row. In LACM 143363, an M^3, the posteroloph is highly crenulated in a manner that is apparently typical for this species. In addition, a single auxiliary crest from the metaloph to the posteroloph divides the metafossette into two subfossettes. That condition is seen again in an M^3 of *E. simpsoni* new species (LACM 143380).

Lower Teeth. The enamel pattern in lower teeth is unusual in that a small, enamel spur may extend in a curve from the lingual apex of the anterolophid to attach to the metalophid near its center. This creates a small fossettid from the lingual corner of the anterofossettid. This unusual element is consistent with the substantial variation seen in the corresponding valley of the upper teeth, the metafossette, and may indicate commensurate variation in this part of the lower teeth. The metalophid and hypolophid are slightly oblique in the posterolin-

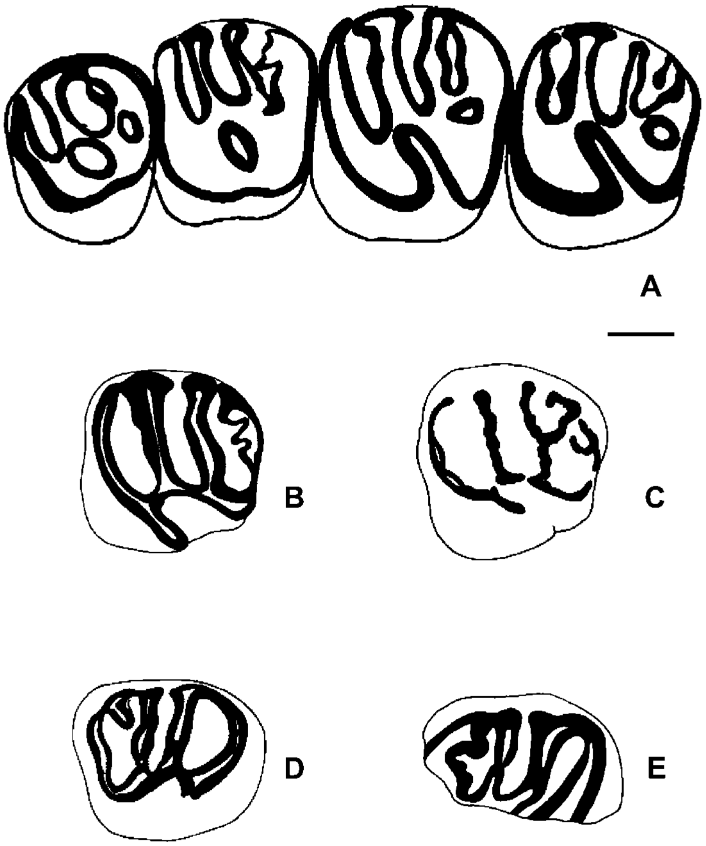


Figure 8 *Eosallamys paulacoutoi.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." P^4–M^3: **A,** LACM 143422r (holotype of genus). M^x: **B,** LACM 143267r; **C,** LACM 143363r. M_3: **D,** LACM 143262r. M_x: **E,** LACM 143265r. Scale = 1 mm.

gual to anterolabial direction. The metaconid is clearly present, even in a tooth that shows moderate wear. Protoconid and hypoconid are of approximately equal size.

Eosallamys simpsoni new species

Figures 9, 12H, 13G, 14; Appendix 2

HOLOTYPE. LACM 143424, right M^x.

REFERRED SPECIMENS. P^4: left, 149451. M^3: left, 143380; right, 149448. M^x: left, 143374, 143376, 143398, 149457, 149459, 149481, 149488; right, 143411, 143429, 143430, 143441 (partial), 149472, 149477. dp_4: left, 143452; right, 143406 (partial), 143407 (partial), 143443 (partial), 149467 (partial). P_4: left, 143311. M_3: left, 143284. M_x: left, 143276, 143416 (partial); right, 143273, 143275, 143412, 143413, 143414, 149491. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. The smaller of two species referred to this genus. Paracone and metacone large and approximately equal in size. Metafossette not heavily invaded by enamel spurs. Hypoflexus broadly open.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Simpsoni,* in honor of George Gaylord Simpson, who was so instrumental to our understanding of the Age of Mammals in South America.

DESCRIPTION. Upper Teeth. In many ways, these teeth are a smaller version of those referred to *Eosallamys paulacoutoi,* and were it not for the significant size difference it would be difficult to separate some of them. The smaller teeth of *E. simpsoni* also have a more primitive appearance, with a bulbous paracone and metacone, but substantial variation in this character is found among the teeth referred to this species. Enamel intrusions into the metafossette may be small (LACM 143429 and 149459) or large enough to be called a neoloph (LACM 143374 and 143398). In the latter two

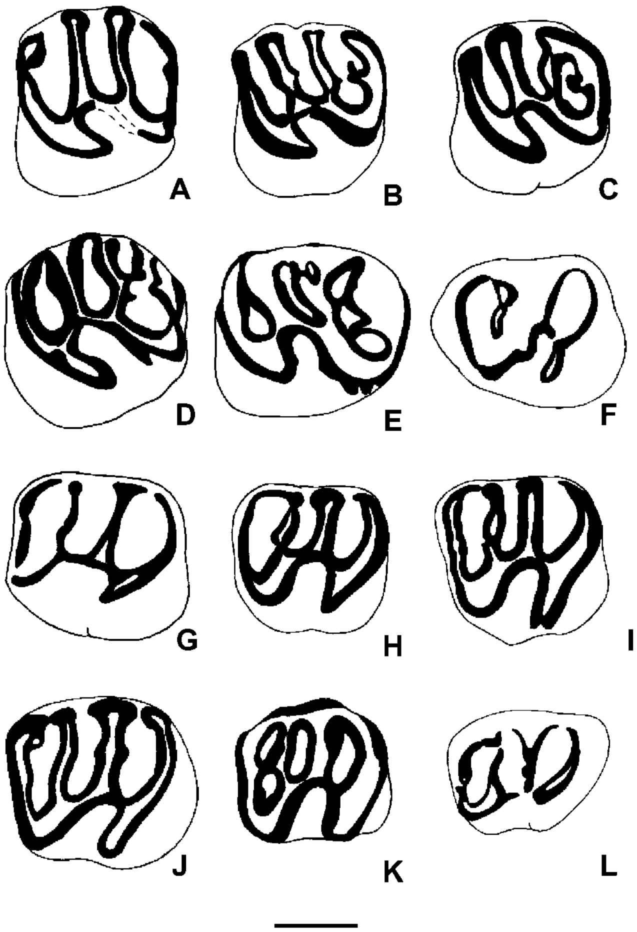


Figure 9 *Eosallamys simpsoni.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." M^x: **A,** LACM 143429r; **B,** LACM 143430r; **C,** LACM 143424r (holotype). M^3: **D,** LACM 143380. M^x: **E,** LACM 143411r. P_4: **F,** LACM 143311. M_x: **G,** LACM 143273r; **H,** LACM 143412r; **I,** LACM 143275r; **J,** LACM 143276; **K,** LACM 143413r. M_3: **L,** LACM 143284. Scale = 1 mm.

specimens, the neoloph is formed by two enamel projections from the posteroloph that meet, but do not completely unite, and therefore do not duplicate the strong and highly characteristic neoloph of *Eobranisamys.*

Lower Teeth. The lower teeth have four lophids, unlike the characteristic three lophids of later echimyids such as *Sallamys.* However, the most frequent site of variation is within the metalophid, and it is probably this lophid that is suppressed in the lower teeth of later echimyids.

An echimyid feature of these lower teeth that seems to be less evident in *E. paulacoutoi* is the relative positions of the hypoflexid and the lingual half of the hypolophid. The hypoflexid terminates near the center of the occlusal surface, where the hypolophid turns to meet the metalophid before continuing to the protoconid. The lingual half of the hypolophid appears to rest upon the lingual terminus of the hypoflexid. The effect is to separate the curve of the hypoflexid from the curve of the metafossettid and to associate the hypoflexid with the hypolophid instead.

Eoespina new genus

TYPE SPECIES. *Eoespina woodi* new species.

INCLUDED SPECIES. Monotypic.

DIAGNOSIS. Upper teeth tetralophodont, rounded crowns with thick, tapered marginal crests, thin internal crests, and large bulbous cusps.

ETYMOLOGY. *Eos,* dawn, Greek; *espina,* Spanish, spine or thorn.

DISCUSSION. Numerous specimens represent the smallest rodent in the Santa Rosa local fauna. They are placed in family Echimyidae, subfamily Heteropsomyinae on the basis of the emended diagnosis of that subfamily by Patterson and Wood

(1982:282–283) and because of their basic similarity to the teeth of *Eosallamys paulacoutoi.*

Upper Teeth. The upper teeth of this genus are similar to those of *Eosallamys* in that they have a tetralophodont pattern with three labial folds, of which the middle fold, the mesoflexus, is the shortest and most narrow. The protoloph and metaloph diverge only slightly toward the labial margin of the tooth. This genus differs from *Eosallamys* and *Eosachacui* new genus (see below) in that the posteroloph lacks the extensive crenulations that partially fill the metafossette of those genera.

Other than the unusual and possibly aberrant teeth of *Eopicure,* in which crests are poorly formed, the upper cheek teeth of *Eoespina* appear to be the most primitive among the Santa Rosan taxa. These teeth are rounded in both occlusal and lateral views. The major cusps are large, cone-shaped, and stand well above the level of the crests in an unworn tooth, and they retain this height distinction until the crown is well worn. All crests are broadly based and taper toward the occlusal surface. The thick anterior and posterior crests combine with the four bulbous cusps to nearly encircle the occlusal surface. The metacone is the smallest principal cusp, although this size difference is less than that in teeth of other Santa Rosan taxa. Two internal crests, the metaloph and labial half of the protoloph, are thin, low, and nearly parallel. These two crests are separate or weakly connected to the lingual half of the protoloph in an unworn tooth. Thus, until moderate wear unites them, there appear to be three short, thin crests within the interior of the occlusal surface (i.e., the two aforementioned labial crests and the oblique, lingual half of the protoloph).

The tetralophodont P^4 is about half the size of either of the first two upper molars. There is considerable variation in the size and placement of the protoloph and metaloph. These crests may appear as a small version of what is seen in a typical upper molar, or both may exist as projections from the labial margin of the tooth. In occlusal outline, the P^4 is round with a nearly continuous marginal crest.

Lower Teeth. All permanent lower teeth are tetralophodont, with little evidence of irregularities in the anterolophid or anteroflexid that typify several other taxa in this fauna. The description of the upper teeth as having large, conical cusps and thick marginal crests applies to the lower teeth as well, although the size distinction between the marginal and interior crests is not as strong. The metaconid is the smallest identifiable cuspid; the metalophid is the smallest crest and in some examples, probably P_4s, it is incomplete. The reduction to near loss of the metalophid is part of the subfamilial diagnosis of Patterson and Wood (1982).

Eoespina woodi new species

Figures 10, 12I, 13H–I; Appendix 2

HOLOTYPE. LACM 143286, left M^x.

REFERRED SPECIMENS. P^4: left, 144301; right, 143432, 143459, 149468. M^2: left, 149441. M^3: left, 143288, 143298; right, 143297. M^x: left, 143291, 143293, 143397, 144300, 149431, 149432, 149471, 149484; right, 143289, 143290, 143295, 143296, 143384, 143455, 143457, 149427, 149433, 149436, 149437. Mandibular fragment, right, with P_4–M_2, 144294. dp_4: left, 149440; right, 143391, 143403, 143404 (partial), 143405, 143448 (partial). P_4: left, 143283. M_1: left, 149425, 149469; right, 149434. M_3: left, 143386, 143438; right, 143282, 143440, 143461. M_x: left, 143389, 143436, 143446; right, 143281, 143327, 143330, 143385, 143390, 143439, 143447, 149429, 149486. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. As for the genus.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Woodi,* in honor of Albert Wood, who contributed so much to our understanding of rodent evolution.

Eosachacui new genus

TYPE SPECIES. *Eosachacui lavocati* new species.

INCLUDED SPECIES. Monotypic.

DIAGNOSIS. Union of the protoloph and metaloph occurs near center of occlusal surface. Mesoflexus widens laterally. Protoloph large, slightly curved, with only a slight flexure at its union with the metaloph. Posteroloph highly variable, with multiple enamel projections into metaflexus, which may extend to metaloph.

ETYMOLOGY. *Eos,* dawn, Greek; *sacha cui,* local Peruvian name for a spiny rat (Echimyidae).

DESCRIPTION. Upper Teeth. The paracone and metacone are seen as enlarged cones on the labial ends of the protoloph and metaloph. The protocone and hypocone are more compressed and incorporated within the anteroloph and posteroloph. The occlusal surface is crossed by four crests, of which the metaloph is the smallest. The two central crests diverge slightly toward the labial surface, with the metaloph placed transversely and the protoloph oblique to the transverse axis. The obliquity of the protoloph is created by the very anterior placement of the paracone, which lies even with, or slightly anterior to, the protocone. The protoloph maintains a constant width from paracone to hypocone. There is a deflection in the protoloph at the point at which the metaloph unites with the protoloph after moderate wear of the tooth surface, but this change of direction is directed toward the protocone rather than toward the anteromedial direction, with the result that this change of direction is less abrupt than is frequently seen in taxa of this local fauna. For example, in *Eobranisamys* and *Eoespina* the great deflection in the path of the

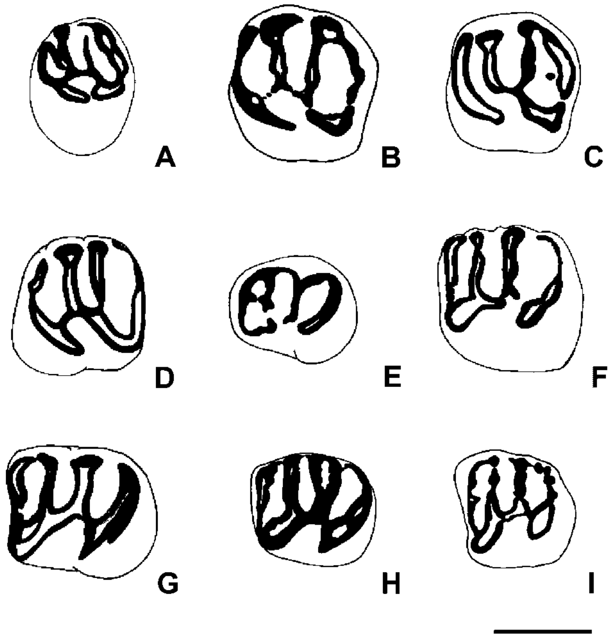


Figure 10 *Eoespina woodi.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." P^4: **A,** LACM 143459r. M^x: **B,** LACM 143286 (holotype of genus); **C,** LACM 143291; **D,** LACM 143384r. P_4: **E,** LACM 143283. M_x: **F,** LACM 143390; **G,** LACM 143446; **H,** LACM 143281r. M_3: **I,** LACM 143440r. Scale = 1 mm.

transverse protoloph creates a more rectangular base of the mesofossette. At an early stage of union, the lingual end of the metaloph appears to turn back toward the deflection of the protoloph and then to fuse with it. When fully united, the metaloph appears to be the principal, most smoothly continuous crest running from the metacone to the hypocone. The union of these two crests has the appearance of a Y, as is seen in *Eosallamys* from this fauna. The large number of irregularities of the posteroloph, in which enamel spurs of various size, number, and position may occupy much of the metafossette, is another similarity to *Eosallamys.* These enamel spurs are particularly strong in the M^3, and they may subdivide the metafossette into two or three smaller fossettes.

Three labial flexuses are present, which, with only moderate wear, create three fossettes. The order of closing is, first the parafossette, then the metafossette, and finally, and only with extreme wear, the mesofossette. The resulting fossettes are roughly oval in outline. The largest is the metafossette. The mesofossette and parafossette are approximately equal in size. The hypoflexus is deep and nearly reaches the center of the occlusal surface. Its curved axis is continuous with that of the parafossette and the two form a single curved valley in the unworn or slightly worn tooth. After considerable wear has occurred, these two flexuses are separated by only a small mure.

Lower Teeth. The occlusal surfaces of lower teeth of *Eosachacui* have four crests and three labial flexids. The anterolophid, hypolophid, and posterolophid are approximately the same size. The metalophid is small, but usually uniform in width and length. In three specimens (LACM 143325, 143329, and 149426; probably M_1s, but possibly P_4s), the metalophid is incomplete at its middle section or turns anteriad at this point to join the anterolophid rather than the hypolophid. When the metalophid unites with the hypolophid, as is typical, it does so midway between the protoconid and the lingual deflection of the hypolophid. In so doing, the angle of union is less than 45 degrees and a Y configuration of the crests occurs, as in the uppers. The lingual half of the hypolophid is transverse to slightly oblique toward the posterior. The lingual half of the hypolophid is equal to or smaller than the lingual half of the anterolophid.

Of the three flexids, the mesoflexid and metaflexid are of nearly equal size and both are smaller than the anteroflexid. On most specimens, the anteroflexid is disrupted by either an irregular margin to the anterolophid or enamel spurs from the anterolophid or metalophid.

One specimen, LACM 143394, which appears to be a P_4 but may be an M_1, is unusual in that there seem to be five crests present rather than four. This is surely an anomalous pattern because there appear to be two protoconids. The more posterior of the two is smaller and more of a buttressing cuspule to the main protoconid. Two crests extend from these two protoconids toward the lingual side of the tooth. The posterior of the two anomalous crests is recognizable as the hypolophid at its union with the metalophid. The anterior of the two crests is composed of two principal cuspules, one of which, the more lingual, is connected to an enamel spur that extends posteriad from the anterolophid. As one of the characters of *Eosachacui* is the presence of cuspules and enamel spurs in the anterofossettid, this is apparently an extreme example of such variation.

The hypoflexid is deep, extending to near the center of the occlusal surface and terminating at the lingual deflection of the hypolophid. As such, the hypoflexid is continuous with the curve of the lingual half of the hypolophid rather than seeming to be the continuation of the curve of the metaflexid.

DISCUSSION. These teeth represent another small heteropsomyine rodent in the fauna that is only slightly larger than *Eoespina* and with which it shares many similarities. In the upper molars, the most significant difference is the presence of enamel variations in the form of spurs or cuspules in the paraflexus versus a comparatively simple paraflexus in *Eoespina.* Also, the deflections of the protoloph in *Eosachacui* are less severe than those seen in specimens referred to *Eoespina,* and the medial extent of the mesoflexus narrows in contrast to a comparatively blunt, square medial margin of this flexus in *Eoespina.*

In the lower teeth, both genera have greatly reduced the metalophid as a precursor condition to the trilophid pattern that is characteristic of younger echimyids. In *Eosachacui,* this crest generally maintains a constant width and presence in the occlusal surface, but it may be broken, or constricted, or it may turn into the anteroflexid rather than join the hypolophid. The anteroflexid of *Eoespina* seldom has additional cuspules or crests. In *Eoespina,* the metalophid appears not to be uniform in either height or thickness. The greatest height and thickness are found at its union with the hypolophid, and toward the metaconid the metalophid may nearly disappear and not be included as part of the occlusal surface. The close positions of the protolophid and metalophid in *Eosachacui,* and a resultant narrow mesoflexid versus a more open mesoflexid in *Eoespina,* might be constant features, but the difference is slight. More variable is the orientation of the lingual half of the hypolophid. It is transverse or slightly oblique toward the posterior in *Eosachacui,* and, in *Eoespina,* it appears to be either transverse or slightly oblique toward the anterior, producing a more rounded mesofossettid.

Eosachacui lavocati new species

Figures 11, 12J; Appendix 2

HOLOTYPE. LACM 143294, left M^x.

REFERRED SPECIMENS. P^4: left, 143433, 143458, 143466. M^3: left, 143401. M^x: left, 143292, 143337, 143383, 143399,143444, 143453; right, 143278, 143285, 143387, 143388, 143454, 149438, 149439. dp_4: left, 143326, 143400, 143449 (partial); right, 143379, 143402. P_4: left, 143394. M_1: left, 143329, 149426; right, 143274. M_3: left, 143395. M_x: left, 143287, 143393, 143408, 143417, 143431, 143442 (partial), 143443 (partial), 149447; right, 143325, 143382, 143421, 149428. All catalogue numbers pertain to LACM collections.

DIAGNOSIS. As for the genus.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Lavocati,* in honor of René Lavocat, for his contributions to our knowledge of rodent evolution.

Subfamily Adelphomyinae Patterson and Pascual, 1968

Eodelphomys new genus

TYPE SPECIES. *Eodelphomys almeidacomposi* new species.

INCLUDED SPECIES. Monotypic.

DIAGNOSIS. Tooth with large entoconid occupying posterolabial corner. Occlusal surface of lower teeth dominated by an extended, straight, diagonal hypolophid that connects entoconid with protoconid. Hypolophid and posterolophid weakly connected by a mure. Metalophid and anterolophid unconnected to hypolophid, but join to create a lens-shaped anterofossettid.

ETYMOLOGY. *Eos,* dawn, Greek; *delphomys,* for sharing similarities with *Paradelphomys* Patterson and Pascual, 1968, and *Adelphomys* Ameghino, 1887, fossil rodents from the Miocene of Argentina.

DESCRIPTION. This single specimen is so distinctive that we have departed from our practice of using only upper teeth as holotypes and of giving names to only those taxa for which numerous specimens are available. The dental pattern of this species is typified by a long hypolophid that runs diagonally across the occlusal surface from a large entoconid to the protoconid, with only a minor curve as it passes the hypoflexid. Smaller lophids parallel the long hypolophid anteriorly and posteriorly without uniting (i.e., without showing a confluence of dentine) until a late wear stage.

DISCUSSION. This genus is referred to the family Echimyidae, subfamily Adelphomyinae because of a dental pattern that is close to that of the Oligocene genus *Paradelphomys,* of that family and subfamily. The occlusal surfaces of teeth from genera in this group are dominated by a strong, diagonal lophid (the hypolophid) that is paralleled by a shorter lophid to the anterior (likely a combined anterolophid and metalophid) and one to the pos-

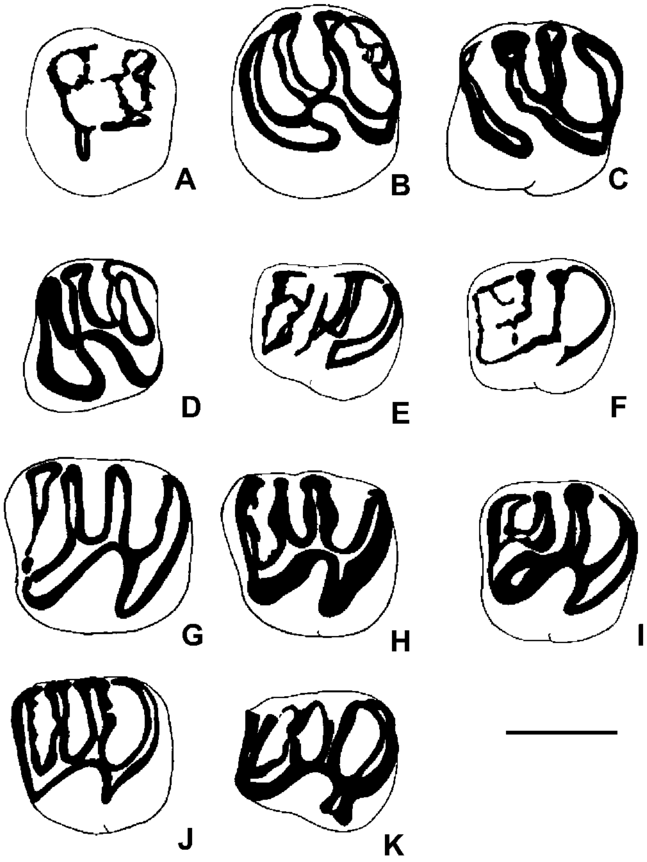


Figure 11 *Eosachacui lavocati.* Variations in dental and wear patterns in upper and lower teeth. A reversed drawing is indicated by "r." P^4: **A,** LACM 143458. M^x: **B,** LACM 143294 (holotype of genus); **C,** LACM 143383; **D,** LACM 143285r. P_4: **E,** 143394. M_x: **F,** 143325r; **G,** LACM 143382r; **H,** LACM 143393; **I,** LACM 143329; **J,** LACM 143287; **K,** LACM 143274r. Scale = 1 mm.

terior (the posterolophid). Both an anterolophid and a metalophid are present in *Eodelphomys,* but in close proximity to each other. This M_3 differs from the molar of *Paradelphomys* in that it is extremely brachydont, tetralophodont instead of trilophodont (the anterior two crests have fused in *Paradelphomys*), and it has a larger entoconid. The anterolophid and metalophid of *Eodelphomys* are separate crests united at their two ends to create an isolated fossettid, the anterofossettid. These crests may have been separate in *Paradelphomys* at a very early wear stage, but they are fused in both teeth of the specimen of *Paradelphomys* described by Patterson and Pascual (1968), a partial mandible with dp_4–M_1, and these crests are smaller than those of *Eodelphomys.*

The holotypical specimen and the specimen described by Patterson and Pascual (1968) are at similar stages of wear. A small mure between the posterolophid and hypolophid is present in *Eodelphomys,* but a potential connection is only suggested in *Paradelphomys,* and it would not have been achieved until late wear.

The combined anterolophid/metalophid of *Paradelphomys* is united with the hypolophid labially in the M_1 and at both ends in the dp_4. This is an earlier union of these crests than is seen in the tooth of *Eodelphomys,* and this earlier union is probably a result of the higher crown in *Paradelphomys.*

The dental pattern of a strong, central lophid matched fore and aft by shorter lophids is also characteristic of *Eoincamys, Incamys,* and some later dasyproctids. However, there are numerous differences that offset the fundamental similarity. The weak connecting mure between the hypolophid and the posterolophid is probably a shared primitive character between *Eodelphomys* and these early dasyproctids in that this mure is part of the interconnected crest pattern in higher crowned molars. The posterolophid of *Eodelphomys* differs from that of teeth in species of *Eoincamys* and *Incamys* in that its labial terminus does not reach the

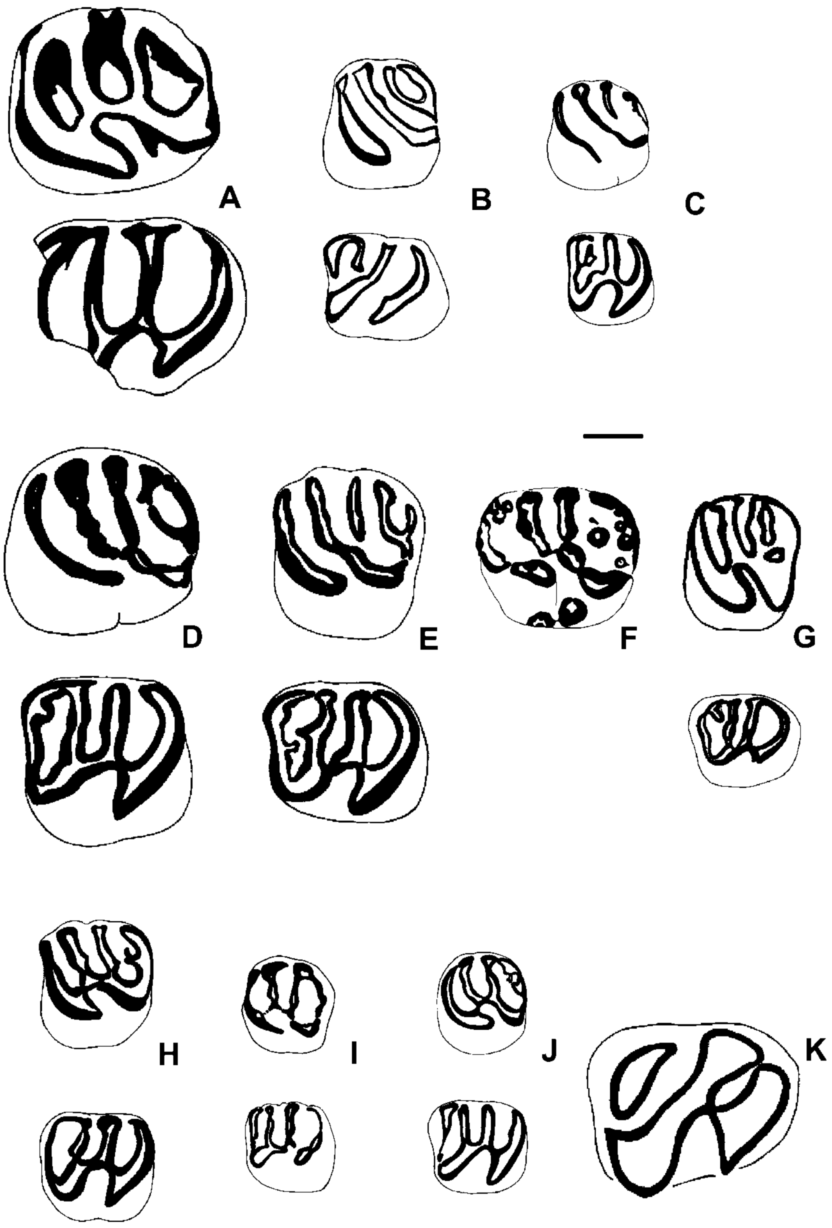


Figure 12 Summary illustration of dental characteristics and size comparison of rodent taxa included in the Santa Rosa local fauna. All teeth are drawn to the same scale. Both upper and lower teeth, if known, are presented for each taxon. All are drawn as left teeth with the anterior to the left and the protocone or protoconid at the lower left of each sketch. Catalogue numbers list the upper tooth and then the lower; the letter "r" indicates a reversed drawing. **A,** *Eopululo wigmorei,* LACM 143269, LACM 143410; **B,** *Eoincamys pascuali,* LACM 143319, LACM 143306; **C,** *Eoincamys ameghinoi,* LACM 143339, LACM 143435; **D,** *Eobranisamys romeropittmanae,* LACM 143359r, LACM 143341; **E,** *Eobranisamys riverai,* LACM 143373, LACM 143366; **F,** *Eopicure kraglievichi,* LACM 143353; **G,** *Eosallamys paulacoutoi,* LACM 143422r, LACM 143262r; **H,** *Eosallamys simpsoni,* LACM 143430r, LACM 143412r; **I,** *Eoespina woodi,* LACM 143286, LACM 143390; **J,** *Eosachacui lavocati,* LACM 143294, LACM 143382; **K,** *Eodelphomys almeidacomposi,* LACM 144298r.

labial margin of the tooth. In *Eodelphomys,* this may be a result of the reduced nature of the posterior half of the M_3, but the same condition is seen in more anterior teeth in *Paradelphomys*. The metalophid is reduced in *Eoincamys* and *Incamys,* whereas it is nearly as large as the anterolophid in *Eodelphomys.*

Eodelphomys almeidacomposi **new species**

Figure 12K; Appendix 2

HOLOTYPE. LACM 144298, mandibular fragment, right, with M_3.

DIAGNOSIS. As for the genus.

MEASUREMENTS. See Appendix 1.

TYPE LOCALITY. Santa Rosa, Peru. LACM locality 6289.

TYPE AND HORIZON AND AGE. ?Yahuarango Formation. ?Eocene.

ETYMOLOGY. *Almeidacomposi,* in honor of Diogenes de Almeida Compos, a friend, colleague, and leading vertebrate paleontologist of Brazil.

Family Echimyidae, Genus and Species Indeterminate A

Appendix 2

REFERRED SPECIMENS. LACM 143409, partial right M^x.

DISCUSSION. A large echimyid in the fauna is indicated by a single specimen. The upper tooth fragment displays a tetralophodont pattern in which the hypoflexus lies in the same axis as the labial portion of the protoloph, and the metaloph joins the protoloph away from the center of the occlusal surface and toward the hypocone. These are characters of *Eosallamys*. Differences that might be diagnostic are the narrow mesofossette and the proximity of the tips of the metaloph and posteroloph. In this tooth, the metaloph and posteroloph would join at an early wear stage, long before the union of the anteroloph and protoloph.

Echimyidae, Genus and Species Indeterminate B

REFERRED SPECIMEN. LACM 143348, left M_x.

DISCUSSION. This single specimen is very similar to those assigned to *Eosallamys*. Very characteristically, the anterofossettid has been divided into labial and lingual subfossettids by a short crest that extends anterolaterally from the metalophid to the anterolophid. Additionally, the metafossettid is similarly divided, although incompletely so, even at this late wear stage. The largest species assigned to *Eosallamys* is *E. paulacoutoi,* to which this specimen could possibly be referred, but it is about 30 percent larger than the lower teeth assigned to that species. The subjective decision at this time is to separate it from *E. paulacoutoi* as perhaps indicative of another echimyid in the fauna.

Echimyidae, Genus and Species Indeterminate C

REFERRED SPECIMEN. LACM 143277, left M^x.

DISCUSSION. This single tooth is referred to the family Echimyidae on the basis of its similarity to *Deseadomys* Wood and Patterson, 1959. As in *Deseadomys,* the metafossette formed well before the parafossette or mesofossette, and, with moderate wear, it is approaching obliteration. The mesofossette is more rectangular than that of *Deseadomys,* although, like *Deseadomys,* the metaloph does turn toward the posteroloph at its labial end in the formation of the metafossette. This specimen exhibits approximately the same amount of wear as that of an upper dentition referred to *Deseadomys arambourgi* (Wood and Patterson, 1959:fig. 4), but at a similar wear stage the hypoflexus of the Santa Rosa specimen has been closed into a hypofossette that matches the insubstantial metafossette. No such correspondence is seen in the referred upper dentition of *Deseadomys,* which displays what is for this wear stage in all rodents a more typically open hypoflexus.

This specimen is within the size range of *Deseadomys arambourgi* (Wood and Patterson, 1959:table 1).

Suborder Hystricognatha Woods, 1976

Family Indeterminate

SPECIMENS. LACM 143271, 143350, 143392, 143425, 143426, 143460, 143462, 143463, 143464, 143465, 143467, and many unnumbered, fragmentary specimens of upper and lower teeth.

DISCUSSION. A number of teeth, approximately 400, are included in the sample from the Santa Rosa local fauna that cannot be identified, most even to family. Well over half of these teeth are incisors, mostly fragments. The remainder are small fragments that consist of as little as one crest, and several specimens are so highly abraded that the dental patterns are totally obscured. The latter specimens may be important in paleoecological reconstruction in that they were found mixed together with completely intact and unabraded specimens. Many of the fragmentary teeth are a result of fracturing *in situ,* followed by separation of pieces during the recovery of the fossils (see Campbell et al., 2004).

DISCUSSION

FAUNAL CHARACTERISTICS

The rodents of the Santa Rosa local fauna appear to represent an early stage in the adaptive radiation of a vertebrate lineage, wherein the members of the newly formed lineages, possibly excepting the Erethizontidae, are not distantly removed from their common origin. The impression derived from the detailed study of these taxa is that the differences

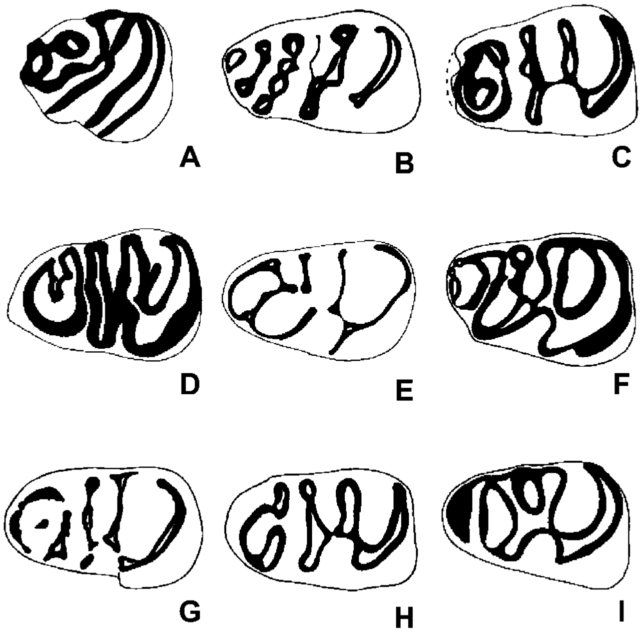


Figure 13 Comparison sketches of deciduous premolar (dp_4) patterns of Santa Rosan rodents. A reversed drawing is indicated by "r." **A,** *Eoincamys pascuali,* LACM 143335; **B,** *Eobranisamys romeropittmanae,* LACM 143352; **C,** *Eobranisamys riverai,* LACM 143371r; **D,** *Eobranisamys riverai,* LACM 143369; **E,** *Eosallamys paulacoutoi,* LACM 143420r; **F,** *Eosallamys paulacoutoi,* LACM 143451; **G,** *Eosallamys simpsoni,* LACM 143452; **H,** *Eoespina woodi,* LACM 143391r; **I,** *Eoespina woodi,* LACM 143405r. Not to scale.

in tooth morphology among the Santa Rosan rodents are slight variations on a theme that in another context might serve to differentiate genera of one family of rodents. Overall, the distinctions among the dental patterns of the several genera are rather subtle. Despite this subtlety of the observed differences, however, they are consistent, and trends linking some Santa Rosan rodents with later taxa can be identified with confidence.

The rodents of Santa Rosa all have a common pattern comprising four principal cusps that are connected by low, broad-based, and tapering crests on both the upper and lower teeth. The cusp patterns of the upper and lower teeth (Fig. 1) appear to be arranged around cusps homologous to those seen in the teeth of taxa within the Sciuromorpha or Myomorpha, in which the paracone/paraconid of the tritubercular pattern has been reduced in all teeth. If one were to mentally reverse the trend toward lophodonty observed in these and younger South American rodents, a version of a hypothetical ancestor would appear in which the dental pattern was bunodont, but possibly not basined, with four primary cusps in which the upper labial and lower lingual cusps were positioned closer to each other than were the opposite pair. The dental configurations and size diversity of all the Santa Rosan rodents described in this paper are compared in Figure 12.

The basic pattern of P^4s in the Santa Rosa sample, excluding those of the readily diagnostic *Eoincamys,* consists of two anterior crests and two posterior crests that converge, respectively, on the protocone and hypocone. Only a small connection, a weak mure, between the protoloph and metaloph developed as wear altered the occlusal pattern. The hypoflexus is nearly encompassed by the protocone and hypocone (the latter being the smaller of the two cusps), and with only slight wear this flexus is entirely enclosed as a small, deep, medial enamel lake. These teeth are so symmetrical that at times, it is difficult to determine which is the anterior surface. The pattern seen in these P^4s is here interpreted as a modification of a molariform pattern that has been compressed onto a nearly circular occlusal surface. Species assignments of the P^4s were based on perceived similarities to upper molar teeth that are of the appropriate size.

The deciduous lower premolars of rodents in the Santa Rosa local fauna are also basically similar, and they are important to the larger considerations of caviomorph relationships. Patterson and Wood (1982:508) stated, "The best opportunity for comparing thryonomyoid and caviomorph antemolar teeth lies in the deciduous dentition, dm^4_4." The dm^4_4 of these authors are the retained, or permanent, dp^4_4 of others, and the latter terminology is so used here. In this study, dp_4s are identified for *Eoincamys, Eobranisamys, Eosallamys,* and *Eoespina* (Fig. 13). Within those genera, referral to species was based on size. The posterior two-thirds of the tooth can be described with the terminology of the lower molars, but the pattern of the anterior one-third of the tooth is highly variable and often obscured by wear. The anterior extension of the enamel pattern is created by two crests that replace the anterolophid of permanent teeth. These two crests apparently originate as two parallel plates that, with only a little wear, might join in a variety of ways. The primary distinctions among the dp_4s of these four genera lie in the positions and inclinations of the hypolophid and metalophid, which match the corresponding elements in the permanent lower teeth of the respective genera.

In *Eoincamys* (Agoutidae), this means that the hypolophid is a diagonal crest that extends across the occlusal surface, the metalophid is reduced, and there is no mure connecting the hypolophid to the posterolophid. For *Eobranisamys* (Agoutidae), by the terminology of this paper, the metalophid appears to be a continuous, transverse crest that is connected to the lingual half of the hypolophid. In the deciduous lower premolars allocated to the two genera of Echimyidae (i.e., *Eosallamys* and *Eoespina*), the hypolophid is slanted in the anterolabial direction for its labial half. The metalophid is somewhat reduced, although larger than that of *Eoincamys*. It is smaller than the metalophid of *Eobranisamys,* and it tends to be inclined slightly toward the anterolingual margin.

Indeed, because of the basic, simple structure seen in the teeth of all of the rodents from Santa Rosa, had South American rodents become extinct after deposition of the Santa Rosa local fauna, it is possible that all of these early rodent genera could have been grouped closely together taxonomically, perhaps within a single family. With younger taxa for comparison, the separation of the Santa Rosan rodents into several families is justified and better reflects the radiation from an ancestral morphotype possibly not much older than Santa Rosan time. The erethizontids are generally considered to be a lone branch that separated early and has continued to the present. *Eopululo,* as our single, most probable erethizontid, is, therefore, more separated taxonomically in this paper than might be justified on dental patterns alone, which is all that is available now.

EARLY DIVERGENCE IN CAVIID RODENTS

Wood (1949) and Wood and Patterson (1959:294–295) gave considerable importance to *Platypittamys* (Deseadan SALMA; Patagonia, Argentina) as a structural ancestor, at least, of the caviid rodents. *Platypittamys* was placed in the Acaremyidae (Octodontoidea) by Wood (1949). The postulated importance of this genus in caviid evolution was not changed in Wood and Patterson (1959:295), but its taxonomic placement was described more cautiously as "primitive Octodontidae." Currently (McKenna and Bell, 1997), *Platypittamys* is placed within the subfamily Acaremyinae, family Octodontidae, although Vucetich and Kramarz (2003), in a cladistic analysis, place *Platypittamys* as a sister taxon to a group consisting of Acaremyidae (as used by them and restricted to three genera) and another group made up of a mixture of "acaremyids," octodontids, and echimyids.

However, the supposed primitive dental pattern of *Platypittamys* and the retention of primitive features in living octodontids (Wood and Patterson, 1959:295) have given, in our estimation, undue importance to the Octodontidae as a basal group in the radiation of the caviids. It is our view that the dental characters of *Platypittamys* are more specialized than those seen in the Santa Rosan rodents in features that herald the highly characteristic modern octodontid dental pattern. These characters would include the large hypoflexus(-id), which, with the mesoflexus(-id), forms a distinct waist between the anterior and posterior halves of a tooth, and the shallow anterior and posterior fossettes and fossettids. In this paper, no Santa Rosan rodents are placed in the Acaremyinae, and we suggest that the Octodontidae, like the Erethizontidae, represents a lineage of South American rodents separate from that which gave rise to all other taxa of caviids. In fact, the overall resemblance of the dental pattern seen in Santa Rosan rodents to the primitive erethizontid pattern, that is, a short hypoflexus(-id) and three opposing fossette(-id)s of nearly equal length and depth, leads us to conclude that the erethizontid dental pattern is closer to the ancestral caviid condition than that seen in the Acaremyinae and that the roots of the caviid radiation go much deeper than the earliest appearance of the acaremyines, including *Platypittamys*. Because the basic Santa Rosan rodent dental pattern appears to be that of an echimyid, we agree with the statement of Vucetich and Kramarz (2003:443), "The Octodontidae probably originated from an ancestor closer to the Echimyidae than the Acaremyidae . . . ."

TETRALOPHODONTY VERSUS PENTALOPHODONTY

All but one of the Santa Rosan rodent genera have tetralophodont upper and lower teeth, the hypothetical ancestral number of lophs proposed by Wood (1949) for erethizontids and caviids. The single exception, *Eobranisamys,* has the basic tetralophodont pattern, but it also has a small, accessory loph that projects from the posteroloph into the metaflexus on its upper teeth, which creates a pentalophodont pattern. This loph is variable in size and location. It is clearly not a primary loph, but rather an addition to the tetralophodont condition created by the alignment of enamel irregularities on the surface of the metaflexus, or from crenulations on the anterior surface of the posteroloph, or both. Similar irregularities cause a noticeably crenulated anterior margin of the posteroloph in two other Santa Rosan genera, *Eopululo* and *Eosallamys*. It might yet prove to be that the original number of lophs in caviids was five, the hypothetical pentalophodont ancestral condition argued by many (Lavocat, 1981; Vucetich and Verzi, 1990; Candela, 1999, 2002), but it appears to us that the variation in what we refer to as the neoloph, and in its counterpart the anterolophid, is greater than what would be expected if it were an additional, or fifth, loph in the process of being lost. In most of the Santa Rosan rodent upper molars, there is an abundance of minor cuspules in the posterior part of the metaflexus, of which only some are connected to the posteroloph and produce a crenulated margin with wear. In our view, this variation is consistent with the establishment of dental patterns proceeding from the union of minor cuspules that, by Santa Rosan time, had perfected a fifth loph in only one genus, *Eobranisamys*.

The basic pentalophodont pattern of upper molars seen in many Old World hystricognaths is, we think, correctly identified with an additional crest placed third in order from the anterior. This is either the mesoloph (Lavocat, 1981, and references therein) or a mesolophule (Flynn et al., 1986; Fig. 2), and it might, in fact, be either in different genera. In this instance (i.e., Old World hystricognaths), it is the fourth crest that extends toward the interior of the crown from a large cusp, the metacone, and which should therefore be called a metaloph. In contrast, the third labial cusp in *Eobranisamys,* at the labial union of the posteroloph and a neoloph, when such a union occurs, appears to us to be an enlargement of the most labial of a series of cuspids that compose the unworn posteroloph. The proposal that this third cusp might be the metacone and the central, or second labial, cusp the mesostyle [as in the theoretical pentalophodont primitive condition of these rodents proposed by Lavocat (1981) and Candela (1999)] is not accepted in this paper because of the overall similarity in cusp placement and prominence among all of the Santa Rosan rodent teeth, including the pentalophodont *Eobranisamys,* and because of the variable nature of the posteroloph in which the minor cuspules comprising the labial enlargement of this loph wear into a highly variable, crenulated anterior border.

Butler (1985) argued that it would be unique among rodents for the paracone and metacone of the caviids to be closer together than the protoconid and hypoconid, rather than alternate with them, as must be true if the dental homologies of Patterson and Wood (1982) are correct. Nonetheless, as we identify the cusps in the Santa Rosan rodents, that is exactly the situation we find, and this organization of the cusps might be a definitive feature of the Caviida. We consider the nonalternating placement of these cusps as a primitive feature similar to the placement of these cusps in some early North American (including Mexico) rodents such as *Protoptychus* Scott, 1895; *Jaywilsonomys* Ferrusquia-Villafranca and Wood, 1969; *Mysops* Leidy, 1871; or *Marfilomys* Ferrusquia-Villafranca, 1989. The most obvious difference between these genera and the Santa Rosan rodents is that the protoloph, as used in this paper, touches the posterolabial margin of the protocone. Further separation of the protoloph from the protocone, either until full separation is achieved or until the protoloph is connected to the protocone only by a short mure, is a short step to the basic dental pattern for upper teeth of Santa Rosan rodents. Although we consider the structural plan of the dental pattern in these North American rodents to be similar to what we might expect to see in pre–Santa Rosan South American rodents, the fact that all of the above are contemporaneous or younger than the structurally more derived Santa Rosan rodents removes them from consideration as possible ancestral lineages for the South American rodents.

To argue for pentalophodonty as the most primitive dental pattern among the Santa Rosan rodents would require one of two hypothetical evolutionary paths for the teeth of all erethizontid and caviid genera, except *Eobranisamys*. *Sensu* Lavocat (1981), the metacone and metaloph were lost and a mesostyle enlarged in all of the tetralophodont forms except *Eoincamys,* in which the mesoloph was lost. Alternatively, *sensu* Flynn et al. (1986), the mesolophule was lost and the metacone moved anteriorly, or the metacone and the labial portion of the metaloph was lost and the labial terminus of the mesolophule was enlarged into a cusp that replaced the metacone. Coincident with these changes suggested by Flynn et al. (1986), the orientation of the lingual portion of the metaloph moved anteriorly to unite with the protoloph, except in *Eoincamys,* in which it moved posteriorly to unite with the posteroloph. Parsimony alone would argue against these possible routes to tetralophodonty. We take the position that the great variation seen on the anterior border of the posteroloph is not a metaloph or metalophule in various stages of reduction, but rather a feature that is common among the teeth of the Santa Rosan rodents. In *Eobranisamys,* alone among the genera of Santa Rosan rodents, this feature has become clarified, prominent, and a characteristic structure.

Additional cusps and crests are common on teeth of those North American and African early Tertiary rodents that have been proposed as morphological prototypes of the caviomorphs. No such additions are evident on the relatively clean cusp morphology of the Santa Rosan rodents. Most notably, there is no clear indication of a mesocone on any rodent molar from Santa Rosa. In unworn teeth from this sample, the crests appear as a series of minor cuspules. It might yet prove to be that one of these minor cuspules is a mesocone, but, if so, it is not very much different from nearby cuspules. With no mesocone there can be no mesoloph (see Wood and Wilson, 1936, for cusp terminology) on any rodent tooth from Santa Rosa. The crest that might be identified as such by those who advocate a pentalophodont ancestor for the caviids originates not from the center of the crown, in the position of the mesocone, but from a labial cone, from which it extends inward with decreasing height. We interpret that labial cone as the metacone; therefore, the primitive pattern would be tetralophodont. For the rodents of Santa Rosa, either simplification of the dental pattern from a pentalophodont condition had occurred, or an abundance of accessory cusp structures in these taxa that would have led to pentalophodonty had not yet developed. On the basis of their extreme brachydonty, in which the dental patterns are not much elevated from a bunodont crown, the overall similarity of the rodent teeth from Santa Rosa to each other, and a predominance in the fauna of tetralophodont upper molars, we prefer the latter argument.

CREST OBLIQUITY AND CHEWING

In rodents, a scissorslike cutting surface is formed by passing oblique crests of upper and lower teeth against each other. As a function of brachydonty and the large primary cusps in all rodent molars from Santa Rosa, this shear is poorly formed, and the flattened, scissorslike cutting surface of Neogene and Recent caviids was not yet developed. Rather, wear appears to have proceeded in a distinct pattern. First, the lingual side of the upper molars and the labial side of the lower molars would wear (see various wear stages of teeth in Appendix 2). Then a sloping surface would extend across the loph(-id)s to the tips of the labial (upper) and lingual (lower) cusps. Further wear flattened the lingual (upper) and labial (lower) portion of the occlusal surface, leading to a steeply sloping wear pattern on the opposite side that extended to the tips of the cusps (paracone/metacone, uppers; metaconid/entoconid, lowers). The tips of these cusps would then wear into a keyhole pattern. This produced a roughly S-shaped, or terraced, wear surface. On upper molars, the wear surface extended from the lingual side of the tooth, across about two-thirds to three-fourths of the tooth, then sloped steeply to the tips of the paracone/metacone.

This terraced wear pattern is different from that observed by Vucetich and Verzi (1996) in that there is no wear on the anterior or posterior sides of the cusps. In fact, there is no indication of a labiolingual stroke to the chewing motion at any wear stage. This suggests that the Santa Rosan rodents had already achieved, or nearly achieved, a form of propalinal chewing. This could be considered grade D of Butler (1985), except that the lateral (upper) and lingual (lower) cusps remain elevated above the wear surface until a late wear stage is reached. In the later wear stages, the S-shaped occlusal surface became flattened and took on an appearance similar to later caviids, except that by this stage, the initial brachydont condition resulted in very shallow fossette(-id)s, as opposed to the deeper fossette(-id)s in younger caviids. This type of chewing might not have been universal among the Santa Rosan rodents, and it still needs to be confirmed by analysis of wear striae on the occlusal surfaces, but it appears to have been the most important mode of chewing in these rodents.

In *Eopululo,* as in all erethizontid rodents, the obliquity of the crests is less severe than in other South American rodents. The occlusal surface is divisible into two equal parts that are separated by a shallow hypoflexus(-id) and a thin, straight mesoflexus(-id). Anterior and posterior halves of the occlusal surface are clearly separated on the basis of positioning and union of the crests. The posterior half is primarily a connection between the metacone and hypocone. The protoloph remains an element of the anterior portion of the tooth that is strongly connected with wear to both the protocone and the metaloph. The combination of two straight central crests and two curved marginal crests on both upper and lower teeth in this genus, combined with the offset of the upper and lower teeth, always positions a straight crest against a curved crest during the chewing motion.

In the upper teeth of the other genera of rodents from Santa Rosa, there is a sweep of crests toward the posterior. This is most dramatic in *Eoincamys,* in which the metaloph sweeps posteriad to unite with the posteroloph rather than with the hypocone. *Eobranisamys, Eosallamys,* and *Eoespina* have similar, but not as extreme, patterns in that the metaloph is the straighter of the two central lophs and the protoloph curves to meet it. In *Eosallamys,* the inclination of the two central crests and the accessory spurs that extend into the metaflexus are diagnostic. *Eoespina* is distinguished by a weak connection of the metaloph to the protoloph, whereas the distinct neoloph of *Eobranisamys* distinguishes that genus.

The lower teeth display generalities similar to the uppers, but with an opposing obliquity. The lower teeth of *Eopululo* have the most equally balanced dental patterns, which consist of four lophids, of which the central two are of approximately equal length, and where the primary connection of the protoconid is with the hypolophid. The hypolophid is connected to the metalophid and the hypoconid (Fig. 12). The posterior lophids of the other rodent genera display a sweep anteriad in which the hypolophid, uniting the entoconid with the protoconid, dominates the pattern. The metalophid becomes the most variable element in the patterns. In *Eoincamys,* the metalophid is short and much separated from the hypolophid. In *Eosallamys, Eobranisamys,* and *Eoespina,* the metalophid appears to be the primary crest, with the hypolophid joining it at its midpoint between the metaconid and protoconid (or, said another way, the hypolophid makes a strong deflection at its point of union with the metalophid). This condition holds in *Eoespina,* even though the metalophid makes a weak connection with the hypolophid.

AGE OF THE SANTA ROSAN RODENTS

Before the discovery of the Santa Rosa local fauna, the oldest extensive samples of South American rodents were from the combined Deseadan SALMA Salla and Lacayani local faunas of Bolivia and the Cabeza Blanca local fauna of Argentina (Vucetich, 1991). The diversity of these faunas indicated that rodents had been present in South America for some time prior to Deseadan time. A single specimen, a partial mandibular ramus from the pre-Deseadan Tinguiririca local fauna of Chile (Wyss et al., 1993), provided support for the view that rodents were in South America well before the Deseadan SALMA. This ramus is hystricognathous, as are all of the partial mandibles found at Santa Rosa. The hystricognathous mandible is one in which the angular process of the mandible is not positioned in the same vertical plane as the tooth row, but instead is positioned lateral to that plane.

The teeth of the Tinguiririca specimen are in an advanced wear stage, but some observations are nonetheless relevant to the discussion of Santa Rosan rodents. In the original description of the specimen, Wyss et al. (1993) suggested that the closest comparison among Deseadan genera was with *Branisamys* of Bolivia. On that basis, the specimen was questionably referred to the Dasyproctidae (Agoutidae, Dasyproctinae, in this paper). With the benefit of the Santa Rosan sample, both in terms of taxonomic diversity and abundant examples of wear stages, we suggest that the Tinguiririca specimen is better placed within the Echimyidae. This specimen shares echimyid features with *Eosallamys* (?Eocene, this paper) and *Sallamys* (Oligocene) in that all lower teeth of these taxa possess a deep hypoflexid, which is equal in length to the opposing flexids and which terminates at the base of the hypolophid, and four slightly oblique lophids, of which the anterior two are the first to fuse and form a single lophid. This is illustrated in *Sallamys,* where four lophids are found only in the earliest dental wear stage, whereas later wear stages show only the characteristic three lophids.

Of some note is that the crown height of the cheek teeth of the Tinguiririca rodent far exceeds that of any Santa Rosan species. Even highly worn, as they are, the cheek teeth of this rodent have as much crown remaining as an unworn tooth of any Santa Rosan rodent. In its degree of hypsodonty, the Tinguiririca specimen more closely matches teeth of *Sallamys,* or other moderately hypsodont Oligocene caviomorphs, than it does the brachydont teeth of the Santa Rosan rodents. As a general trend, hypsodonty is an apomorphic character within the caviids. With only one rodent specimen from the Tinguiririca local fauna, conclusions are tenuous, but on the basis of the degree of fusion of the anterior two lophids of the lower molars and the lesser degree of hypsodonty, we consider the Santa Rosan rodents to be "pre-Tinguiririca" in age.

Wyss et al. (1994:25), in discussing single-crystal ^{40}Ar/^{39}Ar dates relevant to the age of the Tinguiririca fauna, suggested that it is ". . . at least as young as about 31.5 Ma . . . ," but that it ". . . may be as old as late Eocene (circa 37.5 Ma), and might therefore span the Eocene–Oligocene boundary." The former age was determined for deposits immediately above and within the upper part of the fossiliferous horizons, whereas the latter was obtained from immediately below the fossiliferous horizons. Flynn and Wyss (1999) also placed the age between these two dates, indicating a pre-Deseadan, post-Mustersan age on the basis of the occurrence of several higher level taxa.

However, Kay et al. (1999), in recent efforts to date the Casamayoran age fauna at Gran Barranca in Chubut, Argentina, have demonstrated that the Barrancan "subage" of the Casamayoran SALMA is middle late Eocene, rather than late early Eocene as previously thought. Kay et al. (1999) place the age of the Barrancan "subage" at 36.6–35.34 Ma, or 37.60–35.69 Ma, depending on to which subchron of the geomagnetic polarity time scale the plagioclase ^{40}Ar/^{39}Ar date is referred. This means that the age of the overlying Mustersan faunas at the Gran Barranca must also be revised upward, and Kay et al. (1999) suggest that the Mustersan SALMA must now straddle the Eocene–Oligocene boundary, or range from approximately 35 to 32 Ma. This period of time was derived by taking into consideration the "Astraponotéen plus Supérieur" local fauna of the Gran Barranca, which overlies the Mustersan SALMA faunas and appears to be contemporaneous with the Tinguiririca local fauna of Chile (Bond et al., 1996; Flynn and Wyss, 1999), and the fossiliferous beds producing the latter, which are dated to 31.5 Ma. Thus, there would seem to be room for only about a 0.5 Ma time gap between the dated "Tinguiririca" age faunas of Chile and the Mustersan faunas.

The Deseadan SALMA local fauna of Salla, Bolivia, is currently dated to 29.4–25.5 Ma (Kay et al., 1998), whereas the age of the Deseadan SALMA local fauna of Scarritt Pocket in Argentina is currently placed at 29–27 Ma (Flynn and Swisher, 1995). Thus, the post-Mustersan, pre-Deseadan Tinguiririca local fauna would seem to be restricted to a possible temporal range of 32–29.4 Ma, and it is confidently tied only to the date of 31.5 Ma, or early Oligocene. The reported approximately 37.5 Ma age of the horizon immediately below the fossiliferous horizon at the Tinguiririca locality (Wyss et al., 1994) appears to be unrelated to the age of the Tinguiririca local fauna.

The age of the Santa Rosa local fauna is unresolved (Campbell, 2004). This is a consequence of two major factors. First, no currently available stratigraphic data are useful in dating the fossiliferous horizon producing the Santa Rosa local fauna (see Campbell et al., 2004). Second, most of the mammalian taxa are new at the generic level, and many are new at higher taxonomic levels (see other papers in this volume), so it is impossible to correlate the Santa Rosa local fauna with other faunas of known age. We have interpreted the age of the Santa Rosan rodents to be pre-"Tinguiririca n" on the basis of the degree of hypsodonty and the degree of fusion of the anterior two lophids of the lower molars, relative to the single rodent from the Tinguiririca local fauna. The lack of a sizable time gap, if any at all, between "Tinguiririca n" time and the Mustersan SALMA leads us to the conclusion that the Santa Rosan rodents must be at least as old as the Mustersan, and probably early Mustersan.

With their revision of the age of the Casamayoran SALMA, Kay et al. (1999) were able to relate the climatic changes observed in the marine sedimentary record of the South Atlantic with those of continental paleofloras and paleomammals. They suggested that the mammalian faunas experienced a dramatic change in response to climatic change, and one of the ways this was expressed was via a marked increase in the number of hypsodont taxa in South America after 36 Ma and before 32 Ma. They also provided data demonstrating a significant correlation between climatic variables and degree of hypsodonty in sigmodontine rodents. If, and we recognize it is a big if, the early caviomorphs of South America responded to climatic change in the late Eocene in the same way as the mammalian herbivores discussed by Kay et al. (1999), then it is possible that the brachydont rodents of Santa Rosa would fall somewhere in the time span between 36 Ma and "Tinguiririca n" time, or before, prior to the onset of hypsodonty.

Still, we know nothing about the Paleogene floras of western Amazonia, and local conditions may override general faunal tendencies. An example of the latter that might be pertinent is the greater hypsodonty of the Deseadan SALMA rodents of Lacayani, Bolivia, relative to those of the Deseadan SALMA rodents of Salla, Bolivia. Thus, we can only offer this suggestion as a possibility; that is, that there might be a correlation between hypsodonty in early caviids and large-scale climatic change and that the brachydont Santa Rosan rodents predate this period of climatic change. Nonetheless, we are confident that the Santa Rosan rodents are at least Mustersan SALMA in age and that they are probably early Mustersan SALMA in age. They might, quite possibly, be even older. This conclusion is consistent with the age suggested by the marsupials from the Santa Rosa local fauna (Goin and Candela, 2004). For the reasons given, we refer to the age of the Santa Rosa local fauna as ?Eocene.

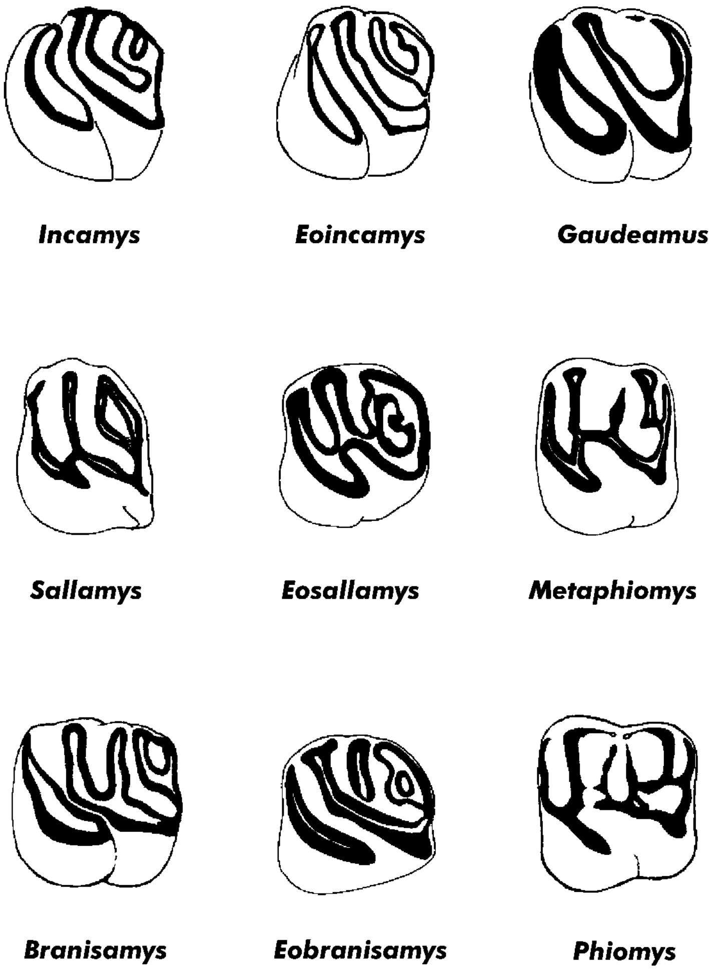
RELATIONSHIPS OF THE SANTA ROSAN RODENTS

In this paper, we describe eight genera and eleven species, with several additional genera and species indicated by fragmentary material. This diversity is equivalent to the most diverse Deseadan localities known (Vucetich, 1991). Even given the similarity observed among the various rodent taxa from Santa Rosa, this diversity indicates that rodents were in South America for some time before deposition of the Santa Rosa local fauna. Although an ?Eocene age assignment does have an element of uncertainty because numerical age dates are lacking, we think it is supported by the stage of evolution of the rodents, in comparison with other early rodents of South America. An ?Eocene age places the rodent fauna of Santa Rosa contemporaneous with or predating taxa that might otherwise have been considered among the ancestral groups from which came the caviids. Furthermore, the replacement of the indistinct time frame "pre-Deseadan" with the equally indistinct time frame "pre-Mustersan," during which the development of typical caviid features of South American rodents would have taken place, has a significant effect on discussions relating to the origin of South American rodents. When one considers that the diversity of the known Deseadan rodent faunas led previous authors to propose a late Eocene radiation of rodents in South America, following an even earlier arrival in South America (Patterson and Wood, 1982; Marshall and Sempere, 1993; Vucetich et al., 1999), it is reasonable to conclude that the highly diverse and significantly older Santa Rosan rodents push the origin of caviids even farther back and into the early Cenozoic.

The complex history of rodent classification reflects the presence in rodents of a mosaic of characters that one might expect in lineages descendent from a common ancestor, as well as differing opinions of character preeminence by those who study these animals. In studies of rodent relationships, the consensus seems to be that the caviids represent a natural group (George, 1993, and references therein; Hartenberger, 1998), but the relationship of caviids to rodents of other continents is less certain. This question is complicated by the anatomical similarity that is so evident among rodents of Europe, Africa, and South America. The origin of these similarities, however, whether phylogenetic or through convergence, is unknown.

The question of the origin of the South American rodents has been extensively discussed, with proponents principally aligned on one of two sides. The advocates of a North American origin were led by Wood (1981, 1985, 1993). Those who were persuaded that Africa had been the original home of South American rodents were led by Lavocat (1974, 1976, 1993). The latter viewpoint is also advanced by Martin (1992, 1994, 2004), who notes the presence of the same three subtypes of multiserial enamel within the Santa Rosan rodents that are seen in all South American caviids and the Eocene/Oligocene thryonomyoids of Africa.

However, the dental features that seem to link caviids with African rodents are seen in the late Eocene/Oligocene rodents (Fig. 14). For example, *Eoincamys* and *Incamys* (Agoutidae) from South



Incamys ***Eoincamys*** ***Gaudeamus***

Sallamys ***Eosallamys*** ***Metaphiomys***

Branisamys ***Eobranisamys*** ***Phiomys***

Figure 14 Comparative upper molar dental patterns of some Santa Rosan genera (middle column) with Oligocene genera from South America (left column) and late Eocene/Oligocene genera from Africa (right column). A reversed drawing is indicated by "r." Sources: *Incamys bolivianus* (M^{1-2}, PU 21728 (in part), Bolivia; Patterson and Wood, 1982:fig. 17B, Agoutidae). *Eoincamys pascuali* (LACM 143319, this paper; Agoutidae). *Gaudeamus aegyptius* (M^{1-2}, YPM 18044r (in part), Egypt, Simons and Wood, 1968:fig. 14A; Phiomyidae). *Sallamys pascuali* (M^1, PU 20982, Bolivia, Patterson and Wood, 1982:fig. 5A; Echimyidae). *Eosallamys simpsoni,* LACM 143424r; this paper; Echimyidae). *Metaphiomys schaubi* (M^2, YPM 21320 (in part), Egypt, Patterson and Wood, 1982:fig. 30F; Phiomyidae). *Branisamys luribayensis* (M^1, PU 21955r (in part), Bolivia, Patterson and Wood, 1982:fig. 24B; Agoutidae). *Eobranisamys romeropittmanae,* LACM 143358r; this paper; Agoutidae). *Phiomys andrewsi* (M^2, YPM 18035r, Egypt, Simons and Wood, 1968:fig. 2D; Phiomyidae). Not to scale.

America resemble *Gaudeamus* Wood, 1968 (Thryonomyidae), from the late Eocene Fayum faunas of Africa. In *Gaudeamus,* the trilophid pattern resembles the pattern of upper molars in *Incamys* after moderate wear has united the metaloph with the posteroloph. Compared with *Eoincamys* and *Incamys,* the dental pattern of *Gaudeamus* might be considered the next step in character development.

Dental patterns of the Eocene/Oligocene African genera *Metaphiomys* Osborn, 1908 (Diamantomyidae Schaub, 1958), and *Phiomys* Osborn, 1908 (Phiomyidae), also bear a general resemblance to those of *Eobranisamys* and *Branisamys* (Agoutidae). However, as discussed in justification of the choice of dental nomenclature used in this paper (see "General Descriptive Odontology" section), we identify the five crests in the upper teeth of *Eobranisamys* as the anteroloph, protoloph, metaloph, neoloph, and posteroloph. The five crests of the "phiomorphs" are the anteroloph, protoloph, mesoloph or mesolophule, metaloph, and posteroloph.

When comparing *Eosallamys* and *Sallamys* (Echimyidae) with *Metaphiomys* or *Phiomys,* it initially appears that similar dental patterns were achieved by reduction of the metaloph and enlargement of the neoloph. However, on closer inspection, it seems more likely that the pattern of *Sallamys* was achieved by a reduction and redirection of the metaloph to meet the posteroloph at its midpoint. These conditions, and a dental spur at the midpoint of the posteroloph (in the position of a neoloph), occur in specimens of *Eosallamys*.

In each example cited above, the closer comparison is between the ?Eocene and Oligocene South American rodents and a lineal relationship is reasonable. Similarities seen between molar patterns of early caviids and contemporaneous African hystricognathi seem to be superficial rather than based on homologies. At best, if one were attempting to strengthen the argument for a relationship between South American and African rodents, it could be postulated that the similar patterns of caviids and some African/Asian rodents might have been independently derived from a more primitive, probably basined, molar pattern.

In Patterson and Wood (1982), Wood states that real or incipient hystricognathy is present in some North American rodents by the late Paleocene in the western United States or the Eocene in Mexico. His use of "incipient hystricognathy" as a character was challenged by Dawson (1977) and Korth (1984); nevertheless, hystricognathous rodents were apparently present in North America by the Eocene (Wood, 1972, 1973). *Prolapsus* Wood, 1973, the North American genus in question, was used to support the hypothesis of a North American origin for the "Caviomorpha" (Caviida). But, hystricognathy appears to be an early feature of the caviids, as indicated by the fact that it is a feature of the partial mandibles in the collection from Santa Rosa, and the presence of this feature in a North American rodent that is approximately contemporaneous to the Santa Rosan rodents cannot be used to support a North American origin of the caviomorphs. It is just as possible that hystricognathy occurred independently or owes its presence in North America to dispersal northward.

Leaving aside the question of hystricognathy, we note that there are no dental patterns that would link early North American rodent genera with those of the Santa Rosa local fauna. For example, although unworn cylindrodont teeth (Cylindrodontidae) have a pattern that is similar to the general structure of Santa Rosan teeth (i.e., both have simple patterns built around four crests), the symmetry of the crests in the cylindrodonts and their characteristic hypsodonty is unlike that of the Santa Rosan rodents. If the caviids had a North American origin, then that source would have had to have entered South America at a very early date, leaving no record of taxa with similar dental characters in North America, or at least no record that has been discovered to date. The characteristic caviid patterns seen in Santa Rosan rodents would then have developed in place in South America from this unknown source.

The Santa Rosan rodents do not provide enough evidence to tip the scales toward either a North American or African origin of the South American rodents. However, the timing of the dispersal event, if that were the source of South American rodents, must have occurred earlier than previously thought. We note that the teeth of the Santa Rosan rodents are readily referable to extant caviid families on the basis of their similarities to Oligocene representatives of these families. However, if, as we suspect, the Santa Rosan rodents date from the early Mustersan or before, then these advanced dental and mandibular features appear at a time when, for the most part, Eocene rodents elsewhere in the world retained evidence of tritubercularity and only incipient hystricognathy. A much earlier placement of the time of origination of the South American rodents may reinvigorate arguments heretofore left dormant for lack of intervening fossils such as are found at Santa Rosa.

For example, in a discussion of South American zoogeography, Croizat (1971, 1979) suggested that during the Cretaceous certain "proto-rodents" in the unified fauna of the Gondwanan continents had progressed toward some hystricognath characters [e.g., perhaps the subtypes of multiserial enamel discussed by Martin (2004)]. These characters were to become fully formed in African and South American rodents only after the separation of those continents and their faunas. In making this suggestion, Croizat placed the "caviomorphs" among the autochthonous fauna of South America, or Faunal Stratum I of Simpson (1950), which includes the Xenarthra, Pyrotheria, Litopterna, Notoungulata, and Marsupialia, a position strengthened somewhat by the discovery of the Santa Rosa local fauna.

An interesting variation on this theme was put forth by Landry (1957:90), but his hypothesis has languished for lack of fossil evidence. Landry suggested that the order Rodentia originated in the late Cretaceous or earliest Paleocene. Furthermore, he tentatively suggested that the hystricomorphs were the result of the first adaptive radiation of rodents; a radiation that was later replaced throughout the world by the sciurognaths, or *Paramys* and its relatives, during the early Eocene. In Landry's hypothesis, New World and Old World hystricomorphs are relics of that first radiation.

Phylogenetic reconstruction based on DNA analysis has placed the separation of the caviids as an early event in the development of the Rodentia, so early that they might very well be treated as taxonomic equivalents to the order Rodentia (Graur et al., 1991; D'Erchia et al., 1996). Although DNA evidence no longer points to a separation of the caviids from the rest of Rodentia as initially proposed (Frye and Hedges, 1995), isolation of this group seems certain to have occurred long before the time of the Santa Rosa local fauna.

Although highly controversial when proposed, the hypotheses of Landry (1957), Croizat (1971, 1979), and Graur et al. (1991) present an alternative scenario for the origin of South American caviids into which the Santa Rosan rodents might be placed. It is widely recognized that the isolation of South America as an island continent during the Tertiary strongly influenced the evolutionary development of the fauna. There are a number of major taxonomic groups that are primarily, or wholly, restricted to a South American distribution during this period of isolation (Pascual et al., 1985), but there is also substantial evidence for faunal exchange between South America and North America and between South America and Africa in the late Mesozoic and early Cenozoic. Furthermore, in each case, this movement was apparently in both directions, as South America contributed taxa to both North America (Estes and Báez, 1985; Gingerich, 1985) and Africa (George and Lavocat, 1993; Goldblatt, 1993). Viewed through the prism of the Santa Rosa local fauna, the autochthonous Tertiary fauna of South America, including rodents, is perhaps better seen as the natural development of an isolated portion of the Gondwanaland fauna rather than comprising just the archaic remnants of more widely distributed, and more rapidly evolving, Old and New World faunas.

The stage of evolution of the rodents from the Santa Rosa local fauna indicates that they are older than the rodents from the Deseadan SALMA of Salla, Bolivia, and the single specimen from Tinguiririca, Chile. Inasmuch as the caviids are generally considered to be conservative in the rate of evolutionary change of their tooth morphology, the small, but significant, differences seen between taxa of the Salla local fauna and Santa Rosa local fauna suggest that the Santa Rosa taxa may be considerably older than those from Salla, in spite of first impressions based on similar features. The diversity at Santa Rosa is not as great as that seen among all known Deseadan rodent faunas in South America taken together, but it is greater than that of the next youngest rodent faunas. We still have only a small sample from Santa Rosa, and intensive screen-washing could produce many thousands of specimens and probably many additional taxa. Nonetheless, the present known diversity at Santa Rosa is sufficient to indicate that rodents were in South America for some time before the accumulation of those deposits. On the basis of the evidence presented above, we are inclined to accept the hypothesis that the caviomorph rodents of South America represent an autochthonous evolutionary lineage derived from an ancestral group that formed part of a greater Gondwanaland fauna.

SUMMARY

The rodents of the Santa Rosa local fauna described in this paper constitute the oldest known rodents from South America. They are dated to the ?Eocene (Mustersan SALMA) on the basis of their more primitive form compared with the post-Mustersan, pre-Deseadan rodent from the Tinguiririca local fauna of Chile. This age is also consistent with the stage of evolution of other mammals in the Santa Rosa local fauna, but there are as yet no other confirming age data. There is great taxonomic diversity in this fauna, with at least eight genera and perhaps as many as seventeen species present, eleven of which are described in this paper. These species are placed within three well-known families of South American rodents—the Erethizontidae, Agoutidae, and Echimyidae—because of identifiable evolutionary trends already underway by Santa Rosan time. Nonetheless, a horizontal classification on the basis only of the features of the teeth of the Santa Rosan rodents could easily justify inclusion of the Santa Rosan rodents within one family. Most of the specimens consist of isolated teeth that range in size from approximately 1 mm to just under 4 mm in width.

The teeth of all of the Santa Rosan rodents are fundamentally similar. They are quadrangular in outline, with rounded corners, and brachydont, and they have low crests among only four recognizable cusps. With the exception of *Eobranisamys,* the teeth, both uppers and lowers, are primarily tetralophodont. Still, a developing fifth loph, a neoloph, is present as a variable feature on many teeth in the Santa Rosa collection. Usually it consists of minor crenulations in the anterior surface of the posteroloph or a series of aligned enamel irregularities within the metaflexus. It might also form from a substantial spur that extends into the metaflexus, or two such spurs that approach each other to form a complete neoloph. Such crenulations and enamel irregularities are present in variable form in several Santa Rosan taxa (e.g., *Eoincamys,* Agoutidae; and *Eosallamys* and *Eoespina,* Echimyidae). The fifth loph on the upper teeth of *Eobranisamys* (Agoutidae) is consistently present, but variable, and it is the best formed fifth loph of those found in any genus within the local fauna. In the Oligocene erethizontid *Protosteiromys* (*P. medianus* in Wood and Patterson, 1959:fig. 30), a complete neoloph (our usage) is present, evidently marking the stabilization in the erethizontids, as well as in some agoutids, of what is a variable feature in most rodents of Santa Rosan age. The overall similarities in crown height and shape and the arrangement of the lophs suggest that these rodents were not far removed from their common ancestry, even though they were highly advanced for Eocene rodents.

Two partial mandibles referred to *Eobranisamys* show evidence of advanced caviomorph features. The rami are fully hystricognathous, and the lower deciduous premolars were still in place and in use as part of a complete lower tooth row that included M_3. Hystricognathy has been found in an early Oligocene rodent of Chile (Wyss et al., 1993) and possibly in Eocene rodents of North America (Wood, 1972), and this trait seems to have been an early characteristic among South American rodents. Hystricognathy might be significant in understanding the history of rodents in North America, but it cannot be used as evidence that South American rodents are derived from North America because the groups on the two continents were roughly contemporaneous.

Furthermore, the two partial mandibles of *Eobranisamys* have dp_4s in place, with moderate to well worn molars. There is no indication of unerupted P_4s beneath the dp_4s, and only deciduous fourth premolars are referred to the genus *Eobranisamys*. The retention of deciduous premolars was cited as a character in common between Caviida and the Old World "Phiomorpha" by Hoffstetter (1975:520, in Patterson and Wood, 1982:498). That view is strengthened by the evidence from these two rami.

The Santa Rosan rodents, primitive as they are when compared with later caviids, are nonetheless highly advanced for Eocene rodents, and a clear progression from the taxa of Santa Rosa toward the Deseadan SALMA taxa of Salla, Bolivia, and Patagonia, Argentina, can be identified. The occlusal patterns of both upper and lower teeth show no lingering evidence of tritubercularity in upper teeth, or basinal expansion of the talonid at the expense of the trigonid and marginal placement of the cuspids in lower teeth. The fundamental dental pattern of rodents from Santa Rosa is one in which there are four large cusps in both upper and lower teeth and in which the labial cusps (in the uppers) or lingual cuspids (in the lowers) are more closely spaced to the labiolingual axis of the tooth. Each molar has four low crests, with a principal crest placed diagonally on the occlusal surface and between the paracone and hypocone (upper teeth), or the entoconid and protoconid (lower teeth). By Santa Rosan time, the basic caviid patterns were set for the families Agoutidae, Echimyidae, and perhaps Erethizontidae. If an Eocene age for the Santa Rosa local fauna is borne out, then the rodents would appear to be much farther along in their evolutionary direction than Eocene rodents in other parts of the world, and it would seem fruitless to seek their ancestry in either North America or Africa, as was the practice when no rodents older than the Oligocene were known from South America.

The early age of these rodents, and their well-defined and characteristic caviid features, is sufficient cause to resurrect hypotheses of caviid divergence that place this group in isolation in the early Cenozoic. This might have occurred as the result of vicariance brought about by the breakup of Gondwana. The obvious and often remarked upon similarities between South American and African hystricognaths would therefore be the manifestations of a once common gene pool. However, that the caviids are related to North American paramyids cannot be ruled out entirely. Certainly, instances of faunal and floral exchange between South America, North America, and Africa in the early Tertiary are growing more evident, and the precursors of the caviids could have come from any direction. Nonetheless, the Santa Rosan rodents suggest that they were diverging from a common center, had not proceeded far in their evolutionary development, and were diverging in ways characteristic of later caviids without displaying similarities to Eocene genera in North America or Africa. From this, we conclude that the caviids constitute a long and separate lineage within Rodentia and that they should be recognized as a component of the autochthonous fauna of South America.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the field companionship and financial support of John G. Wigmore, codiscoverer of the Santa Rosa local fauna. Additional funding for field efforts was provided by the National Geographic Society. Tim Barnhart and Bret Gustafson, Johnson County Community College, assisted with the preparation of the illustrations. Larry Martin, Morton Green, and Robert W. Wilson, University of Kansas Museum of Natural History, read drafts of the manuscript and provided notes and comments. Spirited reviews of the manuscript were offered by Malcolm McKenna and Guiomar Vucetich, for which we are grateful. We thank Francisco Goin for the translation of the abstract into Spanish. The X-ray photographs were made by John Chorn, University of Kansas Museum of Natural History.

LITERATURE CITED

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo La Plata. *Boletín del Museo La Plata (Buenos Aires)* 1:1–26 (del apartado).

Bond, M., G. López, and M. Reguero. 1996. "Astraponotéen plus supérieur" of Ameghino: Another interval in the Paleogene record of South America. *Journal of Vertebrate Paleontology* 16(3)(Suppl.):23A.

Bryant, J.D., and M.C. McKenna. 1995. Cranial anatomy and phylogenetic position of *Tsanganomys altaicus* (Mammalia: Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. *American Museum of Natural History Novitates* 3156:1–42.

Butler, P. 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. In *Evolutionary relationships among rodents. A multidisciplinary analysis,* ed. W.P. Luckett and J.-L. Hartenberger, 381–401. New York: Plenum Press.

Campbell, K.E., Jr. 2004. The Santa Rosa local fauna: A summary. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 155–163.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Candela, A. 1999. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino, 1904. *Palaeovertebrata* 28(1):53–73.

———. 2002. Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): Evolutionary significance. *Acta Palaeontologia Polonica* 47(4): 717–723.

Croizat, L. 1971. De la "pseudovicariance" et de la "disjonction illusoire." *Anuârio da Sociedade Broteriana* 37:115–141.

———. 1979. Review of Biogeographie: Fauna und Flora der Erde und ihre Geschichtliche Entwicklung by P. Banarescu and N. Boscaiu. *Systematic Zoology* 28(2):250–252.

Dawson, M.R. 1977. Late Eocene rodent radiations: North America, Europe, and Asia. *Géobios, Special Memoir* 1:195–209.

D'Erchia, A.M., C. Gissi, G. Pesole, C. Saccone, and V. Arnason. 1996. The guinea-pig is not a rodent. *Nature* 381:597–599.

Estes, R., and A. Báez. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: Evidence for interchange? In *The great American biotic interchange,* ed. F.G. Stehli and S.D. Webb, 140–197. New York: Plenum.

Ferrusquia-Villafranca, I. 1989. A new rodent genus from central Mexico and its bearing on the origin of the Caviomorpha. In *Papers on fossil rodents in honor of Albert Elmer Wood,* ed. C.C. Black and M.R. Dawson. Natural History Museum of Los Angeles County, Science Series 33, 91–117.

Ferrusquia-Villafranca, I., and A.E. Wood. 1969. New fossil rodents from the early Oligocene Rancho Gaitan local fauna, northeastern Chihuahua, Mexico. *The Pearce-Sellards Series, Texas Memorial Museum* 16:1–13.

Flynn, J.J., and C.C. Swisher. 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. *Society of Economic Petrologists and Mineralogists, Special Publication* 54:317–333.

Flynn, J.J., and A.R. Wyss. 1999. New marsupials from the Eocene–Oligocene transition of the Andean main range, Chile. *Journal of Vertebrate Paleontology* 19(3):533–549.

Flynn, L., L.L. Jacobs, and I.U. Cheema. 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. *American Museum Novitates* 2841:1–58.

Frye, M.S., and S.B. Hedges. 1995. Monophyly of the Order Rodentia inferred from mitochondrial DNA sequences of the genes for 12S rRNA, 16s rRNA, and tRNA-valine. *Molecular Biology and Evolution* 12(1):168–176.

George, W. 1993. The strange rodents of Africa and South America. In *The Africa–South America connection,* ed. W. George and R. Lavocat. Oxford Monographs on Biogeography, 7:119–141. New York: Oxford University Press.

George, W., and R. Lavocat (eds.). 1993. *The Africa–South America connection.* Oxford Monographs on Biogeography, no. 7. New York: Oxford University Press, 166 pp.

Gingerich, P.D. 1985. South American Mammals in the Paleocene of North America. In *The Great American Biotic Interchange,* ed. F.G. Stehli and S.D. Webb, 123–137. New York: Plenum Press.

Goin, F., and A. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Goldblatt, P. (ed.). 1993. *Biological relationships between Africa and South America.* New Haven: Yale University Press, 630 pp.

Graur, D., W.A. Hide, and W.H. Li. 1991. Is the guinea-pig a rodent? *Nature* 351:649–652.

Hartenberger, J.-L. 1998. Description of the radiation of the Rodentia (Mammalia) from the late Paleocene to the Miocene—Phylogenetic consequences. *Comptes Rendus de l'Academie des Sciences Serie II, (A)* 326(6):439–444.

Hoffstetter, R. 1975. El origen de los Caviomorpha y el problema de los Hystricognathi (Rodentia). *I Congreso Argentino de paleontologia y bioestratigrafia, Actas* 1(2):505–528.

Hoffstetter, R., and R. Lavocat. 1970. Découverte dans le Déséadien de Bolivie de genres pentalophodontes appuyant les affinités africaines des rongeurs caviomorphes. *Comptes Rendus de l'Académie des Sciences, (D)* 271:172–175.

Kay, R.F., B.J. MacFadden, R.H. Madden, H. Sandeman, and F. Anaya. 1998. Revised age of the Salla beds, Bolivia, and its bearing on the age of the Deseadan South American Land Mammal "Age." *Journal of Vertebrate Paleontology* 18(1):189–199.

Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G.H. Re, M. Heizler, and H. Sandeman. 1999. Revised age of the Casamayoran South American Land Mammal "Age"—Climatic and biotic implications. *Proceedings of the National Academy of Sciences, Washington* 96(23):13235–13240.

Korth, W.W. 1984. Earliest Tertiary evolution and radiation of rodents in North America. *Bulletin of the Carnegie Museum of Natural History* 24:1–71.

Landry, S.O. 1957. The interrelationships of the New and Old World hystricomorph rodents. *University of California Publications in Zoology* 56:1–118.

Lavocat, R. 1974. The interrelationships between the African and South American rodents and their bearing on the problem of the origin of South American monkeys. *Journal of Human Evolution* 3:523–526.

———. 1976. Rongeurs caviomorphes de l'Oligocene de Bolivie. II. Rongeurs du bassin Deseadien de Salla-Luribay. *Palaeovertebrata* 7(3):15–90.

———. 1981. The implications of rodent paleontology and biogeography to the geographical sources and origin of platyrrhine primates. In *Evolutionary biology of the New World monkeys and continental drift,* ed. R.L. Ciochon and A.B. Chiarelli, 93–102. New York: Plenum Press.

———. 1993. Conclusions. In *The Africa–South America connection,* ed. W. George and R. Lavocat. Oxford Monographs on Biogeography, 7:142–150. New York: Oxford University Press.

Leidy, J. 1871. Notice of some extinct rodents. *Proceedings of the Academy of Natural Science, Philadelphia* 1871:230–232.

Marshall, L., and T. Sempere. 1993. Evolution of the Neotropical Cenozoic land mammal fauna in its geochronologic, stratigraphic, and tectonic context. In *Biological relationships between Africa and South America,* ed. P. Goldblatt, 328–392. New Haven, Connecticut, and London: Yale University Press.

Martin, T. 1992. Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire,* pp. 1–168.

———. 1994. African origin of caviomorph rodents is indicated by incisor enamel microstructure. *Paleobiology* 20:5–13.

———. 2004. Incisor enamel microstructure of South America's earliest rodents: Implications for caviomorph origin and diversification. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 131–140.

McKenna, M.C., and S.K. Bell. 1997. *Classification of mammals above the species level.* New York: Columbia University Press, 629 pp.

Osborn, H.F. 1908. New fossil mammals from the Fayûm Oligocene, Egypt. *American Museum of Natural History, Bulletin* 24:265–272.

Pascual, R., M.G. Vucetich, G.J. Scillato-Yané, and M. Bond. 1985. Main pathways of mammalian diversification in South America. In *The great American biotic interchange,* ed. F.G. Stehli and S.D. Webb, 219–247. New York: Plenum.

Patterson, B., and R. Pascual. 1968. New echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. *Museum of Comparative Zoology, Harvard University, Breviora* 301:1–14.

Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149(7):371–543.

Schaub, S. 1958. Simplicidentata. In: *Traité de Paléontologie,* vol. 6, no. 2, ed. J. Piveteau, 659–818. Paris: Masson et Cie.

Scott, W.B. 1895. *Protoptychus hatcheri,* a new rodent from the Uinta Eocene. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1895:269–286.

Simons, E., and A.E. Wood. 1968. Early Cenozoic mammalian faunas, Fayum Province, Egypt. *Peabody Museum of Natural History, Yale University, Bulletin* 28:1–105.

Simpson, G.G. 1950. History of the fauna of Latin America. *American Scientist* 38(3):369–408.

Tullberg, T. 1899. Ueber das System der Nagethiere: eine phylogenetische Studie. *Nova acta regiae Societatis scientiarum upsaliensis* 18(3):1–514.

Vucetich, M.G. 1991. Los roedores de Salla y Lacayani (Bolivia) y su correlación con las otras faunas de edad Deseadense (Oligoceno). In *Fosiles y Facies de Bolivia,* vol. 1, *Vertebrados,* ed. R. Suarez-Soruco. Santa Cruz, Bolivia: Revista Técnica de YPFB, 12(3–4):625–629.

Vucetich, M.G., and A.G. Kramarz. 2003. New Miocene rodents from Patagonia (Argentina) and their bearing on the early radiation of the octodontoids (Hystricognathi). *Journal of Vertebrate Paleontology* 23(2):435–444.

Vucetich, M.G., and D.H. Verzi. 1990. La pentalofodoncia entre los roedores Caviomorpha: Simplesiomorfía o homoplasia? In *Reunión conjunta de la Sociedad Argentina para el Estudio de los Mamíferos (SAREM) y la American Society of Mammalogists (ASM), Buenos Aires,* 42.

———. 1996. A peculiar octodontoid (Rodentia, Caviomorpha) with terraced molars from the Lower Miocene of Patagonia (Argentina). *Journal of Vertebrate Paleontology* 16(2):297–302.

Vucetich, M.G., D.H. Verzi, and J.-L. Hartenberger. 1999. Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). *Comptes Rendu de l' Académie des Sciences, Sciences de la terre et des planétes* 329:763–769.

Wood, A.E. 1949. A new Oligocene rodent from Patagonia. *American Museum of Natural History, Novitates* 1435:1–54.

———. 1968. The African Oligocene Rodentia. Part II of: Early Cenozoic mammalian faunas, Fayum Province, Egypt. *Peabody Museum of Natural History, Yale University, Bulletin* 28:23–105.

———. 1972. An Eocene hystricognathous rodent from Texas: Its significance in interpretations of continental drift. *Science* 175:1250–1251.

———. 1973. Eocene rodents, Pruett Formation, Southwest Texas; their pertinence to the origin of the South American Caviomorpha. *Texas Memorial Museum, the Pierce-Sellards Series* 20:1–40.

———. 1981. The origin of the caviomorph rodents from a source in middle America: A clue to the area of origin of the platyrrhine primates. In *Evolutionary biology of the New World monkeys and continental drift,* ed. R.L. Ciochon and A.B. Chiarelli, 79–91. New York: Plenum Press.

———. 1985. Northern waif primates and rodents. In *The Great American Biotic Interchange,* eds. F.G. Stehli and S.D. Webb, 267–282. New York: Plenum Press.

———. 1993. The history of the problem. In *The Africa–South America connection,* no. 7, ed. W. George and R. Lavocat. Oxford Monographs on Biogeography, 1–7. New York: Oxford University Press.

Wood, A.E., and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120(3):279–428.

Wood, A.E., and R.W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology* 10(5):388–391.

Wyss, A.R., J.J. Flynn, M.A. Norell, C.C. Swisher III, R. Charrier, M.J. Novacek, and M.C. McKenna. 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. *Nature* 365: 463–437.

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 of Natural History, Novitates* 3098:1–31.

Received 2 July 2003; accepted 29 December 2003.

APPENDICES

Appendix 1 Crown measurements of Santa Rosan rodent teeth. Measurements of length by width are taken from greatest anteroposterior lengths and greatest labiolingual widths as measured on the occlusal surface. The holotype of a species is indicated by one asterisk (*); two asterisks (**) indicate the holotype of a genus. Measurements in parentheses are estimates made from damaged specimens. Specimens with pound sign (#) were too broken for measurements, but appear in Appendix 2.

		Length × Width (mm)
Eopululo wigmorei		
143269**	M^x	3.63 × 3.05
143272	M^x	2.97 × 2.84
149489	M^x	3.28 × 3.41
143263#	M_x	
143268#	M_x	
143410	M_x	(4.2) × (3.3)
149465	M_x	(3.7) × (3.0)
Eoincamys pascuali		
143313	P^4	1.49 × 1.79
143321	P^4	1.73 × 1.92
143322	P^4	1.65 × 1.79
143312	M^x	2.06 × 2.44
143314	M^x	1.78 × 1.94
143316	M^x	1.82 × 2.17
143317	M^x	2.31 × 2.49
143318**	M^x	2.18 × 2.11
143319	M^x	1.81 × 2.09
143323	M^x	1.77 × 2.17
143324	M^3	1.53 × 1.70
149463	M^x	1.90 × 2.22
149478	M^x	1.94 × 2.23
143328	dp_4	(1.6) × 1.68
143331	dp_4	— × 1.61
143335	dp_4	1.85 × 1.58
143456	dp_4	(1.6) × 1.57
143301	P_4	1.84 × 1.66
143333	P_4	1.72 × 1.41
143334	P_4	1.73 × 1.70
143336	P_4	1.73 × 1.60
143299	M_x	1.99 × 1.78
143300	M_x	2.10 × 1.78
143303	M_I	1.90 × 1.50
143304	M_x	2.06 × 1.72
143305	M_x	1.81 × 1.61
143306	M_x	2.12 × 1.89
143307	M_x	2.05 × 1.88
143308	M_x	2.16 × 1.55
143309	M_x	2.05 × 1.56
143310	M_x	1.93 × 1.70
143427	M_x	— × (1.8)
143434	M_x	1.61 × 1.50
143504	M_x	1.93 × 1.72
149445	M_3	2.03 × 1.65
149446	M_x	1.90 × 1.82
149449	M_3	2.12 × 1.82
149452	M_x	2.07 × 1.82
149453	M_x	2.06 × 1.77

Appendix 1 Continued.

		Length × Width (mm)
Eoincamys ameghinoi		
149430	P^4	1.26 × 1.63
149473	P^4	1.10 × (1.2)
143279	M^x	1.72 × 1.80
143315	M^3	1.43 × 1.48
143320	M^x	1.47 × 1.53
143338	M^x	1.73 × 1.69
143339*	M^x	1.65 × 1.67
143340	M^3	1.61 × 1.76
143396	M^x	
143437	M^x	1.40 × (1.4)
143468	M^x	1.69 × 1.26
149450	M^x	1.64 × 1.67
149470	M^x	1.66 × 1.74
149495	P^4	1.01 × 1.12
	M^1	1.23 × 1.31
	M^2	1.66 × 1.50
143332	P_4	1.55 × 1.45
143445	P_4	1.32 × 1.38
143280	M_x	1.44 × 1.26
143435	M_x	1.49 × 1.55
143507	M_x	1.33 × 1.23
149435	M_x	1.98 × 1.56
149442	M_x	1.87 × 1.45
149444	M_x	1.51 × 1.25
Eobranisamys romeropittmanae		
143354	M^3	3.14 × 3.04
143355	M^x	2.55 × —
143356	M^x	3.05 × 2.97
143357	M^x	3.01 × (3.0)
143358	M^x	3.22 × 3.07
143359	M^x	3.15 × 3.15
143360	M^x	3.29 × (3.1)
143362	M^x	3.21 × 3.07
143364	M^3	2.94 × 3.04
143365	M^3	2.75 × 3.10
143381	M^3	(3.0) × (3.1)
149482	M^x	2.82 × 2.78
149490	M^3	3.16 × 3.35
149493	M^3	3.38 × 2.91
144296	M^2	3.43 × 3.80
	M^3	3.31 × 3.40
144297**	M^1	3.25 × 3.47
	M^2	3.31 × 3.98
143352	dp_4	3.67 × 2.41
143419	dp_4	3.29 × 2.19
143423	dp_4	— × 2.35
143505	dp_4	
144293	dp_4	3.55 × 2.28
	M_1	3.19 × 3.10
	M_2	3.48 × 3.60
143266	M_x	3.33 × 2.95
143341	M_x	3.11 × 3.03
143342	M_x	3.70 × 3.39
143343	M_x	3.23 × 3.15
143344	M_x	3.15 × 2.92

Appendix 1 Continued.

		Length × Width (mm)
143345	M_x	3.18 × 3.01
143346	M_x	3.28 × 3.14
143347	M_3	3.55 × 2.91
144292	M_1	(2.2) × 2.06
149462	M_x	3.28 × —
149483	M_x	3.23 × 3.20
149487	M_1	3.21 × 3.07
Eobranisamys riverai		
143302	M^3	2.61 × 2.64
143372	M^x	2.49 × 3.04
143373	M^x	2.15 × 2.53
143377	M^x	2.62 × 2.80
143378	M^2	2.65 × 2.94
143428	M^3	2.04 × 2.27
143503*	M^1	2.62 × 2.63
149464	M^x	2.68 × (2.4)
149474	M^x	2.26 × 2.59
143368	dp_4	— × (1.8)
143369	dp_4	2.90 × 2.03
143270	dp_4	— × 1.95
143371	dp_4	2.58 × 1.85
143506	dp_4	2.38 × 1.74
143366	M_x	2.84 × 2.54
143367	M_x	2.62 × 2.42
149456	M_x	3.01 × 2.39
149461	M_x	3.39 × (2.5)
149475	M_x	2.78 × 2.72
149476	M_x	2.98 × 2.68
149485	M_x	2.81 × 2.49
Eopicure kraglievichi		
143264**	M^x	2.75 × 2.30
143353	M^x	2.78 × 2.29
149454	M^x	2.49 × 2.13
149455	M^x	2.96 × 2.12
149466	M^x	2.63 × 2.01
149479	M^x	2.54 × 2.48
Agoutidae, genus and species indeterminate A		
144299	M_x	4.24 × 4.08
Agoutidae, genus and species indeterminate B		
143375	M_x	2.96 × 2.82
Agoutidae, genus and species indeterminate C		
143349	M_x	3.84 × 2.92
143351	M_x	3.64 × 2.99
Eosallamys paulacoutoi		
143415	P^4	2.10 × 2.25
149460	P^4	2.16 × 2.34
149480	P^4	2.35 × 2.58
143267	M^x	2.66 × 2.73
143363	M^3	2.86 × 3.05
144302	M^x	2.50 × 2.43
149494	M^x	2.56 × 2.65
143422**	P^4	2.43 × 2.88
	M^1	2.70 × 2.99
	M^2	3.12 × 3.47
	M^3	2.78 × 3.33

Appendix 1 Continued.

		Length × Width (mm)
143370#	dp_4	— × 2.00
143418	dp_4	— × 2.16
143420	dp_4	2.80 × 1.75
143450	dp_4	2.90 × 1.85
143451	dp_4	2.94 × 2.22
149458	dp_4	(3.2) × (2.0)
149492	P_4	3.20 × 2.65
143262	M_3	3.03 × 2.49
143265	M_x	3.08 × —
143361	M_x	2.59 × —
144524	M_x	2.70 × 2.52
Eosallamys simpsoni		
149451	P^4	1.91 × 1.67
143374	M^x	1.98 × 2.16
143376	M^x	2.35 × 2.61
143380	M^3	2.20 × 2.17
143398	M^x	2.05 × 2.06
143411	M^x	2.34 × 2.32
143424*	M^x	1.88 × 2.04
143429	M^x	2.09 × 2.30
143430	M^x	2.04 × 2.24
143441	M^x	1.94 × —
149448	M^3	1.89 × 1.76
149457	M^3	2.06 × 1.95
149459	M^x	2.36 × 2.30
149472	M^x	2.33 × 2.48
149477	M^x	2.31 × 2.02
149481	M^x	2.20 × 2.11
149488	M^x	(2.8) × (2.7)
143406	dp_4	— × 1.48
143407#	dp_4	
143452	dp_4	2.20 × 1.47
149443#	dp_4	
149467#	dp_4	
143311	P_4	2.32 × 1.94
143273	M_x	2.28 × 2.05
143275	M_x	2.28 × 2.28
143276	M_x	2.24 × 2.04
143284	M_3	1.67 × 1.57
143412	M_x	1.93 × 1.83
143413	M_x	1.86 × 1.77
143414	M_x	2.26 × 2.38
143416#	M_x	
149491	M_x	2.76 × 2.48
Eoespina woodi		
143432	P^4	1.06 × 1.20
143459	P^4	1.08 × 1.42
144301	P^4	1.01 × 1.33
149468	P^4	1.28 × 1.24
143286**	M^x	1.33 × 1.45
143288	M^3	0.99 × 1.31
143289	M^x	1.44 × —
143290	M^x	1.42 × 1.55
143291	M^x	1.36 × 1.56
143293	M^x	1.36 × 1.54
143295	M^x	1.31 × (1.2)

Appendix 1 Continued.

		Length × Width (mm)
143296	M^x	1.41 × 1.50
143297	M^3	1.12 × 1.30
143298	M^3	1.30 × 1.37
143384	M^x	1.29 × 1.37
143397	M^x	— × 1.50
143455	M^x	1.32 × 1.43
143457	M^x	1.36 × 1.73
144300	M^x	1.39 × 1.67
149427	M^x	1.30 × 1.26
149431	M^x	1.17 × 1.33
149432	M^x	1.51 × 1.50
149433	M^x	1.51 × 1.35
149436	M^x	1.49 × 1.58
149437	M^x	1.49 × 1.33
149441	M^2	1.55 × 1.57
149471	M^x	1.48 × 1.29
149484	M^x	1.53 × 1.62
143391	dp_4	1.48 × 0.93
143403	dp_4	1.33 × 0.92
143404#	dp_4	
143405	dp_4	1.32 × 0.96
143448#	dp_4	
149440	dp_4	1.50 × 1.02
143283	P_4	1.33 × 1.21
144294	P_4	1.28 × 1.30
	M_1	1.43 × 1.42
	M_2	1.48 × 1.51
143281	M_x	1.24 × 1.15
143282	M_3	1.26 × 1.17
143327	M_x	1.27 × 1.24
143330	M_x	1.41 × 1.37
143385	M_x	1.43 × 1.53
143386	M_3	1.24 × 1.15
143389	M_x	1.49 × 1.39
143390	M_x	1.46 × 1.40
143436	M_x	1.30 × 1.28
143438	M_3	1.34 × 1.22
143439	M_x	(1.2) × (1.2)
143440	M_3	1.12 × 1.15
143446	M_x	1.53 × 1.42
143447	M_x	1.04 × 1.12
143461	M_3	1.29 × 1.15
149425	M_1	(1.5) × (1.4)
149429	M_x	1.55 × 1.39
149434	M_1	1.24 × 1.40
149447	M_x	1.62 × 2.14
149469	M_1	1.41 × 1.38
149486	M_x	1.21 × 1.30
Eosachacui lavocati		
143433	P^4	1.24 × (1.3)
143458	P^4	1.27 × 1.46
143466	P^4	1.03 × (1.2)
143278	M^x	1.45 × 1.72
143285	M^x	1.48 × (1.6)
143292	M^x	1.39 × 1.60
143294**	M^x	1.52 × 1.74
143337	M^x	1.36 × 1.54
143383	M^x	1.55 × 1.60
143387	M^x	(1.6) × (1.7)
143388	M^x	1.34 × 1.48
143399	M^x	1.46 × 1.66
143401	M^3	1.25 × (1.3)
143444	M^x	1.37 × 1.41
143453	M^x	1.42 × 1.62
143454	M^x	(1.6) × 1.63
149438	M^x	1.55 × 1.45
149439	M^x	1.58 × 1.52
143326	dp_4	— × 1.38
143379	dp_4	1.60 × 1.03
143400	dp_4	1.53 × 1.08
143402	dp_4	(1.5) × 0.98
143449	dp_4	— × 1.15
143394	P_4	1.47 × 1.30
143274	M_1	1.54 × 1.39
143287	M_x	1.43 × 1.34
143325	M_x	1.51 × 1.40
143329	M_1	1.43 × 1.47
143382	M_x	1.70 × 1.65
143393	M_x	1.62 × 1.38
143395	M_3	1.39 × 1.31
143408	M_x	1.56 × 1.50
143417	M_x	1.69 × 1.62
143421	M_x	1.50 × 1.33
143431	M_x	1.64 × 2.04
143442	M_x	1.62 × (1.6)
143443	M_x	(1.6) × —
149426	M_1	1.54 × 1.55
149428	M_x	1.56 × 1.40
149447	M_x	1.62 × 2.14
Eodelphomys almeidacomposi		
144298**	M_3	3.81 × 3.38
Echimyidae, genus and species indeterminate A		
143409	M^x	3.69 × —
Echimyidae, genus and species indeterminate B		
143348	M_x	3.98 × 3.00
Echimyidae, genus and species indeterminate C		
143277	M^x	2.47 × (2.4)
Hystricognatha, genus and species indeterminate		
143271#	M^x	
143350	M_x	1.69 × 1.99
143392	M_x	
143425		
143426		
143460		
143462		
143463		
143464		
143465		
143467		

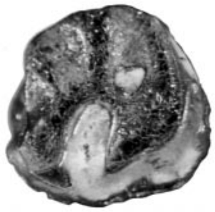
Appendix 2 Photographic catalogue of the Santa Rosan rodents. Upper teeth are followed by lower teeth. Order of species appearance follows that in text. For ease in identification of a tooth, see numerical sequence under taxon in Appendix 1.

Eopululo wigmorei

Upper Teeth

1 mm

143269 **



143272

149489

Eopululo wigmorei

Lower Teeth

1 mm

143263

143268

143410

149465

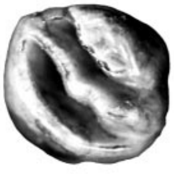
Eoincamys pascuali

Upper Teeth

1 mm

143313

143321



143322

143312

143314

143316

143317

143318 **

143319

143323

Eoincamys pascuali

Lower Teeth

1 mm


143324


149463


149478


143328

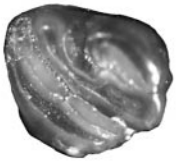

143331


143335


143456


143301


143333


143334


143336


143299


143300


143303


143304


143305


143306


143307


143308


143309


143310

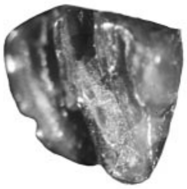

143427


143434


143504


149445


149446


149449

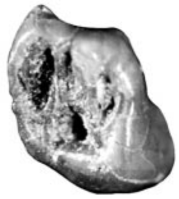

149452

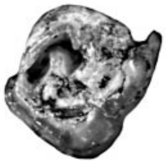

149453

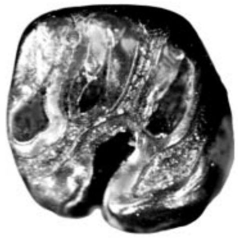
Eoincamys ameghinoi

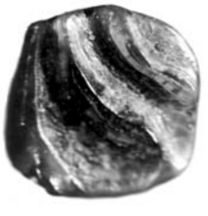
Upper Teeth

1 mm

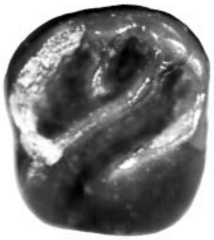

149430


149473


143279

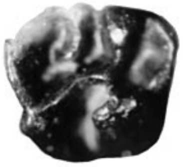

143315


143320


143338

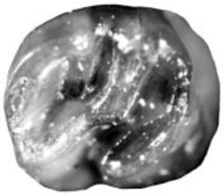

143339 *


143340

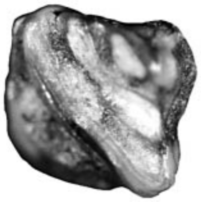

143437

143468

149495



149450



149470

Eoincamys ameghinoi

Lower Teeth

1 mm

143332

143445

143280

143435

143507

149435

149442

149444

Eobranisamys romeropittmanae

Upper Teeth

1 mm

143354

143355

143356

143357

143358

143359

143360

143362

143364

143365

143381

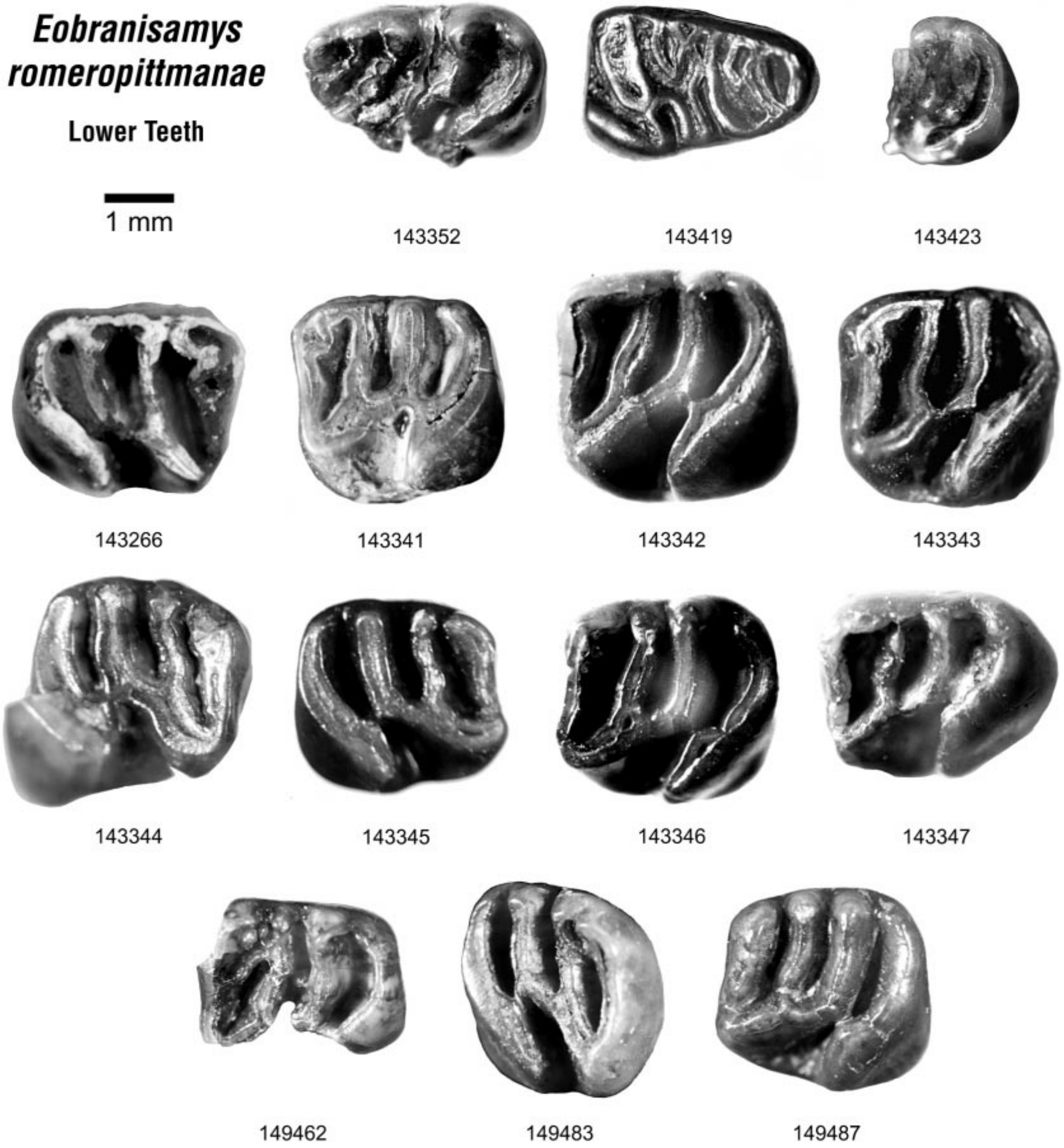
149482

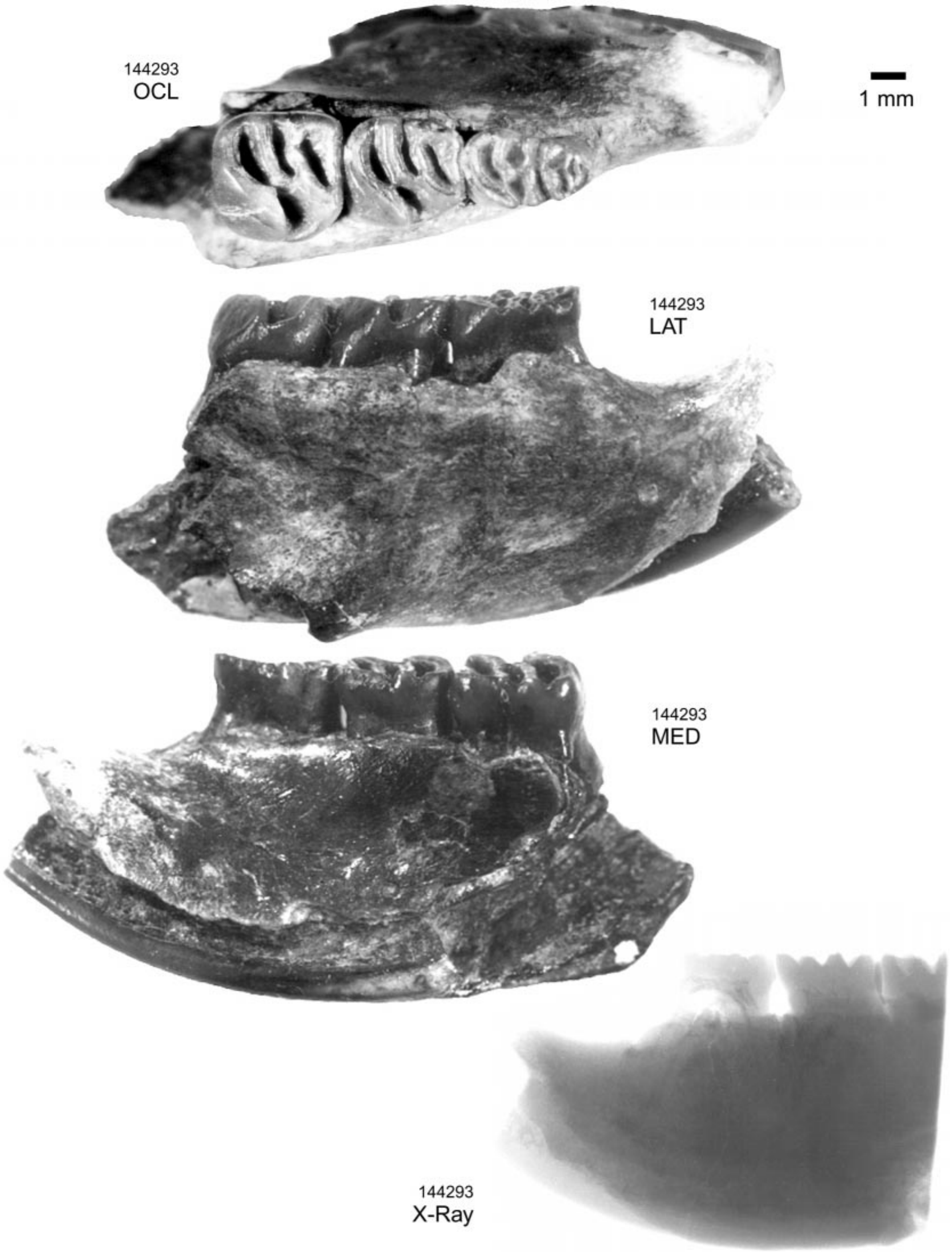
149490

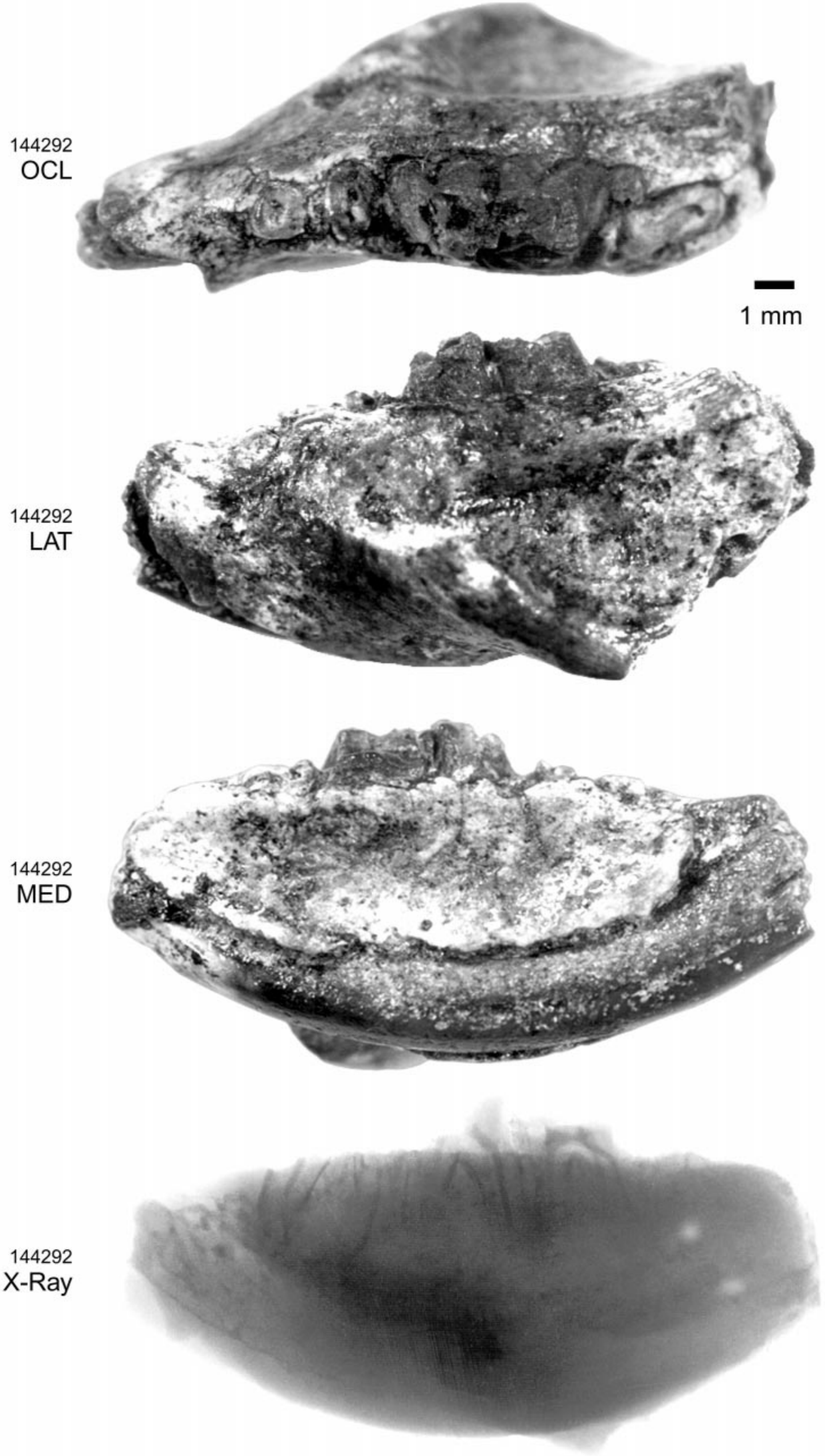
149493

144296

144297 **


Eobranisamys romeropittmanae
Lower Teeth
1 mm
143352
143419
143423
143266
143341
143342
143343
143344
143345
143346
143347
149462
149483
149487


144293
OCL
1 mm
144293
LAT
144293
MED
144293
X-Ray


144292
OCL
1 mm
144292
LAT
144292
MED
144292
X-Ray

Eobranisamys riverai

Upper Teeth

1 mm


143302


143372


143373


143377


143378


143428


143503 *


149474

Eobranisamys riverai

Lower Teeth

1 mm


143270


143368

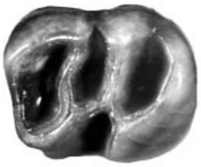

143369

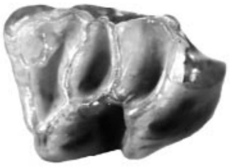

143371


143506

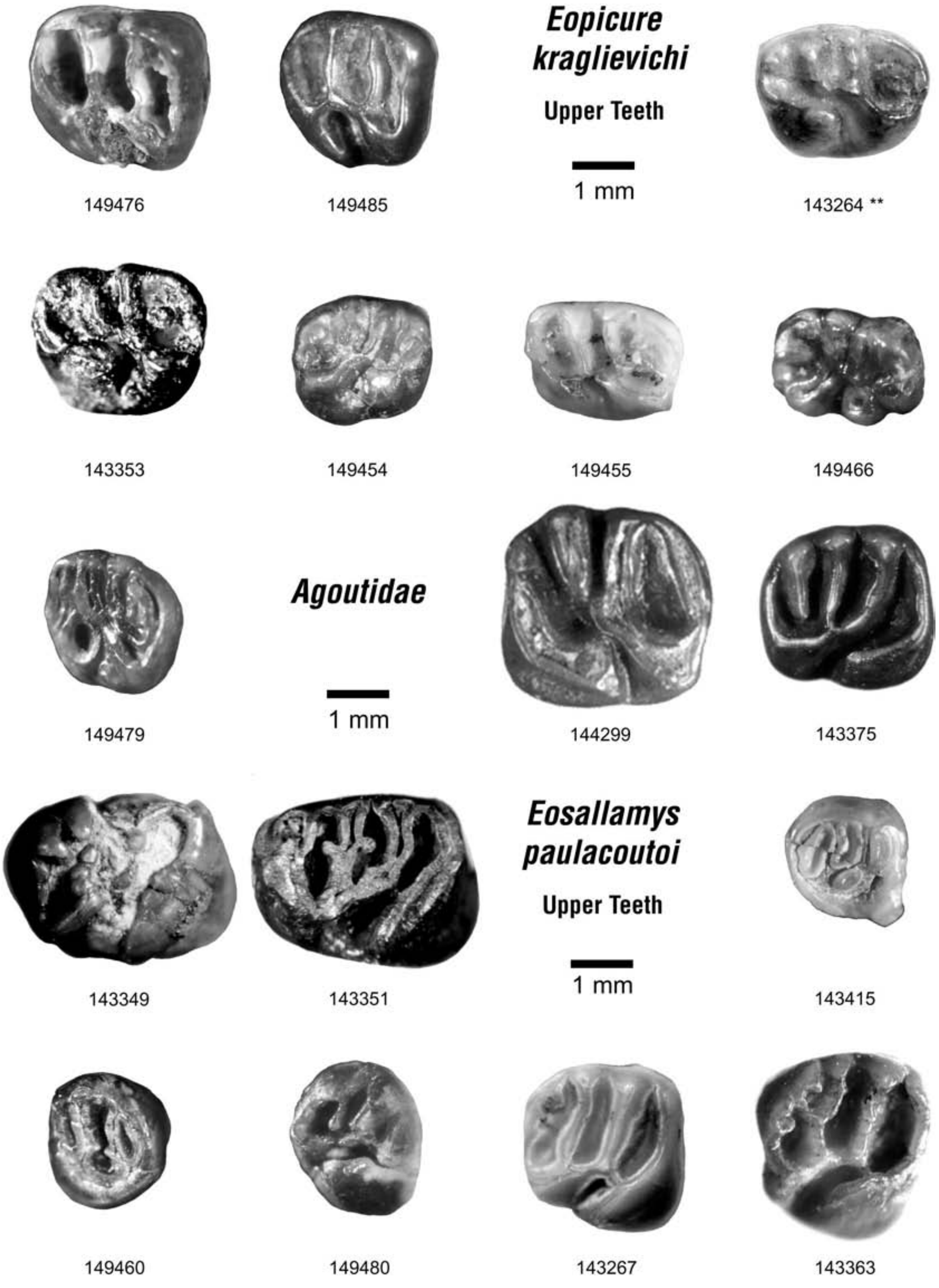

143366


143367


149456


149461


149475


149476
149485
Eopicure kraglievichi
Upper Teeth
1 mm
143264 **
143353
149454
149455
149466
149479
Agoutidae
1 mm
144299
143375
143349
143351
Eosallamys paulacoutoi
Upper Teeth
1 mm
143415
149460
149480
143267
143363


143422 **
LAT


1 mm
143422
OCL


143422
MED

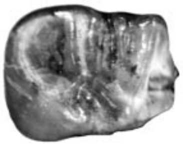

144302


149494

Eosallamys paulacoutoi

Lower Teeth

1 mm


143370


143418


143420

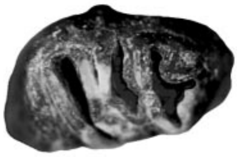

143450


143451

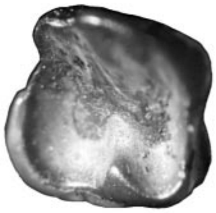

149458


149492


143262


143265


143361


144524

Eosallamys simpsoni

Upper Teeth

1 mm


149451


143374


143376


143380


143398

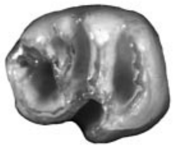

143411


143424 *


143429


143430


143441


149448


149457


149459


149472


149477


149481


149488

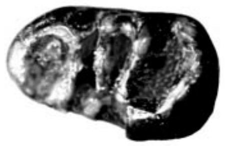
Eosallamys simpsoni

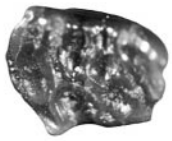
Lower Teeth

1 mm

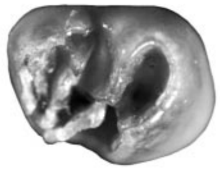

143406

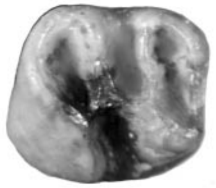

143407


143452


149443

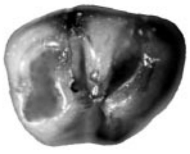

149467


143311


143273


143275


143276


143284


143412


143413


143414


143416


149491

Eoespina woodi

Upper Teeth

1 mm


143432


143459


144301


149468


143286 **

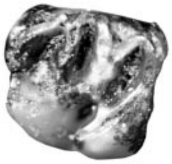

143288

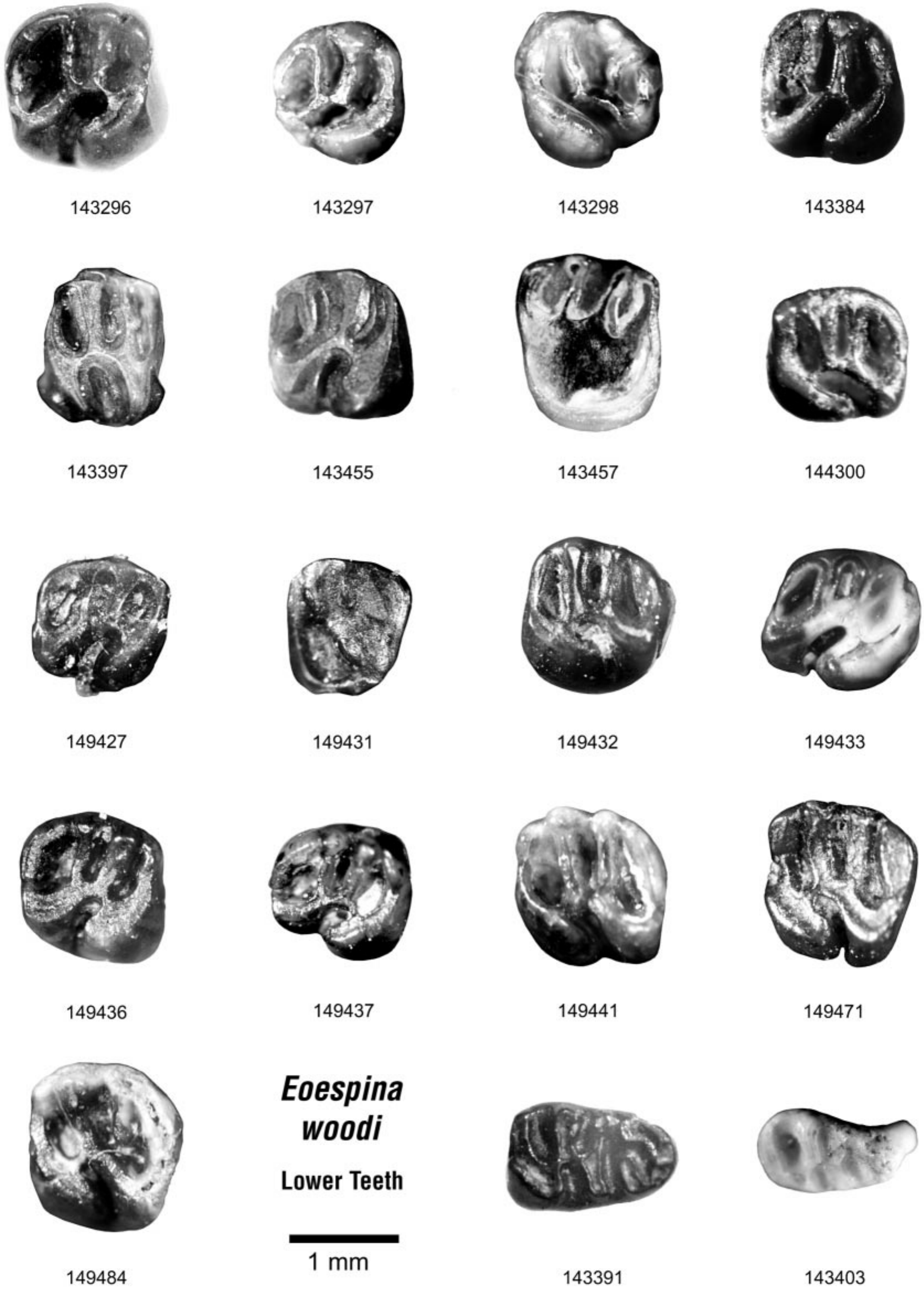

143289


143290


143291


143293


143295


143296
143297
143298
143384
143397
143455
143457
144300
149427
149431
149432
149433
149436
149437
149441
149471
149484
Eoespina woodi
Lower Teeth
1 mm
143391
143403

143404

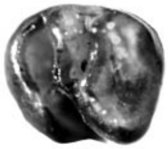
143405

143448

149440

143283

143281



143282

143327

143330

143385

143386

143389

143390

143436

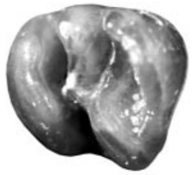
143438

143439

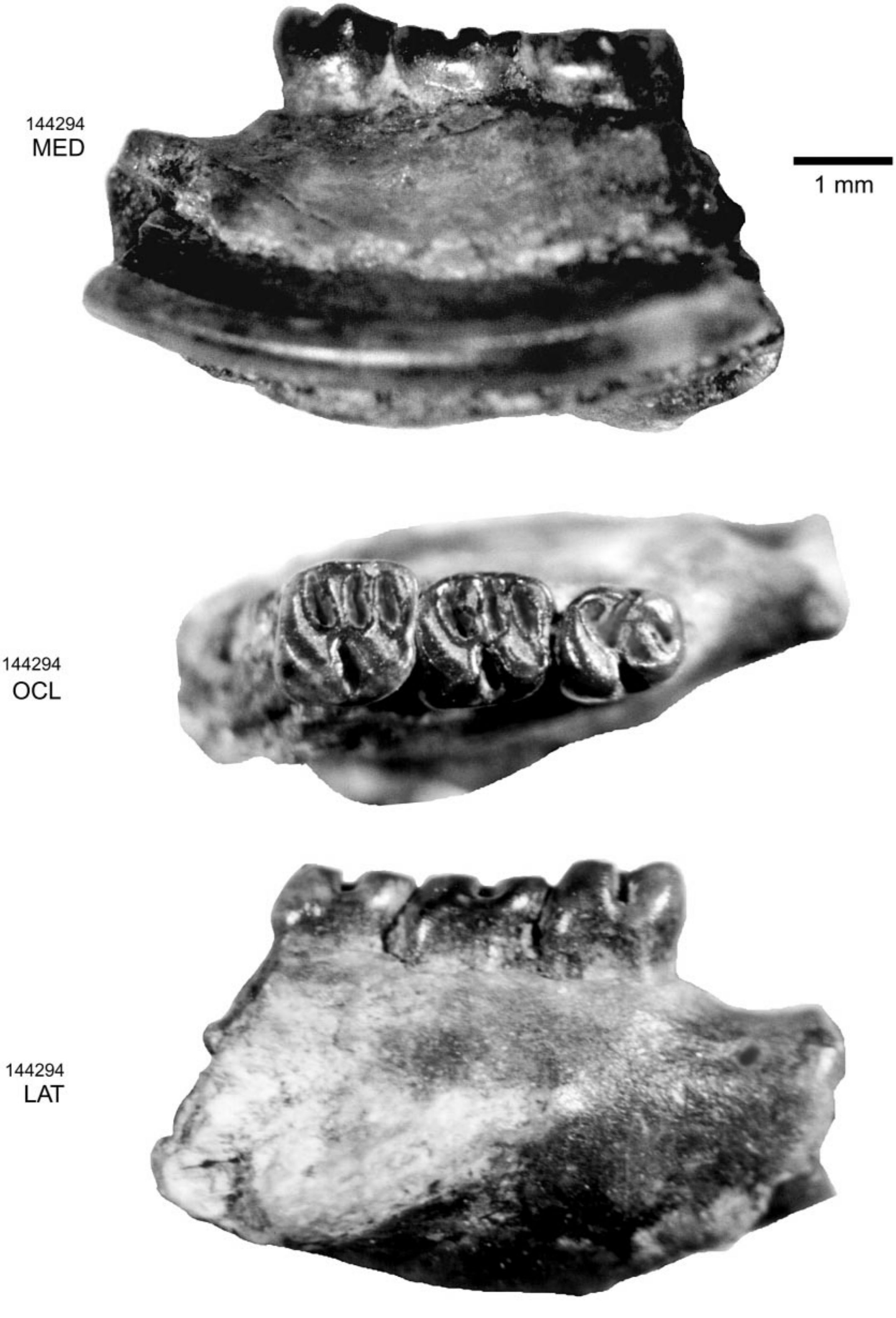
143440

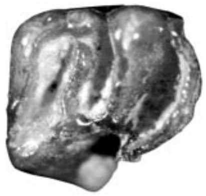
143446

143447

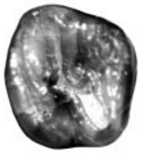


143461


144294
MED
1 mm
144294
OCL
144294
LAT


149425


149429


149434


149469


149486

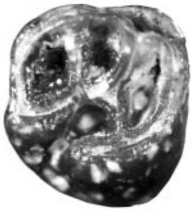
Eosachacui lavocati
Upper Teeth

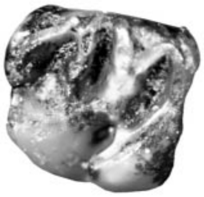
1 mm


143433


143458


143466


143278


143285


143292

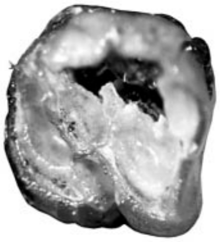

143294 **

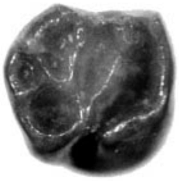

143337


143383


143387


143388

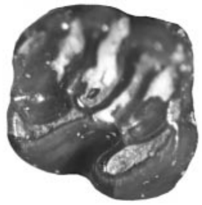

143399


143401


143444

143453

143454



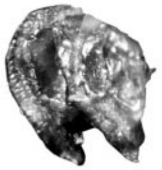
149438

149439

Eosachacui lavocati

Lower Teeth

1 mm



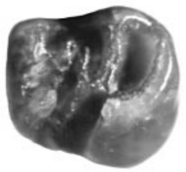
143326

143379

143400

143402

143449



143394

143274

143287

143325

143329

143382

143393

143395

143408

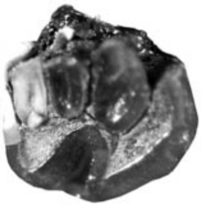
143417


143421

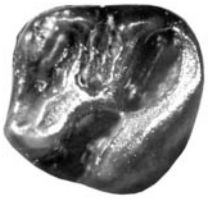

143431


149426


149428


143442


143443


149447

Eodelphomys almeidacomposi

lower tooth

1 mm


144298 **

Echimyidae

1 mm


143409


143348


143277

Hystricognatha

1 mm


143271

Incisor Enamel Microstructure of South America's Earliest Rodents: Implications for Caviomorph Origin and Diversification

Thomas Martin[1]

ABSTRACT. Six isolated rodent incisors from the Paleogene Santa Rosa locality of eastern Peru exhibit a double-layered schmelzmuster with multiserial Hunter–Schreger bands (HSB) in the portio interna (PI), which is typical for caviomorph rodents. All three subtypes of multiserial HSB [parallel to acute angular interprismatic matrix (IPM); acute angular IPM; and rectangular, platelike IPM] observed in Oligocene and younger caviomorphs are present. This variety of schmelzmuster reflects diversity in the ?Eocene Santa Rosa rodent fauna. Two incisors with rectangular, plate-like IPM in the PI indicate the presence of members of Octodontoidea, a caviomorph superfamily characterized by this autapomorphic character. The high diversity of incisor enamel microstructure can be explained by postulating several waves of immigration from Africa, where the same subtypes of HSB occur in Eocene–Oligocene Thryonomyoidea, or a longer evolutionary history of South American caviomorphs.

RESUMEN. Seis incisivos aislados de roedores procedentes de la localidad paleógena de Santa Rosa, en el este del Perú, exhiben un schmelzmuster de dos capas, con bandas de Hunter–Schreger (HSB) multiseriales en la porción interna (PI), un rasgo típico de los rodores caviomorfos. Se aprecian en ellos los tres subtipos de HSB multiserial observados en los caviomorfos oligocenos y más jóvenes: matriz interprismática (IPM) orientada desde paralela hasta en ángulo agudo, IPM en ángulo agudo y, finalmente, IPM rectangular, en forma de lámina o placa. Esta variedad de schmelzmuster refleja diversidad en la fauna ¿eocena? de roedores de Santa Rosa. Dos incisivos con IPM rectangular en forma de lámina o placa indican la presencia de miembros de los Octodontoidea, una superfamilia de caviomorfos caracterizada por este rasgo autapomórfico. La alta diversidad en la microestructura del esmalte de estos incisivos puede ser explicada ya sea postulando varias oleadas inmigratorias a partir de Africa, en donde los mismos subtipos de HSB aparecen en los Thryonomyoidea del Eoceno–Oligoceno, o bien a partir de una más larga historia evolutiva de los caviomorfos sudamericanos.

INTRODUCTION

Incisor enamel microstructure is an important character for phylogeny and systematics in Rodentia (Korvenkontio, 1934; Koenigswald, 1980; Martin, 1993, 1997). The enlarged and ever-growing dI^2/dI_2 (Luckett, 1993) of rodents are highly modified teeth adapted for high stresses, which is reflected by a very complex enamel microstructure (Fig. 1) that is unparalleled among mammals. Mammalian tooth enamel consists of needlelike hydroxyapatite crystallites that are a few micrometers long. In most nonholotherian Mesozoic mammals, the hydroxyapatite crystallites are oriented perpendicular to the enamel–dentine junction (EDJ) and are arranged more or less parallel to each other (Sander, 1997). In Holotheria, first known in Late Jurassic Dryolestidae (Martin, 1999b), the crystallites are bundled into fiberlike elements of 3–5 μm diameter known as enamel prisms (Lester and Koenigswald, 1989; Wood and Stern, 1997). Enamel prisms originate at the EDJ and run through the entire enamel thickness to the outer enamel surface (OES). The current model holds that each enamel prism is formed by a single cell (ameloblast) during its migration from the basal membrane to the OES (Moss-Salentijn et al., 1997).

Enamel prisms are an important innovation in the evolutionary history of mammalian teeth because ameloblasts construct composite enamel tissue (Pfretzschner, 1988). In Mesozoic Holotheria and many other basal mammals, the enamel prisms are embedded in a thick matrix of crystallites, which are oriented parallel to each other but are not bundled. The crystallites form the so-called interprismatic matrix (IPM). In these early mammals, enamel prisms run parallel to each other from the EDJ to the OES, and the IPM crystallites run parallel to the prism long axes. This enamel type is called radial enamel and characterizes, besides Mesozoic Holotheria, many Paleogene mammals and some Recent mammals as well [e.g., Lipotyphla and

---

[1] Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin, Malteserstraße 74-100, D-12249 Berlin, Germany. Email: tmartin@zedat.fu-berlin.de

Science Series, Number 40, pp. 131–140
Natural History Museum of Los Angeles County, 2004

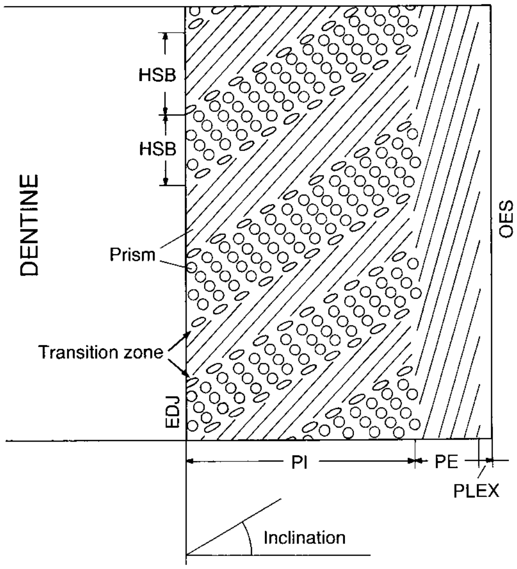


Figure 1 Schematic drawing of rodent incisor enamel as seen in longitudinal section. The tip of the incisor is pointing upward. EDJ, enamel–dentine junction; HSB, Hunter–Schreger band; OES, outer enamel surface; PE, portio externa; PI, portio interna; PLEX, prismless external layer (after Martin, 1999a).

Chiroptera (Koenigswald, 1997)]. When eutherian teeth reach a certain size or are exposed to an increased stress pattern (e.g., crushing and grinding), enamel microstructure acquires a higher level of complexity (Koenigswald et al., 1987). Decussating enamel prisms strengthen the enamel and increase its resistance against crack propagation (Pfretzschner, 1988). Decussating prisms are arranged in layers that generally are 10–15 prisms thick (Koenigswald and Pfretzschner, 1987). Within one layer, the prisms run parallel to each other; in adjacent layers, they decussate at a high angle (about 90 degrees). The prism layers are oriented parallel to the occlusal surface and surround the tooth crown. In longitudinal section, they appear as bands, which are referred to as Hunter–Schreger bands (HSB).

In the highly specialized, ever-growing incisors of rodents, enamel covers only the anterior surface of the tooth (Figs. 1, 2). Together with the softer, underlying dentine that wears at a faster rate, the enamel cover forms a self-sharpening cutting edge. Because of the high stresses incisor enamel experiences during gnawing, the enamel microstructure reaches a very high level of complexity. In general, rodent incisor HSB are thinner than those of other mammals. Rodent incisor enamel microstructure evolved independently from that of the cheek teeth (Koenigswald and Clemens, 1992), and it is particularly useful for phylogenetic studies because incisor form and function are very similar in different rodent groups in comparison to rodent cheek teeth.

On the basis of HSB thickness, Korvenkontio (1934) distinguished in rodent incisors three types of HSB: multiserial, pauciserial, and uniserial. Multiserial HSB are three to seven prisms wide, pauciserial one to six (average three prisms), and uniserial only one prism thick (Martin, 1993). Major groups of Rodentia can be characterized roughly by HSB type: for example, hystricognaths by multiserial HSB, paramyids and ischyromyids by pauciserial HSB, and myomorphs by uniserial HSB. On the basis of HSB thickness, Korvenkontio (1934) interpreted multiserial HSB as the most primitive, and pauciserial and uniserial as more derived enamel types. Later, Martin (1992, 1993) demonstrated that pauciserial HSB are the most primitive condition and that structural characters such as orientation and thickness of the IPM are crucial for assessing primitive and derived stages. The HSB thickness alone is of little value.

A plesiomorphic condition is thick IPM surrounding each single enamel prism and running parallel to the prism long axes. This IPM orientation characterizes pauciserial HSB and is found in the most basal rodents, such as early Paleogene ischyromyids and ctenodactyloids, as well as in the outgroup [e.g., Paleocene condylarths (Koenigswald et al., 1987)]. Other characters of pauciserial HSB include the low inclination of HSB, missing transition zones, and low enamel thickness [for details, see Martin (1993)].

In uniserial HSB, band thickness is reduced to a single prism. So far, this highly derived enamel type has been detected only in Rodentia, where it characterizes sciurids, myomorphs, geomyoids, glirids, and certain theridomyids (Koenigswald, 1980; Martin, 1999a; Kalthoff, 2000).

In multiserial HSB, the number of prisms may be slightly increased compared with pauciserial HSB, but mostly overlaps the same range (three to five prisms per band). This demonstrates that HSB thickness is not a suitable character for distinction between pauciserial and multiserial HSB. The most important difference is the orientation of the IPM, which runs at an angle to prism long axes in multiserial HSB. In rare cases, the IPM may run parallel to prism long axes, but in those instances, it is much thinner than in pauciserial HSB, and it does not surround each single prism. Another important character of multiserial HSB is the presence of transition zones between HSB (Wahlert, 1984; Koenigswald and Pfretzschner, 1987), where prisms switch from one HSB to the next higher on their way from the EDJ to the OES (Fig. 1). Multiserial HSB characterize hystricognath rodents, such as caviomorphs, Thryonomyoidea, Pedetidae, and derived Ctenodactyloidea (Martin, 1992, 1993, 1995). Within caviomorphs, the Octodontoidea are characterized by a plate-like IPM, which runs at a right angle to the prisms. This enamel type is considered to be the most derived on the basis of biomechanical considerations and evolutionary occurrence.

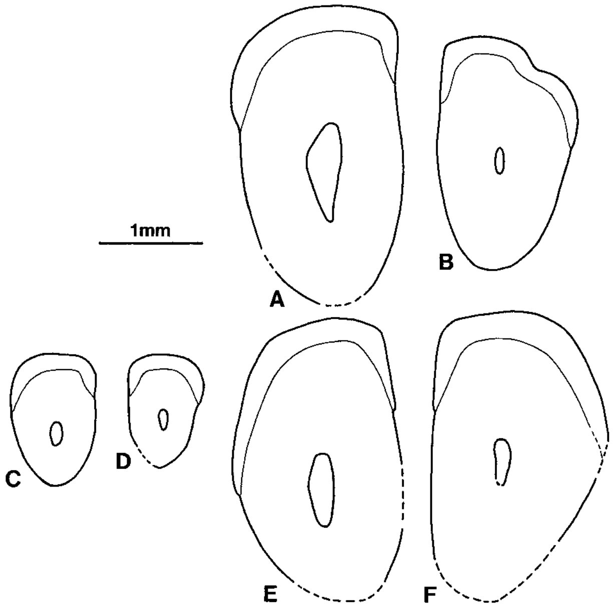


Figure 2 Cross sections of rodent incisors from Santa Rosa. **A,** LACM 145444, upper; **B,** LACM 145447, upper; **C,** LACM 145446, lower; **D,** LACM 145445, lower; **E,** LACM 145442, lower; **F,** LACM 145443, lower. (Drawing by M. Bulang-Lörcher).

METHODS AND MATERIALS

The enamel preparation technique has been described in detail elsewhere (Martin, 1992, 1993). Small pieces of rodent incisors a few millimeters long were embedded in polyester resin. Enamel samples were cut in longitudinal and cross section, ground, polished, and subsequently etched with 2 N hydrochloric acid for 2–4 seconds to make morphological details visible. After rinsing and drying, samples were sputter-coated with gold and studied with a scanning electron microscope (SEM) at magnifications between ×500 and ×2000. The enamel samples are housed in the author's enamel collection under the reference numbers given (MA plus number). For a glossary of terms see Koenigswald and Sander (1997) and Martin (1999a).

Rodent incisors (Fig. 2) studied from the ?Eocene Santa Rosa locality, Natural History Museum of Los Angeles County (LACM) locality 6789 (collected by K.E. Campbell, C.D. Frailey, and L. Romero-Pitman; July 1995): LACM 145442, left lower incisor, MA 259; LACM 145443, left lower incisor, MA 260; LACM 145444, right upper incisor, MA 261; LACM 145445, right lower incisor, MA 262; LACM 145446, right lower incisor, MA 263; LACM 145447, right upper incisor, MA 264.

RESULTS

INCISOR MORPHOLOGY

Among the incisors, three size classes can be distinguished (Fig. 2). Upper incisor LACM 145444 (Fig. 2A) (anterior–posterior diameter 2.9 mm) and lower incisors LACM 145442 and 145443 (Figs. 2E–F; diameter of both about 2.8 mm) belong to the largest group. They are very similar in cross-sectional shape and are characterized by the strong overlap of the enamel cover on the lateral side. Upper incisor LACM 145447 (Fig. 2B) is slightly smaller (diameter 2.5 mm) and characterized by a groove on the lateral part of the enamel cover that appears as an enamel indentation in cross section. Lower incisors LACM 145446 (Fig. 2C; diameter 1.25 mm) and LACM 145445 (Fig. 2D; diameter 1.1 mm) are much smaller, and their enamel cover does not extend very far on the lateral side.

ENAMEL MICROSTRUCTURE

Upper Incisors (Table 1)

LACM 145444 (MA 261). Incisor enamel is two-layered (Figs. 3A–B) with multiserial HSB in the portio interna (PI; Fig. 1) and radial enamel in the portio externa (PE; Fig. 1). HSB comprise three to five prisms, and the thin IPM runs parallel to the prism long axes. Transition zones between HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB are inclined 20 degrees apically. In the PE, inclination of prisms is 55 degrees. Enamel thickness is 235 μm, and PE composes 15–20 percent of the entire enamel thickness (42–48 μm). A prismless external layer (PLEX; Fig. 1) is missing.

LACM 145447 (MA 264). Incisor enamel is two-

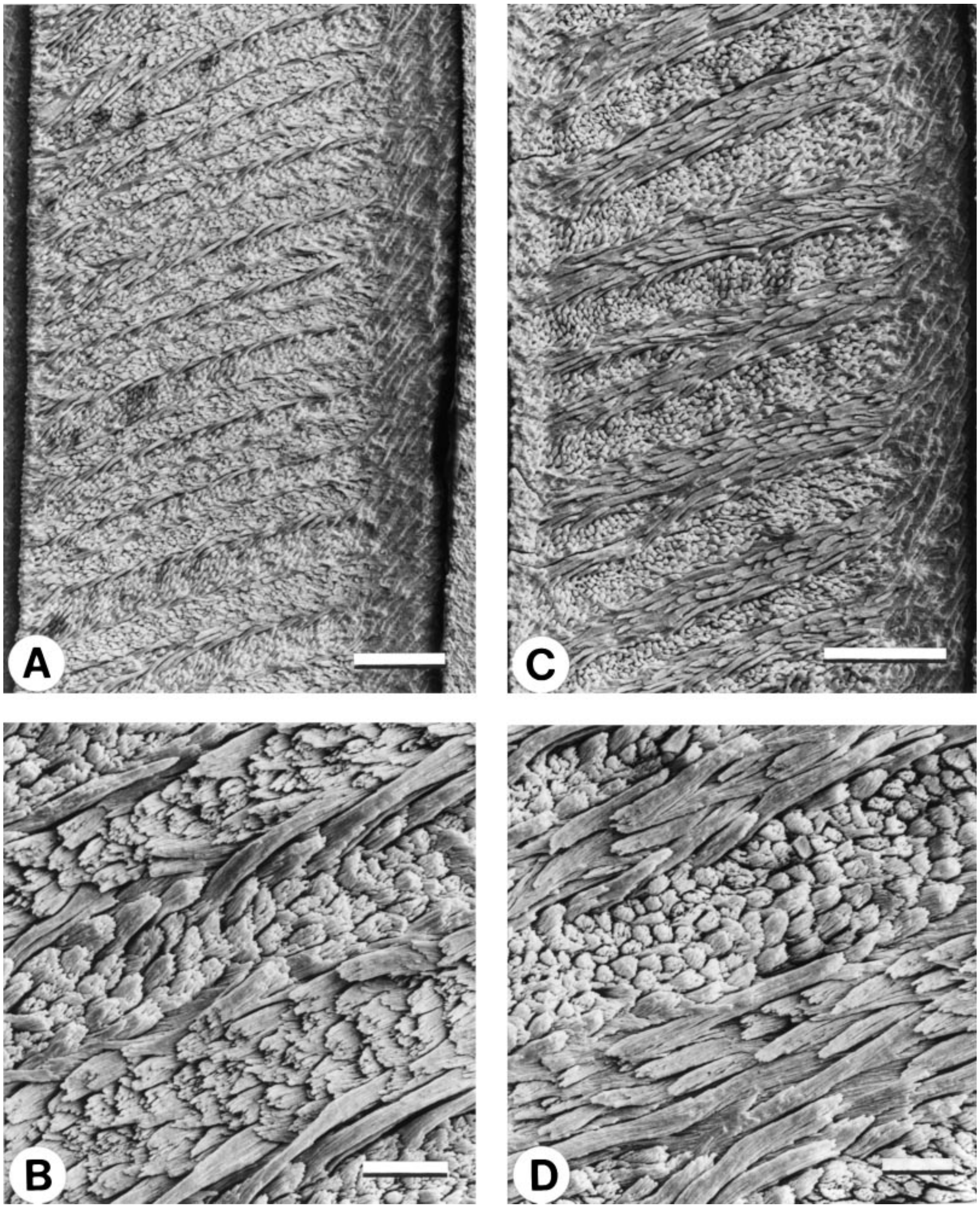


Figure 3 SEM micrographs of incisor enamel longitudinal sections of upper rodent incisors from Santa Rosa. In all sections, EDJ (enamel–dentine junction) is to the left and the tip of the incisor is to the top. **A,** LACM 145444 (MA 261), overview, scale bar = 50 μm; **B,** LACM 145444 (MA 261), detail of PI (portio interna) with HSB (Hunter–Schreger bands); thin IPM (interprismatic matrix) runs parallel to the prism long axes, scale bar = 10 μm; **C,** LACM 145447 (MA 264), overview, scale bar = 50 μm; **D,** LACM 145447 (MA 264), detail of PI with HSB; thin IPM runs at a small angle or parallel to the prism long axes, scale bar = 10 μm.

layered with multiserial HSB in the PI and radial enamel in the PE (Figs. 3C–D). HSB comprise three to six prisms, and the thin IPM runs at a very acute angle or parallel to the prism long axes. Transition zones between the HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB inclination is 15–20 degrees. In the PE, prisms are inclined 55 degrees apically. Enamel thickness is 190 μm, and PE composes 15 percent of the entire enamel thickness (30 μm). A PLEX is missing. The outer surface of the enamel layer is not smooth, but bears a groove on the lateral side that is clearly visible in the overview of the incisor cross section (Fig. 2B). The groove has no influence on the enamel microstructure.

Lower Incisors (Table 1)

LACM 145446 (MA 263). Incisor enamel is two-layered with multiserial HSB in the PI and radial enamel in the PE (Figs. 4A–B). HSB comprise three to four prisms, and IPM runs at a very low angle to the prism long axes and anastomoses regularly. Transition zones between the HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB inclination is 40 degrees, and, in the PE, prisms are inclined 65 degrees apically. Enamel thickness is 135 μm, and PE composes 20 percent of the entire enamel thickness.

LACM 145445 (MA 262). Incisor enamel is two-layered with multiserial HSB in the PI and radial enamel in the PE (Figs. 4C–D). HSB comprise three to four prisms, and IPM runs at an acute angle to the prism long axes and anastomoses regularly. Transition zones between adjacent HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB inclination is 35 degrees, and, in the PE, prisms are inclined 65 degrees apically. Enamel thickness is 130 μm, and PE composes only 15 percent of the entire enamel thickness (20 μm). A PLEX is missing.

LACM 145442 (MA 259). Incisor enamel is two-layered with multiserial HSB in the PI and radial enamel in the PE (Figs. 5A–B). HSB comprise three to four prisms, and the platelike IPM runs at a right angle to the prism long axes and anastomoses only accidentally. Transition zones between the HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB inclination is 35 degrees, and, in the PE, prisms are inclined very steeply (70 degrees) apically. Enamel thickness is 230 μm, and the thin PE composes only 15 percent of the entire enamel thickness (35 μm). A PLEX is missing.

LACM 145443 (MA 260). Incisor enamel is two-layered with multiserial HSB in the PI and radial enamel in the PE (Figs. 5C–D). HSB comprise three to four prisms, and the plate-like IPM runs at a right angle to the prism long axes and anastomoses only accidentally. Transition zones between the HSB are well developed. Prism cross sections are oval in the PI and lancet-shaped in the PE. HSB inclination is 25 degrees, and, in the PE, prisms are inclined very steeply apically (70 degrees). Enamel thickness is 240 μm, and the thin PE composes only 12–15 percent of the entire enamel thickness (30 μm). A thin PLEX is present.

DISCUSSION

The Santa Rosa rodents play a crucial role in our understanding of the origin and diversification of caviomorphs because they likely represent the old-

Table 1 Incisor enamel features of the specimens from Santa Rosa.

Specimen number	Incisor	Schmelzmuster	Prisms per HSB	Inclination of HSB (deg)	Enamel thickness (μm)	Percentage of PE thickness	PE prism inclination (deg)	IPM in PI
LACM 145444	Upper	Multiserial	3–5	20	235	15–20	55	Parallel
LACM 145447	Upper	Multiserial	3–6	15–20	190	15	55	Parallel to acute angular
LACM 145446	Lower	Multiserial	3–4	40	135	20	65	Parallel to acute angular
LACM 145445	Lower	Multiserial	3–4	35	130	15	65	Acute angular
LACM 145442	Lower	Multiserial	3–4	35	230	15	70	Rectangular
LACM 145443	Lower	Multiserial	3–4	25	240	12–15	70	Rectangular

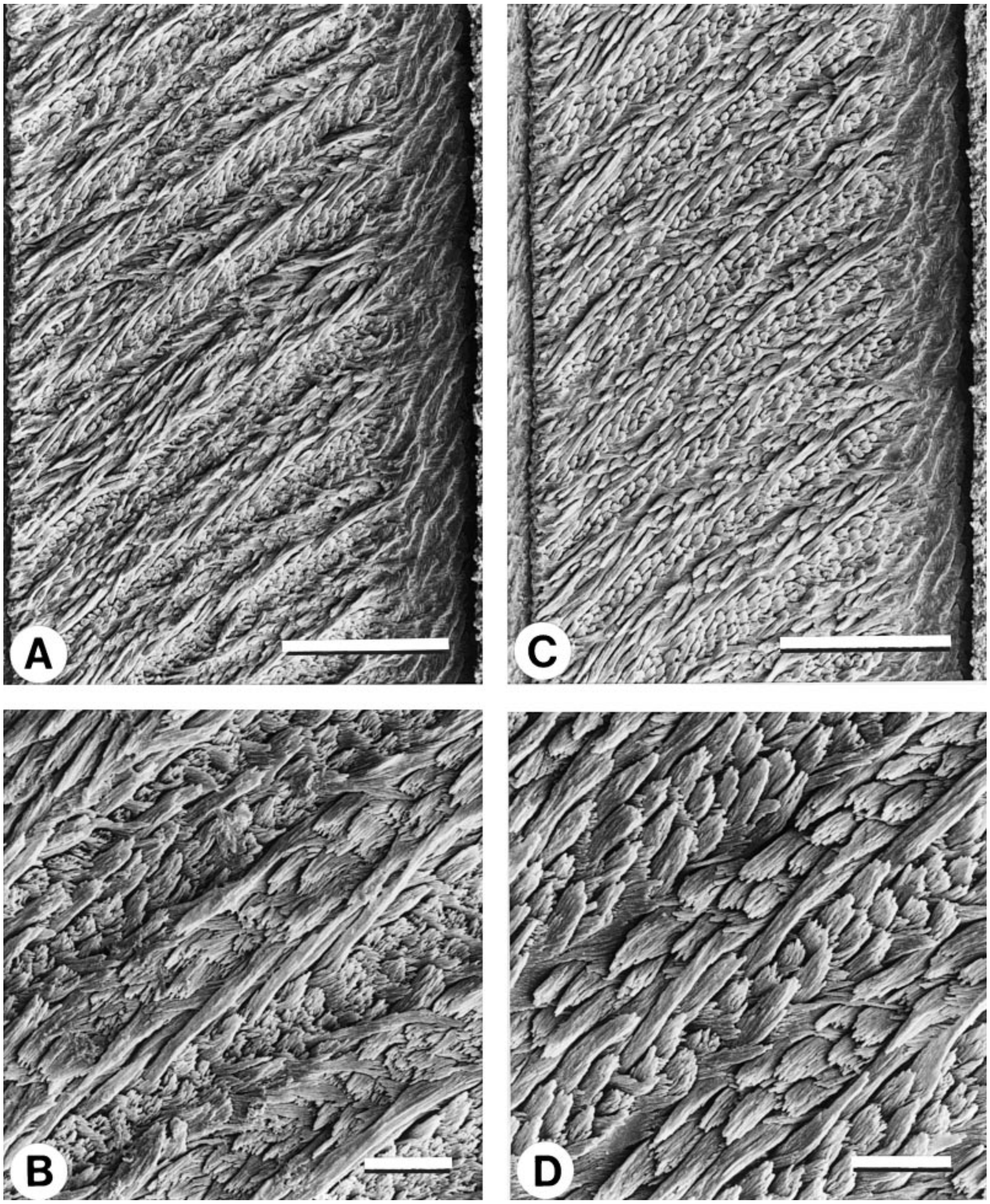


Figure 4 SEM micrographs of incisor enamel longitudinal sections of lower rodent incisors from Santa Rosa. In all sections, EDJ (enamel–dentine junction) is to the left and the tip of the incisor is to the top. **A,** LACM 145446 (MA 263), overview; scale bar = 50 μm; **B,** LACM 145446 (MA 263), detail of PI (portio interna) with multiserial HSB (Hunter–Schreger bands); IPM (interprismatic matrix) runs at an acute angle to the prism long axes and anastomoses regularly, scale bar = 10 μm; **C,** LACM 145445 (MA 262), overview, scale bar = 50 μm; **D,** LACM 145445 (MA 262), detail of PI with multiserial HSB; IPM runs at an acute angle to the prism long axes and anastomoses regularly, scale bar = 10 μm.

est rodents known from South America. There has been a long-standing discussion on the origin of the South American caviomorphs (see Frailey and Campbell, 2004) because South America was an island continent during the late Mesozoic and most of the Cenozoic eras. Historically, caviomorph rodents seemed to appear suddenly in the fossil record together with platyrrhine primates during the Deseadan South American Land Mammal Age (SALMA; Simpson, 1980), which was for a long time

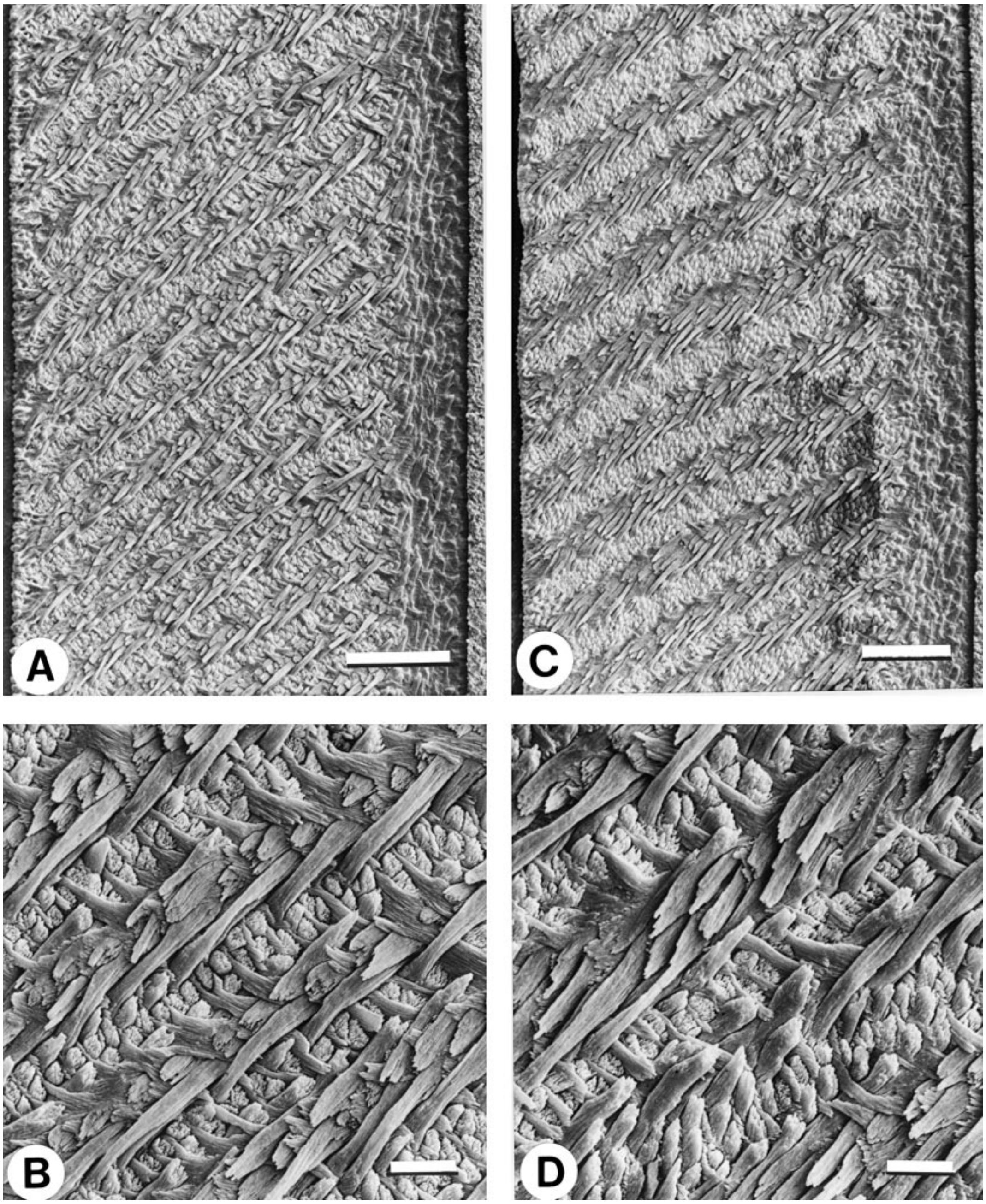


Figure 5 SEM micrographs of incisor enamel longitudinal sections of lower rodent incisors from Santa Rosa. In all sections, EDJ (enamel–dentine junction) is to the left and the tip of the incisor is to the top. **A,** LACM 145442 (MA 259), overview, scale bar = 50 μm; **B,** LACM 145442 (MA 259), detail of PI (portio interna) with multiserial HSB (Hunter–Schreger bands); plate-like IPM (interprismatic matrix) runs at a right angle to the prism long axes and does not anastomose, scale bar = 10 μm; **C,** LACM 145443 (MA 260), overview, scale bar = 50 μm; **D,** LACM 145443 (MA 260), detail of PI with multiserial HSB; plate-like IPM runs at a right angle to the prism long axes and does not anastomose, scale bar = 10 μm.

regarded as early Oligocene, but which more recently has been placed in the late Oligocene to early Miocene (MacFadden et al., 1985) or late early Oligocene to early Miocene (Marshall et al., 1986). The level of the Salla beds in Bolivia, from which the earliest platyrrhine primate *Branisella* comes, is now dated between 27.02 and 25.82 Ma (Kay et al., 1998), and those authors place all of the fossiliferous Salla beds in the Oligocene. Recently, a mandible of a supposed dasyproctid from Tinguiririca (Chile) has been described (Wyss et al., 1993), which predates the Deseadan level and has been dated radiometrically at 31.5 Ma, possibly extending back to ~37.5 Ma (early Oligocene or late Eocene). The Santa Rosa local fauna of eastern Peru is the first known Paleogene mammalian paleofauna of tropical South America. On the basis of the evolutionary stage of the marsupials (Goin and Candela, 2004) and rodents (Frailey and Campbell, 2004), the age of the Santa Rosa local fauna is placed at late Eocene (Mustersan SALMA) or, less probably, early Oligocene (post-Mustersan, pre-"Tinguirirican" age), following the change in the age of the Mustersan SALMA by Kay et al. (1999). The Santa Rosa local fauna was collected from fine- to coarse-grained bed load or channel deposits within massive red bed clays that are exposed in the left bank of the Rio Yurúa, approximately 7 km north of Breu and 7.5 km south of the Brazilian border, Departamento de Ucayali, Peru. The source red beds are tentatively referred to the Paleocene–Eocene Yahuarango Formation (Campbell et al., 2004).

Two classical hypotheses have been put forward for the origin of caviomorphs. Either they are descendants of North American ischyromyids (Wood and Patterson, 1959; Wood, 1981, 1985; Patterson and Wood, 1982) or African Thryonomyoidea ("Phiomorpha")(Lavocat, 1969, 1971, 1974). On the basis of a study of incisor enamel microstructure, Martin (1992, 1994) presented a clear case for the origin of caviomorphs from Paleogene Thryonomyoidea because both share the same derived characters of multiserial schmelzmuster in the incisors. In this regard, the incisor enamel microstructure of the Santa Rosan rodents plays a crucial role because, as the oldest South American rodents known so far, they give valuable information on the evolutionary history of caviomorph schmelzmuster. All rodent incisors from Santa Rosa studied to date exhibit a double-layered enamel with multiserial HSB, which is typical for caviomorph rodents (Martin, 1992). Among the six investigated incisors, all three subtypes of multiserial HSB are present, which are also observed in Oligocene and younger caviomorphs. This indicates that the ?Eocene Santa Rosa rodent fauna was already diversified. The observations at the enamel microstructure level are also supported by the macromorphological diversity of the investigated incisors; at least three groups can be distinguished (Fig. 2) by differences in size and shape.

The incisor enamel schmelzmuster observed in the Santa Rosan rodents are by no means more primitive than those of Deseadan SALMA or later caviomorphs (Martin, 1992). None of the Santa Rosan incisors exhibit pauciserial HSB or a schmelzmuster transitional from the pauciserial to the multiserial condition. This supports the hypothesis that the caviomorph ancestors are descendants of an African stock belonging to the stem lineage of Thryonomyoidea and caviomorphs (Martin, 1992, 1994) and that the first African immigrants into South America introduced the multiserial schmelzmuster. Outside of South America, Eocene–Oligocene stem lineage representatives of African Thryonomyoidea, advanced Ctenodactyloidea, and Pedetidae are the only rodents showing schmelzmuster with multiserial HSB in the incisors (Martin, 1992, 1994). Northern Hemisphere Ischyromyoidea are characterized by more primitive schmelzmuster with pauciserial HSB, and in this clade, a multiserial schmelzmuster never evolved (Martin, 1993).

Among caviomorph rodents, the superfamily Octodontoidea (comprising Octodontidae, Ctenomyidae, Abrocomidae, Echimyidae, Capromyidae, and Myocastoridae) is characterized by the presence of rectangular, plate-like IPM in the HSB (Martin, 1992). It is considered the most derived type of HSB on the basis of biomechanical considerations and evolutionary occurrence. This derived enamel subtype was found in two of the Santa Rosan incisors (LACM 145442 and 145443; Fig. 5), which also are very similar to each other in size and gross morphology (possibly belonging to the same species), indicating that members of the Octodontoidea were already present. Other typical characters of the octodontoid incisor schmelzmuster that were observed in the specimens from Santa Rosa are the high inclinations of HSB in the PI and of the radially oriented prisms in the PE.

The diversity of the incisor schmelzmuster found in the rodents from Santa Rosa makes it probable that the immigration event took place a considerable time span before that stratigraphic level. Depending on the age of the Santa Rosa local fauna, an early or middle Eocene age for the arrival of the immigrants could be projected. However, the oldest record of multiserial HSB in African "phiomorph" incisors from Bir el Ater, Algeria (Martin, 1993), is late Eocene (Jaeger et al., 1985). In the Bir el Ater "phiomorphs," only multiserial HSB with acute angular IPM have been detected; the first multiserial HSB with rectangular, plate-like IPM appear in late Eocene/early Oligocene "phiomorphs" from the Fayum (Martin, 1992). Another possibility for the origin of caviomorphs in South America is the assumption of several waves of immigration of African ancestors shortly before the Santa Rosan level. In this case, it would have to be assumed that the caviomorph stem-lineage immigrants were taxonomically diverse and that they already possessed different subtypes of multiserial HSB.

A different hypothesis for the origin of caviomorphs is presented by Frailey and Campbell (2004). From among the many, mainly isolated rodent teeth from Santa Rosa, they distinguish at least eight genera with possibly 17 species in three families (Erethizontidae, Agoutidae, and Echimyidae). According to the advanced molar morphology of the Santa Rosan caviomorphs, compared with contemporaneous rodents from other parts of the world (e.g., a four-crested molar pattern), an early separation of the caviomorph lineage (late Cretaceous or, at the latest, early Paleocene) is postulated. The caviomorphs are regarded as an autochthonous South American group that had been separated by the breakup of Gondwanaland from a common Gondwanan stock. In this case, the similarities between South American and African hystricognaths (including enamel microstructure characters) would be the result of a once common gene pool.

ACKNOWLEDGMENTS

I thank K.E. Campbell, Natural History Museum of Los Angeles County, for providing the rodent incisors from Santa Rosa for study and for the invitation to contribute to this volume. He and C.D. Frailey permitted me to cite from their chapters in this volume on the geology and rodent fauna of Santa Rosa. I thank Francisco Goin for providing a Spanish translation of the abstract. L. Flynn, W.v. Koenigswald, and J.H. Wahlert gave useful comments on the manuscript. This study was supported by a Heisenberg grant from the Deutsche Forschungsgemeinschaft (Ma 1643/5-1).

LITERATURE CITED

Campbell, K.E., C.D. Frailey, and L. Romero-Pittman. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Frailey, C.D., and K.E. Campbell. 2004. Paleogene rodents from Amazonian Peru: The Santa Rosa local fauna. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 71–130.

Goin, F.J., and A. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Perú. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Jaeger, J.-J., C. Denys, and B. Coiffait. 1985. New Phiomorpha and Anomaluridae from the late Eocene of north-west Africa: Phylogenetic implications. In *Evolutionary relationships among rodents,* ed. W.P. Luckett and J.-L. Hartenberger, 567–588. New York: Plenum Press.

Kalthoff, D.C. 2000. Die Schmelzmikrostruktur in den Inzisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). *Palaeontographica A* 259:1–193.

Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G.H. Re, M. Heizler, and H. Sandeman. 1999. Revised age of the Casamayoran South American Land Mammal "Age"—Climatic and biotic implications. *Proceedings of the National Academy of Sciences, Washington* 96(23):13235–13240.

Kay, R.F., B.J. McFadden, R.H. Madden, H. Sandeman, and F. Anaya. 1998. Revised age of the Salla beds, Bolivia, and its bearing on the age of the Deseadan South American Land Mammal "Age." *Journal of Vertebrate Paleontology* 18:189–199.

Koenigswald, W.v. 1980. Schmelzmuster und Morphologie in den Molaren der Arvicolidae (Rodentia). *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 539:1–129.

———. 1997. Brief survey of enamel diversity at the schmelzmuster level in Cenozoic placental mammals. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 137–161. Rotterdam: Balkema.

Koenigswald, W.v., and W.A. Clemens. 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scanning Microscopy* 6:195–218.

Koenigswald, W.v., and H.U. Pfretzschner. 1987. Hunter–Schreger-Bänder im Zahnschmelz von Säugetieren (Mammalia), Anordnung und Prismenverlauf. *Zoomorphology* 106:329–338.

Koenigswald, W.v., J.M. Rensberger, and H.U. Pfretzschner. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* 328:150–152.

Koenigswald, W.v., and P.M. Sander. 1997. Glossary of terms used for enamel microstructures. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 267–280. Rotterdam: Balkema.

Korvenkontio, V.A. 1934. Mikroskopische Untersuchungen an Nagerincisiven, unter Hinweis auf die Schmelzstruktur der Backenzähne. *Annales Zoologici Societatis Zoologicae-Botanicae Fennica Vanamo* 2:1–274.

Lavocat, R. 1969. La systématique des rongeurs hystricomorphes et la dérive des continents. *Comptes Rendus de l'Academie Scientifique, Paris D* 269:1496–1497.

———. 1971. Affinités systématiques des caviomorphes et des phiomorphes et origine africaine des caviomorphes. *Anais da Academia Brasiliera de Ciencias* 43(Suppl.):515–522.

———. 1974. The interrelationships between the African and South American rodents and their bearing on the problem of the origin of South American monkeys. *Journal of Human Evolution* 3:323–326.

Lester, K.S., and W.v. Koenigswald. 1989. Crystallite orientation discontinuities and the evolution of mammalian enamel or, when is a prism? *Scanning Microscopy* 3:645–663.

Luckett, W.P. 1993. An ontogenetic assessment of dental homologies in therian mammals. In *Mammal phylogeny, Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials,* ed. F.S. Szalay, M.J. Novacek, and M.C. McKenna, 182–204. Berlin, New York, Heidelberg: Springer-Verlag.

MacFadden, B., K.E. Campbell, R.L. Cifelli, O. Siles, N.M. Johnson, C.W. Naeser, and P.K. Zeitler. 1985. Magnetic polarity stratigraphy and mammalian fauna of the Deseadan (late Oligocene–early Miocene) Salla beds of northern Bolivia. *Journal of Geology* 93:223–250.

Marshall, L.G., R.L. Cifelli, R.E. Drake, and G.H. Curtis. 1986. Vertebrate paleontology, geology, and geochronology of the Tapera de Lopez and Scarritt Pocket, Chubut Province, Argentina. *Journal of Paleontology* 60:920–951.

Martin, T. 1992. Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire,* 1–168.

———. 1993. Early rodent incisor enamel evolution: Phylogenetic implications. *Journal of Mammalian Evolution* 1:227–253.

———. 1994. African origin of caviomorph rodents is indicated by incisor enamel microstructure. *Paleobiology* 20:5–13.

———. 1995. Incisor enamel microstructure and phylogenetic interrelationships of Pedetidae and Ctenodactyloidea (Rodentia). *Berliner geowissenschaftliche Abhandlungen E* 16:693–707.

———. 1997. Incisor enamel microstructure and systematics in rodents. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 163–175. Rotterdam: Balkema.

———. 1999a. Evolution of incisor enamel microstructure in Theridomyidae (Rodentia). *Journal of Vertebrate Paleontology* 19:550–565.

———. 1999b. Dryolestidae (Dryolestida, Mammalia) aus dem Oberen Jura von Portugal. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 550:1–119.

Moss-Salentijn, L., M.L. Moss, and M.S. Yuan. 1997. The ontogeny of mammalian enamel. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 5–30. Rotterdam: Balkema.

Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149:371–543.

Pfretzschner, H.U. 1988. Structural reinforcement and crack propagation in enamel. In *Teeth revisited: Proceedings of the VII International Symposium on Dental Morphology.* Paris 1986, ed. D.E. Russell, J.P. Santoro, and D. Sigogneau-Russell. *Mémoirs du Muséum national d'Histoire naturelle C* 53:133–143.

Sander, P.M. 1997. Non-mammalian synapsid enamel and the origin of mammalian enamel prisms: The bottom-up perspective. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 41–62. Rotterdam: Balkema.

Simpson, G.G. 1980. *Splendid isolation: The curious history of South American mammals.* New Haven: Yale University Press, 266 pp.

Wahlert, J.H. 1984. Hystricomorphs, the oldest branch of the Rodentia. *Annals of the New York Academy of Sciences* 435:356–357.

Wood, A.E. 1981. The origin of the caviomorph rodents from a source in middle America: A clue to the area of origin of the platyrrhine primates. In *Evolutionary biology of the New World monkeys and continental drift,* ed. R.L. Ciochon and A.B. Chiarelli, 79–91. New York: Plenum Press.

———. 1985. The relationships, origin, and dispersal of the hystricognathous rodents. In *Evolutionary biology among rodents,* ed. W.P. Luckett and J.-L. Hartenberger, 475–513. New York: Plenum Press.

Wood, A.E., and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120:282–428.

Wood, C.B., and D.N. Stern. 1997. The earliest prisms in mammalian and reptilian enamel. In *Tooth enamel microstructure,* ed. W.v. Koenigswald and P.M. Sander, 63–84. Rotterdam: Balkema.

Wyss, A.E., J.F. Flynn, M.A. Norell, C.C. Swisher III, R. Charrier, M.J. Novacek, and M.C. McKenna. 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. *Nature* 365: 434–437.

Received 2 July 2003; accepted 29 December 2003.

A Possible Bat (Mammalia: Chiroptera) from the ?Eocene of Amazonian Perú

Nicholas J. Czaplewski[1] and Kenneth E. Campbell, Jr.[2]

ABSTRACT. An isolated, tribosphenic lower molar was recovered by screen-washing lowland, continental deposits of probable Eocene age along the Río Yurúa in eastern Perú. The tooth appears to represent a member of the Chiroptera, and it shows similarities to the teeth of species of the family Noctilionidae, but it is incomplete and insufficient for a familial identification. It forms part of the Santa Rosa local fauna, the first known Paleogene mammalian fauna from Amazonia. If correctly identified, the specimen is the oldest known fossil bat in South America and only the third record of a bat from the Paleogene of that continent.

RESUMEN. A partir del lavado de muestras sedimentarias de depósitos continentales de probable edad eocena, procedentes del Río Yurúa en el este del Perú, ha sido recuperado un molar tribosfénico aislado. El diente parece representar a un miembro de los Chiroptera y muestra similitudes con aquéllos de las especies de Noctilionidae, si bien el resto es incompleto e insuficiente como para asegurar su identificación familiar. Forma parte de la fauna local de Santa Rosa, la primera fauna de mamíferos conocida para el Paleógeno de la Amazonia. Si el ejemplar ha sido correctamente identificado, constituye el murciélago más antiguo conocido para América del Sur y el tercer registro de un murciélago paleógeno para este continente.

INTRODUCTION

Small mammals are relatively unknown as fossils in Cenozoic deposits of lowland tropical South America. Previously, only the middle Miocene beds at La Venta, Colombia (Kay et al., 1997), and the upper Miocene Acre Conglomerate of southwestern Amazonia (Frailey, 1986; Kay and Frailey, 1993; Czaplewski, 1996) have produced large numbers of tiny bones and teeth of small vertebrates ("microvertebrates"), including marsupials, primates, bats, and rodents. However, the technique of screen-washing to recover microvertebrates is just beginning to be applied on a wider scale to South American sedimentary deposits. Even for large mammals, relatively few specimens are known from the tropical portion of the continent (see faunal list for western Amazonia in Campbell et al., 2000). For the Paleogene, previous records of microvertebrates from the lowland tropics are virtually nonexistent.

The remains of vertebrates were discovered at Santa Rosa in 1995 in the left bank of the Río Yurúa near its confluence with the Río Beu (Campbell et al., 2004). The locality is at 9°29′39″ S, 72°45′48″ W, approximately 7 km (by air) north of Breu and 7.5 km (by air) south of the Perú–Brazil border (see Campbell et al., 2004:fig. 1). The elevation is about 215 m above mean sea level. A preliminary sample of sediments from the locality was processed by screen washing and yielded hundreds of rodent and marsupial teeth and jaws, prompting a return visit to the locality in 1998 to collect additional concentrated matrix (Campbell et al., 2004). The fossiliferous deposits occur as small fluvial lenses (<30 cm thick) in a cutbank consisting of about 5 m of red clay unconformably overlain by buff sands. The fluvial lenses contain coarse sand, calcareous nodules, and clay pebbles. The stage of evolution of certain of the other vertebrate fossil groups in the Santa Rosa fauna, especially the marsupials and rodents, suggests a probable late Eocene age for the fauna (Frailey and Campbell, 2004; Goin and Candela, 2004), and the beds in which the fossils occur at the Santa Rosa locality are interpreted as belonging to the Paleocene–Eocene Yahuarango Formation (Campbell et al., 2004).

Among the microvertebrate materials screen-washed from the Santa Rosa locality is an enigmatic tooth from a tiny, insectivorous mammal. Although the specimen is damaged, it is important for its geologic age, its occurrence in the Amazon Basin, and the possibility that it might represent the oldest fossil bat from South America. Only two Paleogene bats have previously been reported from South America. An incomplete skeleton of the molossid bat *Mormopterus faustoi* Paula Couto, 1956,

---

[1] Oklahoma Museum of Natural History, 2401 Chautauqua Avenue, and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73072-7029. Email: nczaplewski@ou.edu

[2] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: kcampbel@nhm.org

Science Series, Number 40, pp. 141–144
Natural History Museum of Los Angeles County, 2004

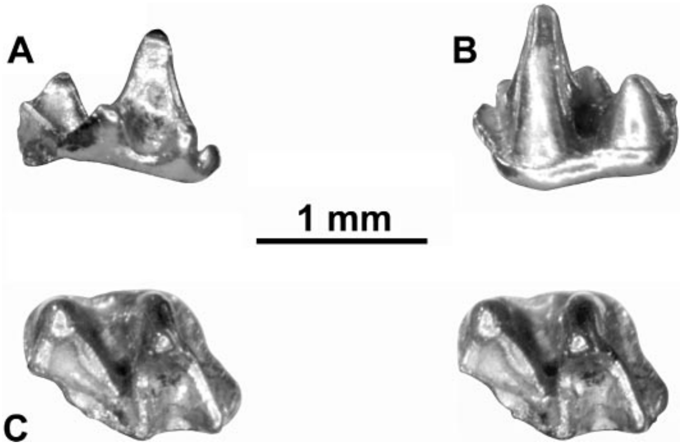


Figure 1 Left lower molar (LACM 140623) attributed to Chiroptera from the Santa Rosa local fauna, Perú. **A,** lingual view; **B,** labial view; **C,** occlusal view (stereo pair).

was reported from the bituminous shales of the Upper Oligocene Tremembé Formation in southeastern Brazil (Paula Couto, 1956, 1983; Paula Couto and Mezzalira, 1971; Legendre, 1984, 1985). A second skeleton of a bat was also reported from the Tremembé Formation (Leonardos, 1924; Mezzalira, 1964, 1966, 1989), but its familial identity is indeterminate (Czaplewski, personal observation). Although the second Tremembé skeleton is more nearly complete than that of *M. faustoi,* it is crushed, and only small fragments of the teeth remain. The Tremembé specimens are considered to be of the Deseadan South American Land Mammal Age (SALMA).

SYSTEMATIC PALEONTOLOGY

Infraclass Eutheria Huxley, 1880

Order Chiroptera Blumenbach, 1779

Family, Genus, and Species Indeterminate

Figure 1

SPECIMEN. Natural History Museum of Los Angeles County (LACM) 140623, left lower molar.

LOCALITY AND AGE. Santa Rosa, Río Yurúa, Departamento de Ucayali, Perú; ?Yahuarango Formation. ?Eocene. LACM locality 6289.

DESCRIPTION. The molar is tribosphenic. It bears an anteroposteriorly compressed trigonid with protoconid, paraconid, and metaconid. The talonid portion includes a hypoconid, but the posterolingual corner is broken. Therefore, the hypoconulid and entoconid are missing, so it is not possible to know the morphology of these important cusps. The remaining portion of the talonid is slightly less compressed than the trigonid. The protoconid is the tallest of the trigonid cusps, followed by the metaconid and paraconid. The bases of the paraconid and metaconid are at about the same level in lingual view. The hypoconid is about half the height of the protoconid. The tooth measures approximately 1.25 mm (estimated because of breakage) in anteroposterior length, 1.02 mm in transverse width of the trigonid, and approximately 1.02 mm (estimated) in transverse width of the talonid.

The major cusps are slender. There are strong, continuous anterior, labial, and posterior cingulids (Fig. 1). A tiny, weak lingual cingulid is present across the foot of the trigonid valley. There is a small swelling at the lingual extremity of the anterior cingulid. A tiny interdental contact wear facet occurs on the anterior wall of the paraconid. The labial valley between protoconid and hypoconid extends across the tooth as a groove anterior to the cristid obliqua and up toward the apex of the metaconid. The cristid obliqua extends from the hypoconid toward, but does not reach, the apex of the metaconid. Instead, it descends from the hypoconid down into the groove between talonid and trigonid, toward the base of the metaconid. In anterior view, the notch in the paracristid has an angle of about 90 degrees. In posterior view, the notch in the protocristid forms an angle of slightly less than 90 degrees. Only half of the postcristid is preserved, but enough of it is present to indicate that, in occlusal view, the angle between it and the cristid obliqua is less acute than the angle formed by the paracristid and protocristid. The hypoconulid (assuming it was present) and the entoconid were probably close to each other (i.e., the hypoconulid was not medially placed). A distal metacristid with a small wear facet extends posterolabially from the metaconid. The posterolabial trend of the metacristid is similar to that in the posterior molars of some bats and different from that of the anterior molars, suggesting that the tooth could possibly be an M_3.

DISCUSSION. The Santa Rosa specimen has a typical dilambdodont morphology that is generally seen in Paleogene insectivorous mammals of many kinds, including certain metatherians, chiropterans, adapisoriculids, talpoids, nyctitheriids, soricids, plagiomenids, mixodectids, galeopithecids, and tupaiids. Little attempt was made at comparisons with this bewildering array of mammals in which convergence of characters of the lower molars is probably rampant. Except for metatherians and the Oligocene bats from the Tremembé Formation (see above), the taxa mentioned are unknown as fossils in the Paleogene of South America. The Santa Rosa specimen is referred with uncertainty to the Chiroptera because it has a well-developed labial cingulid on the lower molars. A strong labial cingulid is probably a synapomorphy of early bats (Hand et al., 1994); it is lacking in metatherians.

The Santa Rosa tooth differs from lower molars of most bats and insectivores in its cristid obliqua, which terminates on the base of the metaconid instead of on the middle of the posterior wall of the trigonid below the notch in the protocristid. Only one New World family of bats, the Noctilionidae, has lower molars in which the cristid obliqua is shifted lingually onto the metaconid (Czaplewski, 1996). In the Old World, this feature also occurs in Nycteridae and Megadermatidae. However, in *Noctilio* Linneaus, 1766 (the only genus in the family Noctilionidae), the cristid obliqua is much more prominent than in the Santa Rosa fossil.

Other differences between the Santa Rosa tooth and those of *Noctilio* are that the talonid of molars of *Noctilio* is much wider than the trigonid (of equal width in LACM 140623), and the two moieties of the tooth are more transversely oriented (i.e., at right angles to the long axis of the tooth row) instead of slightly obliquely oriented. Also lacking in the Santa Rosa tooth, but present in molars of *Noctilio* is a wall-like distal metacristid–entocristid that closes off the talonid valley lingually. These characters are present in specimens of the extant *N. albiventris* Desmarest, 1818 from the middle Miocene of Colombia, which is the earliest fossil record of a noctilionid (Czaplewski, 1997). At this time, it is impossible to say whether the characters of the Santa Rosa tooth might represent a transitional grade in the development of these characters of noctilionids. The differences seem to preclude assigning LACM 140623 to the Noctilionidae.

The lower molars of a few Paleogene lipotyphlan insectivores, such as adapisoriculids, nyctitheriids, talpids, and proscalopids, resemble LACM 140623 in some of its details. Certain talpids and proscalopids possess lower molars with a well-developed labial cingulid and a labial valley that reaches most of the way across the tooth to the metaconid. However, in these taxa, the occlusal outline is usually in the shape of a parallelogram with crests strongly oblique to the long axis of the tooth row, more so than in LACM 140623, and the cristid obliqua reaches all the way to the apex of the metaconid, unlike the condition in the Santa Rosa tooth.

Many nyctitheriids and adapisoriculids have a prominent mesial cingulid like LACM 140623, but they lack the labial cingulid on lower molars. The lipotyphlans of the genus *Wyonycteris* Gingerich, 1987, of the late Paleocene in North America and the Paleocene–Eocene boundary of Europe (Smith, 1995) are generally similar in morphology and size to LACM 140623. *Wyonycteris chalix* Gingerich, 1987, was originally thought to be a bat, but Hand et al. (1994) discussed its similarities with several other groups of insectivorous placental mammals and argued that it is not a bat. Smith (1995, 1997), who named an additional species, *Wyonycteris richardi* Smith, 1995, felt that *Wyonycteris* is not a typical bat and thought that it probably represents a derived member of the Adapisoriculidae or Nyctitheriidae. In *W. chalix,* the configuration of the cristid obliqua, the groove paralleling the cristid obliqua, and the lingual cingulid are virtually identical to those in LACM 140623. *Wyonycteris richardi,* on the other hand, lacks a lingual cingulid at the base of the trigonid valley, and it does not develop a small swelling at the lingual end of the anterior cingulid. But the molars of species of *Wyonycteris* differ from the Santa Rosa tooth in having a more oblique orientation of cristids, slightly less acute notches in the paracristid and protocristid, a relatively larger paraconid, and in completely lacking a labial cingulid.

LACM 140623 is tentatively considered to represent a lower molar of a chiropteran. In the absence of more diagnostic material, it is not possible to identify the specimen accurately. The broken talonid cusps would be critical for determining whether the tooth might represent an archaic, generalized bat or a member of a modern clade of bats. Nevertheless, it is an important specimen in that it suggests the presence in the Santa Rosa local fauna of an order of mammals barely known (or, if not Chiroptera, unknown) in the Paleogene of South America. If it truly belongs to a bat, there is a remote possibility—on the basis of one dental character, the configuration of the cristid obliqua—that the Santa Rosa tooth represents a transitional form between primitive bats and the endemic Neotropical family Noctilionidae. It might also constitute the oldest record of Chiroptera in South America.

ACKNOWLEDGMENTS

We thank Tiffany Naeher for help in making the photographs, Gregg Gunnell for making available a cast of *W. chalix,* and Francisco Goin for providing a Spanish translation of the abstract. The assistance and cooperation of Ing. Hugo Rivera Mantilla, Director Técnico of INGEMMET, and Ing. Oscar Palacios, Director General de Geología of INGEMMET, are gratefully acknowledged. We also thank Suzanne Hand, Bernard Sigé, and Thierry Smith for thoughtful reviews and helpful comments that improved the manuscript.

LITERATURE CITED

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2000. The late Miocene gomphothere *Amahuacath-*

erium peruvium (Proboscidea: Gomphotheriidae) from Amazonian Peru: Implications for the Great American Faunal Interchange. *Instituto Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín* 23:1–152.

———. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Czaplewski, N.J. 1996. Opossums (Didelphidae) and bats (Noctilionidae and Molossidae) from the late Miocene of the Amazon Basin. *Journal of Mammalogy* 77:84–94.

———. 1997. Chiroptera. In *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia,* ed. R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn, 410–431. Washington, D.C.: Smithsonian Institution Press.

Desmarest, A.G. 1818. Article "Noctilion ou bec de lievre." Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique; par une société de naturalistes, Nouveau Edition 23, 14–16. Deterville, Paris.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Rio Acre region, western Amazonia. *Contributions in Science* 374:1–46.

Frailey, C.D., and K.E. Campbell, Jr. 2004. Paleogene rodents from Amazonian Peru: The Santa Rosa local fauna. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 71–130.

Gingerich, P.D. 1987. Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan* 27:275–320.

Goin, F.J., and A. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Hand, S., M. Novacek, H. Godthelp, and M. Archer. 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology* 14:375–381.

Kay, R.F., and C.D. Frailey. 1993. Large fossil platyrrhines from the Rio Acre local fauna, late Miocene, western Amazonia. *Journal of Human Evolution* 25:319–327.

Kay, R.F., R.H. Madden, R.L. Cifelli, and J.J. Flynn (eds.). 1997. *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia.* Washington, D.C.: Smithsonian Institution Press, 592 pp.

Legendre, S. 1984. Identification de deux sous-genres et compréhension phylogénique du genre *Mormopterus* (Molossidae, Chiroptera). *Comptes Rendus de l'Académie de Sciences, Série II, Paris* 298:715–720.

———. 1985. Molossidés (Mammalia, Chiroptera) cénozoïques de l'Ancien et du Nouveau Monde; statut systématique; intégration phylogénique des données. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 170:205–227.

Leonardos, O.H. 1924. Os folhelhos petrolíferos do Vale do Paraíba. *Engenharia, Rio de Janeiro* 1(3):21–24.

Mezzalira, S. 1964. Novas ocorrências de vegetais fósseis cenozóicos no Estado de São Paulo. *IGG [Instituto Geográfico e Geológico], São Paulo* 15:73–94 (1961–1962).

———. 1966. *Os fósseis do Estado de São Paulo,* São Paulo: Instituto Geográfico e Geológico, Boletim, 45: 1–132.

———. 1989. *Os fósseis do Estado de São Paulo,* 2nd ed. revisão atual. São Paulo: Secretaria do Meio Ambiente, Instituto Geológico, Série Pesquisa 1989, 142 pp.

Paula Couto, C. de. 1956. Une chauve-souris fossile des argiles feuilletées Pléistocènes de Tremembé, État de São Paulo (Brésil). *Actes du IV Congrès International du Quaternaire, Roma-Pise, août-septembre 1953* 1:343–347.

———. 1983. Geochronology and paleontology of the basin of Tremembé-Taubaté, State of São Paulo. *Iheringia, série Geologia, Porto Alegre* 8:5–31.

Paula Couto, C. de, and S. Mezzalira. 1971. Nova conceituação geocronológica de Tremembé, Estado de São Paulo, Brasil. *Anais da Academia Brasileira de Ciências* 43(Suppl.):473–488.

Smith, T. 1995. Présence du genre *Wyonycteris* (Mammalia, Lipotyphla) à la limite Paléocène–Éocène en Europe. *Comptes Rendus de l'Académie des Sciences, Paris* 321:923–930.

———. 1997. Les insectivores *s.s.* (Mammalia, Lipotyphla) de la transition Paléocène–Éocène de Dormaal (MP 7, Belgique): Implications biochronologiques et paléogéographiques. *Mémoires et Travaux de l'E.P.H.E., Institut Montpellier* 21:687–696.

Received 2 July 2003; accepted 29 December 2003.

Enigmatic Mammal from the Paleogene of Perú

Francisco J. Goin,[1,3] Emma Carolina Vieytes,[2]
María Guiomar Vucetich,[1] Alfredo A. Carlini,[1] and Mariano Bond[1]

ABSTRACT. We describe an isolated molariform tooth excavated from ?Eocene deposits at Santa Rosa, Perú. The specimen most probably belongs to a mammal, and it may correspond to a left upper last molar. Analysis of its enamel and dentine microstructure leads to no definite conclusion as to its relationships, or even as to its enamel–dentine structural patterns. Taphonomic processes, for example, digestion of the specimen by a predator, might be involved in some of its peculiar characteristics. Its unique gross morphology prevents us from assigning it to any known mammal group with confidence. Several features of its cusp and crest morphology resemble the general pattern of Late Cretaceous–Eocene gondwanatherian mammals, especially that of *Ferugliotherium windhauseni* (Ferugliotheriidae).

RESUMEN. Se describe un molariforme aislado procedente de niveles paleógenos de la localidad de Santa Rosa, Perú. El ejemplar pertenece más probablemente a un mamífero, y podría corresponder a un último molar superior izquierdo. El análisis de su microestructura no permite arribar a conclusiones definitivas sobre sus relaciones, o siquiera sobre el patrón estructural del esmalte y la dentina. Se sugiere que procesos tafonómicos, como la digestión del ejemplar por un depredador, podrían estar relacionados con algunas de sus peculiares características. Su morfología general, verdaderamente única, impide asignarlo a cualquiera de los grupos conocidos de mamíferos; varios rasgos de sus cúspides y crestas recuerdan más a la estructura dentaria de los mamíferos Gondwanatheria, del Cretácico Superior–Eoceno, especialmente a la de *Ferugliotherium windhauseni* (Ferugliotheriidae).

INTRODUCTION

Among the thousands of vertebrate specimens from the Paleogene of Santa Rosa, Perú (see Campbell, 2004), there is a single, multicuspate molariform tooth of uncertain allocation. The specimen is very odd in that its external surface lacks the characteristic brightness of enamel; some of the cusps' internal slopes, as well as the external surface, are irregularly perforated by small holes and grooves, and its morphology is sufficiently strange to preclude any definite assignment to any known group of mammals. In spite of its poor state of preservation, its unusual morphology merits description. The purpose of this paper is to describe the new specimen and to discuss its most relevant features and possible affinities.

SYSTEMATICS

Mammalia Indeterminate

Figures 1–4

MATERIAL. LACM 149371. Isolated molariform tooth lacking its roots. Natural History Museum of Los Angeles County, Vertebrate Paleontology Collections. LACM 149371 was picked from concentrate obtained during the second, or 1998, field expedition to Santa Rosa. Fieldwork was carried out by Kenneth E. Campbell, Jr., Carl D. Frailey, and Manuel Aldana.

MEASUREMENTS. Maximum length = 2.65 mm; maximum width = 2.20 mm; labial height = 1.05 mm; lingual height = 1.30 mm.

LOCALITY, GEOLOGY, AND AGE. The Santa Rosa fossil locality is located about 2 km north of the village of Santa Rosa, on the west bank of the Río Yurúa near its confluence with the Río Beu, in Provincia Atalaya, Departamento Ucayali, eastern Perú (9°29′39″ S, 72°45′48″ W; Campbell et al., 2004). LACM 149371 comes from fine- to coarse-grained bed load or channel deposits that probably belong to the Yahuarango Formation [also known as, or included within, the Huayabamba Formation, lower red beds, lower Capas Rojas, lower Puca, or Huchpayacu Formation (Campbell et al., 2004)]. The age of the Santa Rosa local fauna has

---

[1] Departamento Paleontología Vertebrados, Museo de la Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. Email: fgoin@museo.fcnym.unlp.edu.ar, vucetich@museo.fcnym.unlp.edu.ar, palvert@museo.fcnym.unlp.edu.ar, acarlini@museo.fcnym.unlp.edu.ar

[2] Departamento Zoología Vertebrados, Museo de la Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. Email: cvieytes@museo.fcnym.unlp.edu.ar

[3] Correspondence

Science Series, Number 40, pp. 145–153
Natural History Museum of Los Angeles County, 2004

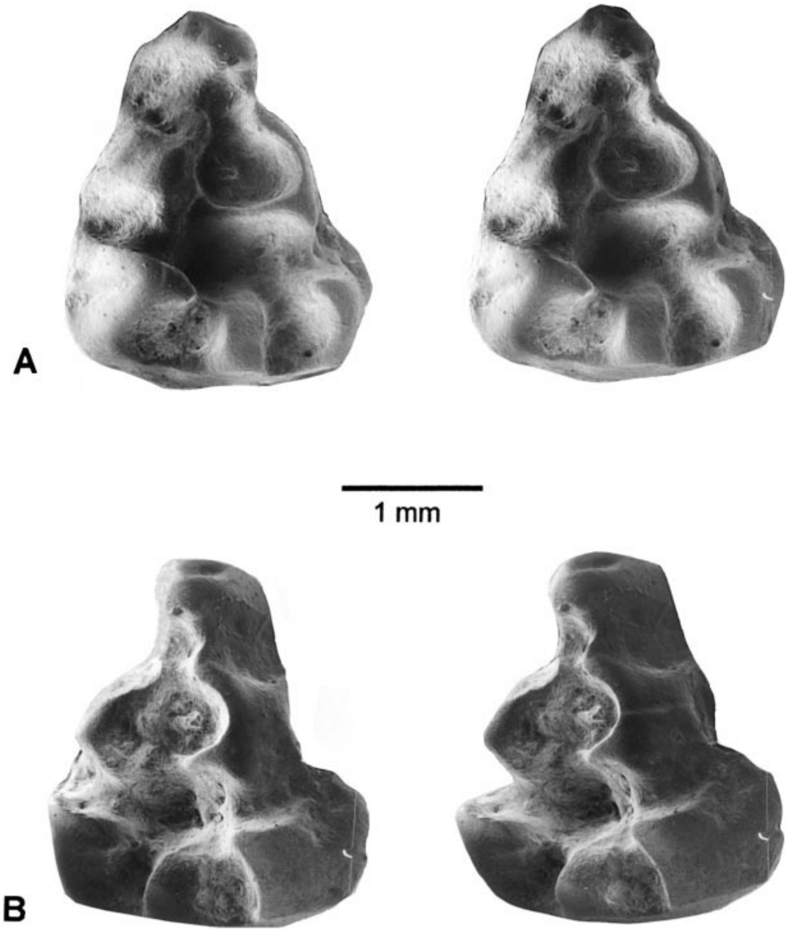


Figure 1 Stereopairs of LACM 149371. **A,** Occlusal view; **B,** occlusal-lingual view. (See Fig. 2 for postulated spatial orientation of the specimen).

been estimated as ?Eocene (Mustersan South American Land Mammal Age) on the basis of the stage of evolution of the marsupials (Goin and Candela, 2004) and rodents (Frailey and Campbell, 2004).

GROSS MORPHOLOGY. For descriptive purposes only, cusps have been designated with capital letters, A to F, with the tips of the cusps in a dorsal position. The nomenclature for these cusps, as well as the presumed labiolingual and anteroposterior axes of the tooth, are shown in Figure 2A. We cannot be positive that these axes are correct, but they will be assumed to be correct for the purpose of the descriptions that follow. When LACM 149371 is observed under the stereomicroscope, the opaque, porous aspect of the whole crown is noticeable. The characteristic brightness of an enamel surface is not observable at all, except for small vitreous patches at the tips of some cusps. Another unusual feature of the crown is the irregular presence of holes and grooves on its surface. They are scattered along the external faces of the crown, and several small, circular holes are also present on the inner slopes of the cusps, as well as on the intercusp valleys (Fig. 3F).

In occlusal view (Figs. 1A–B, 2A, 3A), the specimen has a triangular shape. It has six or seven peripheral cusps, with contiguous cusps connected to each other by low ridges. The cusps surround two deep fossae, as well as a third, much smaller and shallower fossa. The fossae are centrally located and separated from each other by crests. The labial face of this tooth (Fig. 3B) is low, whereas the other two become progressively higher toward the lingual corner (Fig. 3C). No cingulum of any kind is observable in occlusal or any other view of the crown.

The crown pattern is complex. Most of the cusp slopes that face other cusps are smooth and rather rounded, whereas those facing the center of the crown are steep and flat. The most conspicuous feature of the intercusp morphology is that deep val-

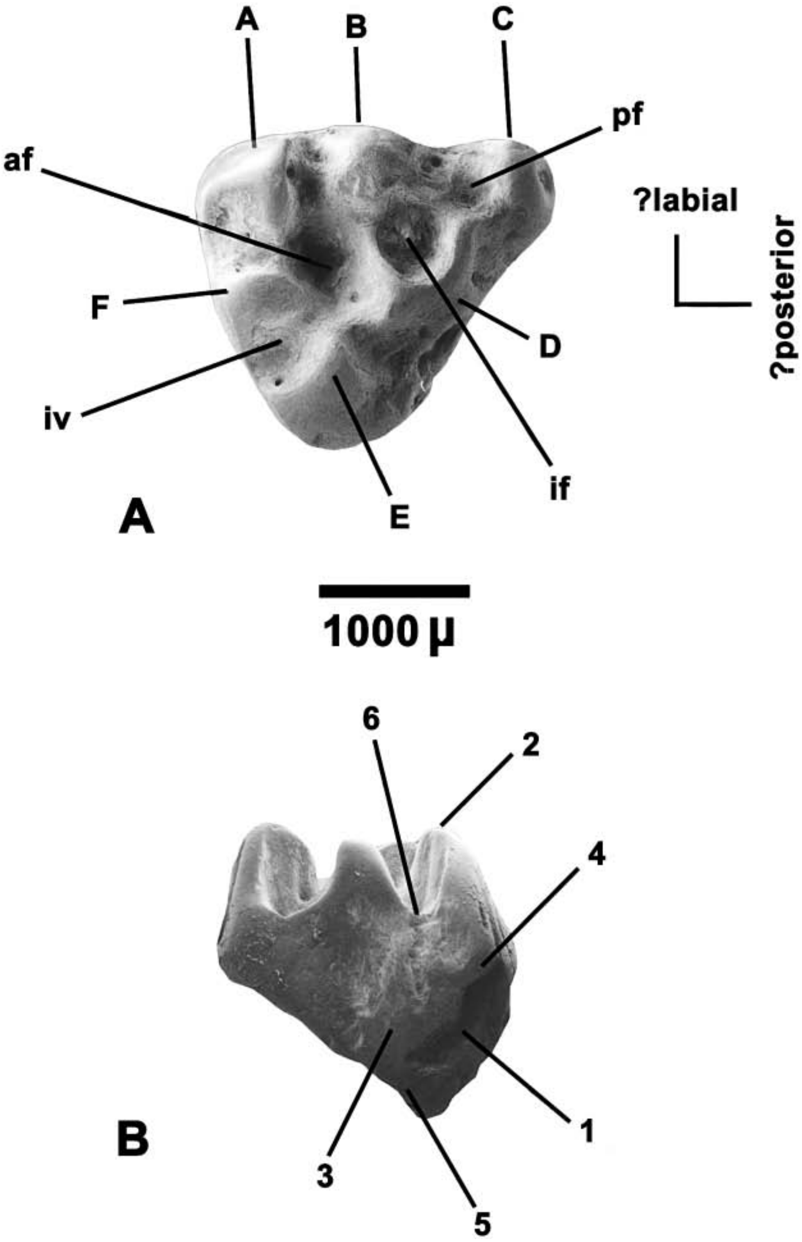


Figure 2 LACM 149371. **A,** Occlusal view; **B,** anterior view. Features labeled in **A** are the following: A–F, cusps mentioned in the text; af, anteriormost fossa; if, intermediate fossa; pf, posteriormost fossa; iv, intercusp valley. In **B,** the following areas of the crown were examined for the microstructure analysis: **1,** basal crack on the anterolingual edge of the tooth; **2,** tip of cusp E (see Figs. 3A–B); **3,** area left of the crack on the anterolingual face of the crown (see Figs. 3C, E, F); **4,** area above the crack noted as site 1 (see Fig. 3D); **5,** area below the same crack (see Fig. 3G); **6,** intercusp valley between cusps E and F (see Fig. 3H).

leys on the external surface of the crown separate contiguous cusps, but low ridges or crests internal to these valleys connect them.

Cusp A, the largest and highest cusp of the tooth, is triangular in occlusal view, with its posterior face flat and sloping steeply ventrad (Fig. 2). Cusp B is more rounded in section; its anterior face is slightly concave. A deep, external valley separates cusps A and B. Lingual to this valley is a low ridge connecting both cusps and surrounding the anterior fossa at its anterolabial corner. Cusp B projects posteriad with a relatively long, moderately sloped

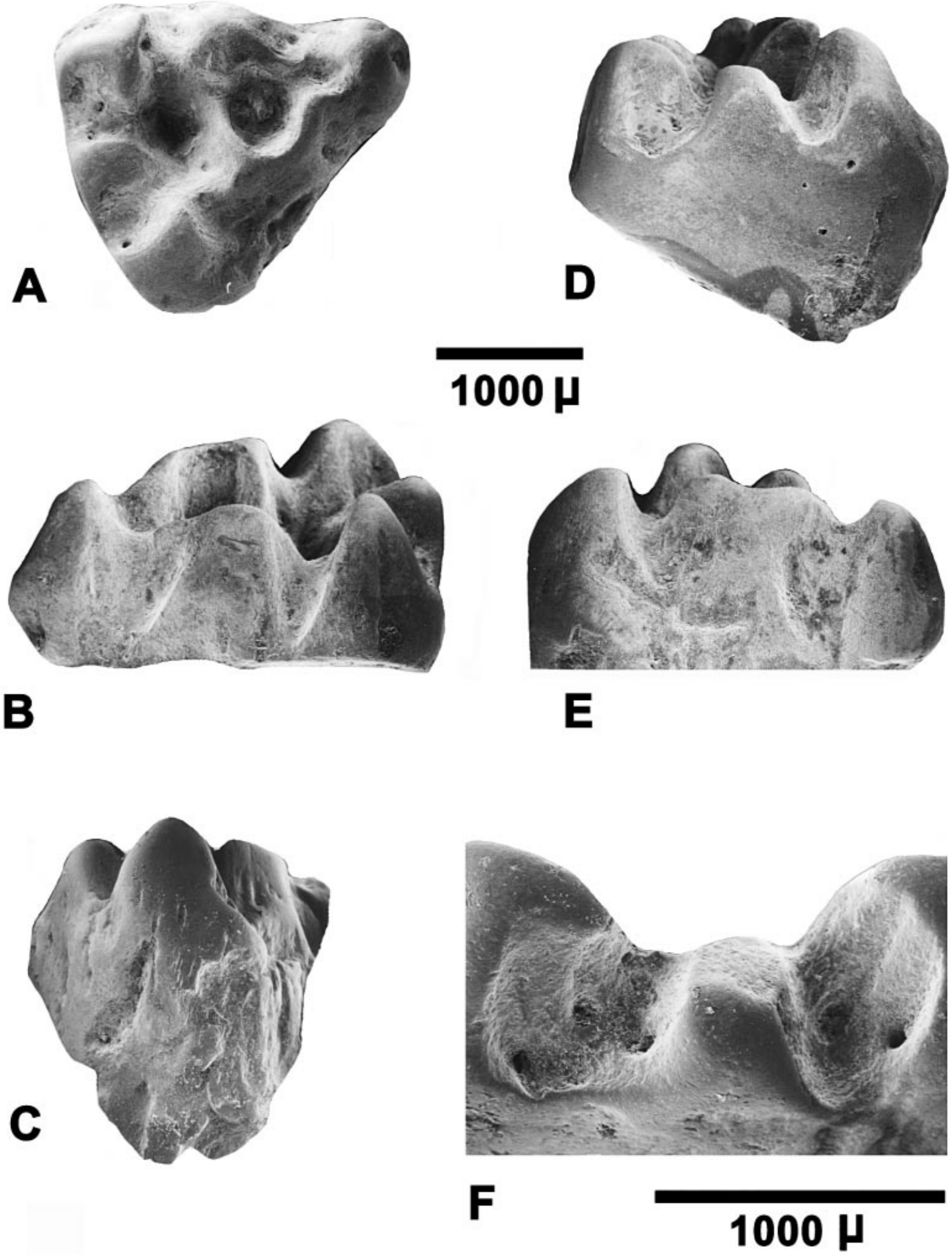


Figure 3 LACM 149371. **A,** Occlusal view; **B,** labial view; **C,** lingual view; **D,** anterolingual view; **E,** posterolingual view. Scale for A–E is the same. **F,** Detail of the anterolingual face of the crown shows the small holes, or dissolution points, that penetrate the tooth's surface. The anterolingual face shown in **D** differs from that of Figure 1B, in that, in the latter photograph, the base of the crown has been polished to the left of the crack.

---

crest that reaches the most posterior fossa, which is the smallest of the fossae. Posterior to this fossa is cusp C, the lowest of the tooth, which is subcircular in section. Its anterior slope, which faces the small fossa, is almost flat. Posterolingually, cusp C is separated from cusp D by a deep valley and its labial face is marked by a deep groove.

Cusp D is very odd, and may, in fact, represent two subtriangular cusps fused at their bases. This structure is crest shaped, and it surrounds the medial fossa of the tooth lingually. Two crests originating from cusp D separate the three fossae. The most anterior crest, the longest and deepest one, almost reaches the base of cusp B. Cusp E is located at the lingual corner of the tooth; it is subtriangular in cross section. Its anterolabial face is almost flat, and it borders a deep valley separating it from cusp F. Cusp E is separated from cusps D and F by means of external valleys and connected to them by internal crests. Cusp F is rounded in section, and it borders the largest fossa anteriorly.

The three aligned, successively smaller and shallower fossae are subcircular in section (Figs. 1A, 2A). The largest is almost centrally located, and it is surrounded by four of the five cusps. The most posterior fossa is extremely small, shallow, and bordered posteriorly by cusp C.

Ventrally, the crown and roots are broken. Pulp cavities for four roots can be distinguished. These cavities are large and subcircular in section. One of them, more suboval in profile than the others, seems to be filled with sediment. The two anterior roots, as well as the two posterior roots, seem to be partially confluent with each other. A much smaller cavity, located medially at the labial side of the tooth, suggests the probable existence of a fifth root. Finally, there is a slight depression at the anterolabial corner of the tooth; whether it represents an additional root is impossible to determine.

ENAMEL AND DENTINE MICROSTRUCTURE. We analyzed the specimen to determine its microstructure, but without embedding it in artificial resin because of its unique condition. Treatment was restricted to three areas of the crown: (1) on a large crack located on the anterior face, (2) at the tip of cusp E, and (3) the ventral face (see Fig. 2B). The first and third areas were polished with grit powder no. 1000 and then etched for 5–6 seconds with 10 percent HCl to make morphological details visible. Acid was applied to the tip of the cusp without polishing.

The results of the microstructure analysis were inconclusive. Most examined areas of the tooth (anterior face, tip of cusp, and ventral face) have a homogeneous internal structure. At intermediate magnifications (×750–1000), we could distinguish flat, tubule-like structures that are parallel to each other and rise toward the external surface at an angle of approximately 45 degrees (Fig. 4G). Additionally, either prisms or prism-like structures, together with interprismatic structures, were observed (Figs. 4A–F). At higher magnifications (×3500–10,000), however, neither the prisms nor the matrix crystals could be distinguished. In transverse view, prism-like structures were observed; in this view, they are suboval in section (Fig. 4A). Again, at higher magnifications, the crystalline structure of these forms was not distinguishable (Fig. 4B). All structures seemed to be degraded to some extent, making it impossible, at least on the polished surfaces, to obtain more precise observations. On an unpolished, but acid-treated surface of the crown (equivalent to a tangential plane), the observed pattern is reminiscent of Hunter–Schreger bands of the enamel of mammals (Fig. 4C). However, this pattern is not uniform across the surface of the crown. In other areas, the observed pattern was that of the prism-like structures. In short, enamel structures are not unequivocally distinguishable. In none of the examined areas of the tooth could we observe a dentine–enamel junction.

DISCUSSION

LACM 149371 is enigmatic in many ways. Regarding its taxonomic assignment, the most plausible hypothesis for us is that it corresponds to a mammal. Its crown is sufficiently complex to eliminate the possibility that it may belong to another vertebrate group, including several with complex, mammal-like postcanine dentitions (e.g., crocodiles; see Clark et al., 1989). The complexity of the crown suggests that it is a molar. Its triangular shape, root number (four or five), and cusp disposition suggest that most probably it is an upper molar. The flat aspect and low crown of its longest face suggest that it corresponds to the labial face (Fig. 3B). In turn, the dramatic narrowing of the crown toward the smallest of the cusps (C) suggests that it may correspond to the posterior end of the tooth. In short, the tooth may be a last upper left molar.

Several features suggest some degree of chemical degradation of both the general morphology and microstructure of this specimen. The dull, porous aspect of the crown, as well as the absence of prismatic structures at various points, suggests that the enamel is partially lacking or that it is highly modified. The grooves and holes that penetrate several areas of the crown surface are suggestive of dissolution points. Taphonomic processes may be involved in the apparent degradation of these structures. One possibility is that the specimen was deposited under the influence of acidic underground water (see, e.g., Fernandez Javo et al., 1998). Several patterns of molar digestion by avian predators have been proposed (Andrews, 1990). Some canids and felids also digest small mammalian molars to the same, or even greater, degree of destruction. Crocodilian digestion of mammalian teeth is also known as a factor producing enamel denudation (Fisher, 1981). If this were the case for LACM 149371, it would explain the unusual features noted above. Although we were unable to observe such preservation anomalies among available marsupial remains from the same matrix sample, other specimens of teeth from the Santa Rosa collection do show evidence of acid etching and enamel denudation (K. Campbell, personal communication). At least some of the observed microstructure features of the tooth could correspond to dentine, not to enamel. It has been noted that in some mammals, such as gondwanatherians (Sigogneau Russell et al., 1991), the dentine tubules can be filled with calcified, dense, cylindrical structures.

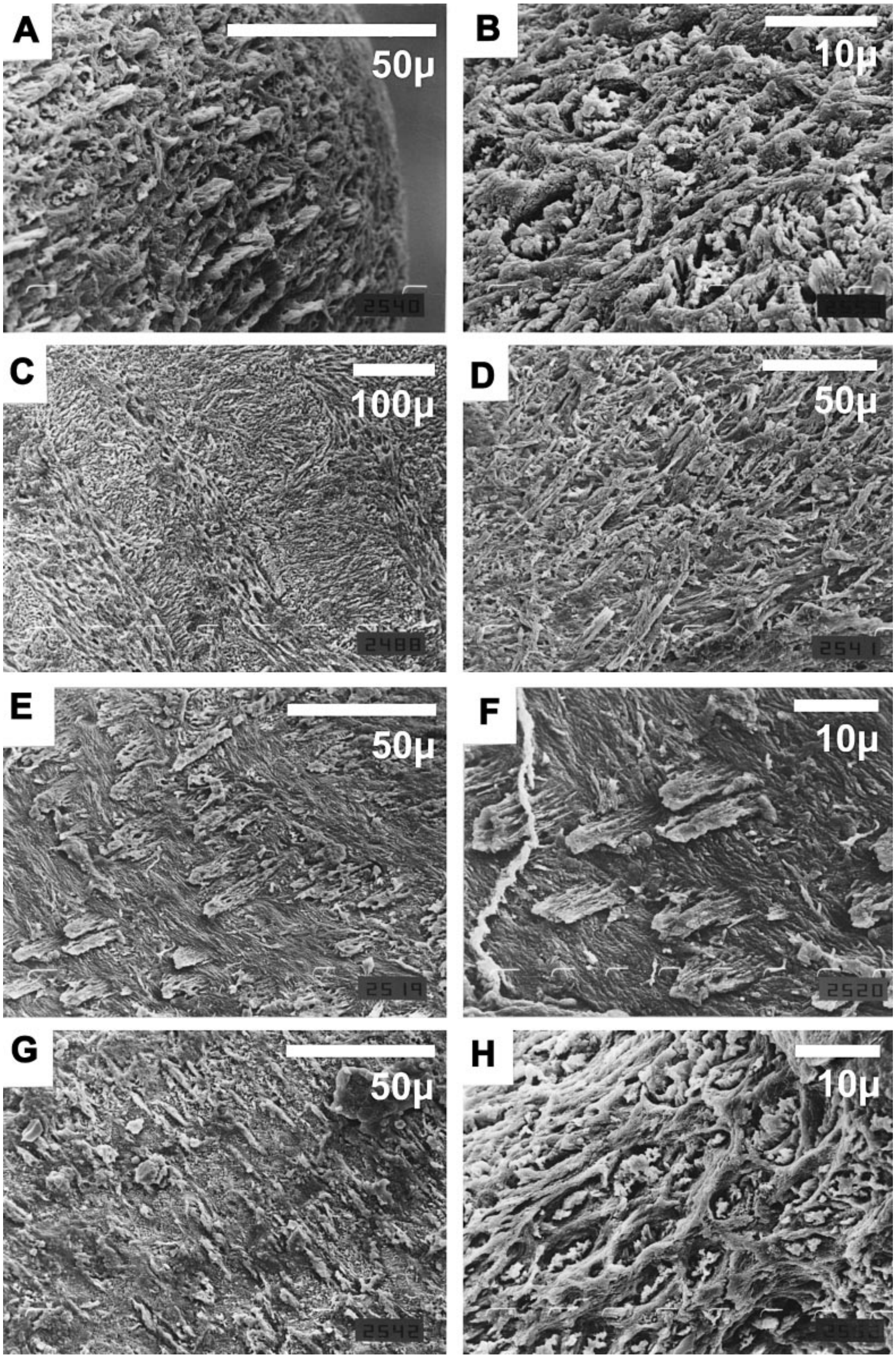


Figure 4 Scanning electron micrographs showing different microstructure patterns in LACM 149371. **A,** Detail of cusp E showing ?enamel prisms emerging from the ?interprismatic matrix at the cusp surface; **B,** detail of **A**; **C,** unpolished area left of the crack on the anterolingual face, showing a pattern similar to that of Hunter–Schreger bands; **D,** ?enamel prisms, parallel to each other, above the crack on the anterolingual face of the crown; **E,** polished area to the left of the

The unusual shape of the valleys and ridges separating and connecting the cusps, especially the three anterior cusps (A, F, and E; Fig. 3D), remind us of the condition seen in several allotherians. In the multituberculate *Essonodon browni* Simpson, 1927, for instance, the cusp arrangement of M_2 is not that of aligned cusps, but one of peripheral cusps around the crown; several of these cusps are anteroposteriorly compressed. Other multituberculates, such as *Meniscoessus robustus* Cope, 1882, show a similar pattern in the intercusp relationship (external valleys, internal ridges; see, e.g., Clemens, 1963; Archibald, 1982). None of these, however, show any indication of fossae between cusps. Moreover, molars of multituberculates are usually quadrangular, not triangular in shape, and they usually show a longitudinal valley between two parallel cusp series.

The same cusp features mentioned above for LACM 149371 remind us of the pattern observable among gondwanatherian mammals. Originally regarded as multituberculates (see, e.g., Krause et al., 1992; Kielan-Jaworowska and Bonaparte, 1996), gondwanatherians were considered more recently by Pascual et al. (1999) to be Mammalia *incertae sedis*. In particular, the cusp shape and intercusp morphology of LACM 149371 resembles that of *Ferugliotherium windhauseni* Bonaparte, 1986a (Gondwanatheria, Ferugliotheriidae), from the upper Cretaceous Los Alamitos Formation in northern Patagonia. No upper molars of these gondwanatherians are known; thus, it is impossible to make any direct comparison with LACM 149371. Nonetheless, it should be noted that several cusps in *Ferugliotherium* Bonaparte, 1986a, are anteroposteriorly compressed and have low ridges or crests that connect with the center of the crown, as in the Peruvian mammal. *Ferugliotherium* has only incipient fossae because it has quite brachydont molariform teeth. Other gondwanatherians, such as the Sudamericidae, include forms (*Sudamerica* Scillato Yané and Pascual 1985, *Gondwanatherium* Bonaparte, 1986b) with high-crowned molariform teeth. Interestingly, *Sudamerica ameghinoi* Scillato Yané and Pascual, 1985, from the lower Paleocene of Patagonia, has two to three fossae in its molariform teeth. Even though they are not very deep, they are clearly observable in lightly worn teeth (Koenigswald et al., 1999).

Comparisons with early tribosphenic mammals (early Australosphenida and Boreosphenida *sensu* Luo et al., 2001, 2002) lead to no definite conclusion other than their sharing of triangular-shaped upper molars. Among early australosphenidans, upper molars of *Ambondro* Flynn et al., 1999, and *Steropodon* Archer et al., 1985, are unknown, whereas those of *Ausktribosphenos* Rich et al., 1997, and more modern monotremes are definitely away from the pattern of the Peruvian mammal. The same can be said of its comparison with early boreosphenidans, which include Metatheria, Eutheria, and "tribotheres" (see Luo et al., 2002). All of these taxa show a more "typical" tribosphenic arrangement of cusps, crests, notches, basins, and cingula (see below).

No metatherian mammal known to us matches the morphology of LACM 149371. Even if we assume that the natural orientation of the tooth was as suggested in Figure 2A, the intercusp morphology is not observable in fossil or living metatherians. Neither are deep fossae limited by shallow cristae transverse to the main axis of the tooth seen in known metatherians. Borhyaenoids, microbiotherians, didelphoids, caenolestoids, and polydolopimorphians of the families Bonapartheriidae, Prepidolopidae, and Gashterniidae have well-known molar patterns, none of which match that of LACM 149371 (see, e.g., Marshall, 1978, 1980, 1981, 1982a, 1982b; Pascual, 1980; Pascual and Bond, 1981). Finally, none of the high-crowned molars of taxa of the Patagoniidae and Argyrolagidae have fossae of any kind (Simpson, 1970).

Assignment of this specimen to a still unknown, early edentate seems to us equally speculative on the basis of the available evidence. Toothed edentates are either homodont and simple-crowned (e.g., armadillos, sloths), or they have complicated crowns without peripheral cusps surrounding central fossae (e.g., glyptodonts). There is no evidence of multicuspate crowns among dasypodoids, whose molars are suboval in section and have simple crowns. Among glyptodontoids, even though the lobed aspect of their teeth could suggest a primitive multicusp pattern, their size, hypsodonty, and crown pattern are far from that of LACM 149371. Vermilinguans (Pilosa) lack teeth, either among extinct forms or as early (fetal or abortive) dentitions. Unworn teeth of early tardigradans (Pilosa) are single-cusped, and their crowns are subelliptical, reniform, or subrectangular in section (see Hoffstetter, 1958, 1982; Paula Couto, 1979).

Some early South American native "ungulates" match the size of LACM 149371. Moreover, this tooth does remind us, in a very general sense, of some upper premolars of "condylarths" and basal litopterns, as well as notioprogonid and typotheriid notoungulates (Cifelli, 1983; Muizon and Cifelli, 2000; Soria, 2001). It could be the case that this specimen is actually an upper right molariform tooth of some unknown form of these ungulates, with an anterolabially salient parastyle. If this were the case, however, cusp A (posterolabial, or "meta-

←

crack on the anterolingual face, showing prism- and matrix-like structures set almost at right angles; **F,** detail of area depicted in **E,** showing ?crystallites; **G,** ?filled dentine tubules below the crack on the anterolingual face; **H,** detail of the (unpolished) surface of the intercusp valley between cusps E and F.

cone" in this interpretation) differs from that of all known ungulates in being transversely oriented with respect to the anterior "paracone." Even though other features also remind us of some ungulates, the presence of a "metacone" makes it markedly different from all of them.

Rodent affinities for this specimen are also highly speculative, even though some resemblances with early forms can be noted. One of these is the early Eocene *Ivanantonia efremovi* Shevyreva, 1989, from Mongolia, which is of uncertain affinities among basal rodents. Lower molars of *Ivanantonia* Shevyreva, 1989, show some anteroposterior alignment of the cusps that, in its case, border a large, central groove. Hartenberger et al. (1997) suggested affinities between *Ivanantonia* and the late Eocene, North American *Nonomys* Emry and Dawson, 1972. Interestingly, *Nonomys* shows in its anteriormost cheek tooth (M^1) a parastylar area ("anterocone lobe" *sensu* Emry, 1981) that is well projected anteriorly. LACM 149371 also shows a prominent projection, which is also interpreted here as external, but posterior instead of anterior. Nonetheless, *Nonomys* lacks the central fossae of the Peruvian mammal, whereas the latter lacks any indication of a cingulum. In none of the other known early Tertiary Glires (see, e.g., Dashzeveg and Russell, 1988; Dashzeveg et al., 1998) could we find the peculiar features observable in LACM 149371.

In short, of all mammals compared with the Peruvian molariform tooth, we regard the Gondwanatheria, and especially the Ferugliotheriidae, as our best estimate as to its possible allocation. If this proves to be the case, LACM 149371 would represent one of the latest known occurrences of a gondwanatherian mammal. The youngest record of sudamericid, but not of ferugliotheriid, gondwanatherians was reported from the middle Eocene of the Antarctic Peninsula (Reguero et al., 2001).

ACKNOWLEDGMENTS

We thank K.E. Campbell for loaning us LACM 149371 for study and for his help with the English version of this paper. Patricia Sarmiento and Rafael Urréjola were very helpful in making the scanning electron micrographs. The following colleagues gave us useful comments on the studied specimen: Rosendo Pascual, Adriana Candela, Javier Gelfo, Claudia Montalvo, and Edgardo Ortiz Jaureguizar. Finally, we thank Zofia Kielan-Jaworowska, Thomas Martin, Malcolm McKenna, and an anonymous reviewer for their useful criticisms and comments on the manuscript.

LITERATURE CITED

Andrews, P. 1990. *Owls, caves and fossils.* Chicago: The University of Chicago Press, 231 pp.

Archer, M., T.F. Flannery, A. Ritchie, and R.E. Molnar. 1985. First Mesozoic mammal from Australia—An Early Cretaceous monotreme. *Nature* 318:363–366.

Archibald, J.D. 1982. A study of mammalia and geology across the Cretaceous–Tertiary boundary in Garfield County, Montana. *University of California Publications in Geological Sciences* 122:1–286.

Bonaparte, J.F. 1986a. Sobre *Mesungulatum houssayi* y nuevos mamíferos cretácicos de Patagonia, Argentina. *Actas IV Congreso Argentino de Paleontolgía y Bioestratigrafía (Mendoza)* 2:48–61.

———. 1986b. A new and unusual Late Cretaceous mammal from Patagonia. *Journal of Vertebrate Paleontology* 6:264–270.

Campbell, K.E., Jr. 2004. Introduction. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 1–2.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

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

Clark, J.M., L.L. Jacobs, and W. Downs. 1989. Mammal-like dentition in a Mesozoic crocodylian. *Science* 244:1064–1066.

Clemens, W.A., Jr. 1963. Fossil mammals of the type Lance Formation, Wyoming. Part I. Introductions and Multituberculata. *University of California Publications in Geological Science* 48:1–105.

Cope, E.D. 1882. Mammalia in the Laramie Formation. *American Naturalist* 16:830–831.

Dashzeveg, D., J.-L. Hartenberger, T. Martin, and S. Legendre. 1998. A peculiar minute Glires (Mammalia) from the Early Eocene of Mongolia. In *Dawn of the age of mammals in Asia,* ed. C. Beard and M.R. Dawson. *Bulletin of the Carnegie Museum of Natural History* 34:194–209.

Dashzeveg, D., and D.E. Russell. 1988. Paleocene and Eocene Mixodontia (Mammalia, Glires) of Mongolia and China. *Palaeontology* 31:129–164.

Emry, R.J. 1981. New material of the Oligocene muroid rodent *Nonomys,* and its bearing on muroid origins. *American Museum Novitates* 2712:1–14.

Emry, R.J., and M.R. Dawson. 1972. A unique cricetid (Rodentia, Mammalia) from the early Oligocene of Natrona County, Wyoming. *American Museum Novitates* 2508:1–14.

Fernandez Javo, Y., C. Denys, P. Andrews, T. Williams, Y. Dauphin, and L. Humphrey. 1998. Taphonomy and palaeoecology of Olduvai Bed—I (Pleistocene, Tanzania). *Journal of Human Evolution* 34:137–172.

Fisher, D. 1981. Crocodilian scatology, microvertebrate concentrations and enamel-less teeth. *Paleobiology* 7:262–275.

Flynn, J.J., M. Parrish, B. Rakotosamimanana, W.F. Simpson, and A.R. Wyss. 1999. A middle Jurassic mammal from Madagascar. *Nature* 401:57–60.

Frailey, C.D., and K.E. Campbell, Jr. 2004. Paleogene rodents from Amazonian Peru: The Santa Rosa local fauna. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 71–130.

Goin, F.J., and A.M. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Perú. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Hartenberger, J.-L., D. Dashzeveg, and T. Martin. 1997. What is *Ivanantonia efremovi* (Rodentia, Mammalia)? *Paläontologische Zeitschrift* 7:135–143.

Hoffstetter, R. 1958. Xenarthra. In *Traité de Paléontologie,* ed. J. Piveteau, 6(2):535–636. Paris: Masson & Cie.

———. 1982. Les Edentes Xenarthres, un groupe singulier de la faune Neotropicale. In *Proceedings of the first meeting on paleontology, essential of historical geology (Venice, 1981),* ed. E. Montanaro Gallitelli, 385–443. Modena: S.T.E.M. Mucchi.

Kielan-Jaworowska, Z., and J.F. Bonaparte. 1996. Partial dentary of a multituberculate mammal from the Late Cretaceous of Argentina and its taxonomic implications. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Nueva Serie* 145: 1–9.

Koenigswald, W.v., F.J. Goin, and R. Pascual. 1999. Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal *Sudamerica ameghinoi. Acta Palaeontologica Polonica* 44:263–300.

Krause, D.W., Z. Kielan-Jaworowska, and J.F. Bonaparte. 1992. *Ferugliotherium* Bonaparte, the first known multituberculate from South America. *Journal of Vertebrate Paleontology* 12:351–376.

Luo, Z.-X., R.L. Cifelli, and Z. Kielan-Jaworowska. 2001. Dual origin of tribosphenic mammals. *Nature* 409: 53–57.

Luo, Z.-X., Z. Kielan-Jaworowska, and R.L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47:1–78.

Marshall, L.G. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences* 117:1–89.

———. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana, Geology, New Series* 5:1–145.

———. 1981. Review of the Hathlyacyninae, an extinct subfamily of South American "dog-like" marsupials. *Fieldiana, Geology, New Series* 7:1–120.

———. 1982a. Systematics of the South American marsupial family Microbiotheriidae. *Fieldiana, Geology, New Series* 10:1–75.

———. 1982b. Systematics of the extinct South American marsupial family Polydolopidae. *Fieldiana, Geology, New Series* 12:1–109.

Muizon, C. de, and R.L. Cifelli. 2000. The "condylarths" (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): Implications on the origin of the South American ungulates. *Geodiversitas* 22:47–150.

Pascual, R. 1980. Nuevos y singulares tipos ecológicos de marsupiales extinguidos de América del Sur (Paleoceno tardío o Eoceno temprano) del Noroeste argentino. *II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología, Buenos Aires, Actas* 2:151–173.

Pascual, R., and M. Bond. 1981. Epidolopinae, subfam. nov. de los Polydolopidae (Marsupialia, Polydolopoidea). *II Congresso Latino-Americano de Paleontología, Porto Alegre, Anais* 1981:479–488.

Pascual, R., F.J. Goin, D.W. Krause, E. Ortiz Jaureguizar, and A.A. Carlini. 1999. The first gnathic remains of *Sudamerica*: Implications for gondwanathere relationships. *Journal of Vertebrate Paleontology* 19: 373–382.

Paula Couto, C. de. 1979. *Tratado de Paleomastozoologia*. Rio de Janeiro: Academia Brasileira de Ciencias, 590 pp.

Reguero, M.A., S.A. Marenssi, and S.N. Santillana. 2001. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: Biogeographic relationships. *Ameghiniana* 38(Suppl.): 16R–17R.

Rich, T., P. Vickers-Rich, A. Constantine, T.F. Flannery, L. Kool, and N. van Klaveren. 1997. A tribosphenic mammal from the Mesozoic of Australia. *Science* 278:1438–1442.

Scillato Yané, G.J., and R. Pascual. 1985. Un peculiar Xenarthra del Paleoceno medio de Patagonia (Argentina). Su importancia en la sistemática de los Paratheria. *Ameghiniana* 21:173–176.

Shevyreva, N.S. 1989. New rodents (Ctenodactyloidea, Rodentia, Mammalia) from the Lower Eocene of Mongolia. *Paleontological Journal* 23(3):57–68.

Sigogneau Russell, D., J.F. Bonaparte, R.M. Frank, and V. Escribano. 1991. Ultrastructure of dental hard tissues of *Gondwanatherium* and *Sudamerica* (Mammalia, Gondwanatheria). *Lethaia* 24:27–38.

Simpson, G.G. 1927. Mammalian fauna of the Hell Creek Formation of Montana. *American Museum Novitates* 267:1–7.

———. 1970. The Argyrolagidae, extinct South American marsupials. *Bulletin of the Museum of Comparative Zoology* 139:1–86.

Soria, M.F. 2001. Los proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales* 1:1–167.

Received 2 July 2003; accepted 29 December 2003.

The Santa Rosa Local Fauna: A Summary

Kenneth E. Campbell, Jr.[1]

As noted by Patterson and Pascual (1972:249) over three decades ago, "The [South American Tertiary] record has one great deficiency: it is very largely restricted to the southern parts of the continent." Although this deficiency has been reduced somewhat for the Neogene of northern South America by progress in recording paleofaunas at La Venta, Colombia (Kay et al., 1997) and in western Amazonia (Frailey, 1986; Campbell et al., 2000), for the Paleogene record, it remains little changed. No low-latitude, tropical paleofauna had been recorded from the Paleogene prior to the Santa Rosa local fauna, and the geographically closest Paleogene localities are those at Laguna Umayo, Peru (latest Cretaceous or earliest Paleocene); Tiupampa, Bolivia [early Paleocene, Tiupampian South American Land Mammal Age (SALMA)]; and Salla and Lacayani, Bolivia (late Oligocene, Deseadan SALMA; see Goin and Candela, 2004; fig. 1). Thus, before the discovery of the Santa Rosa locality, well over one-half of the South American continent was unrepresented by Paleogene vertebrate faunas. For reviews of South American faunas and their ages, see Pascual and Ortiz-Jaureguizar (1990), Marshall and Sempere (1993), and Flynn and Swisher (1995).

The Santa Rosa local fauna, with its abundant and diverse fossil assemblage, is a dramatic first look at Paleogene faunas of low-latitude, low-elevation, tropical South America. This fauna has presented a wonderful opportunity for understanding tropical Paleogene faunas, but at the same time, because there are no other benchmarks against which to place the Santa Rosa local fauna, many limitations are placed on our interpretations of it. Perhaps the most important limiting factor is the lack of an accurate age for the paleofauna (see "Age of the Santa Rosa Local Fauna"). Dating faunas by the stage of evolution of their constituent taxa, as was done for the mammals from Santa Rosa, can only provide an approximate age, and it has a potential for a large margin of error, especially when there is only one Paleogene fauna for one-half a continent. Without an accurate age for the paleofauna, it is not possible to place it within an overall scheme of evolutionary patterns for South American paleofaunas with confidence.

Another important limiting factor is that because so many of the taxa are unique, it is difficult to know where to place them in their respective lineages. For the Santa Rosa local fauna, this difficulty applies to taxa within well-known mammalian groups, such as the marsupials (Goin and Candela, 2004), and even to taxa within the larger group Mammalia (Goin et al., 2004). This factor complicates interpretation of the paleofauna as a whole because it is not known whether these unique taxa are a result of isolation, environmental stability in the tropics, or some other reason.

I review here some of the most significant aspects of the Santa Rosa local fauna as reported in this volume and present a perspective of its role in our understanding of Paleogene tropical South America.

GEOLOGY

To anyone inexperienced in Amazonian geology, one single word descriptor would probably come to mind: monotonous. Red clays, silts, and fine sands abound, and few stratigraphic horizons stand out as being significantly different from all others. To the practiced eye, however, subtle nuances do appear that allow differentiation of formations (Rüegg, 1947, 1956; personal observation). Further complicating the interpretation of stratigraphy in lowland Amazonia is the fact that long stratigraphic sections are nonexistent, and only intermittent outcrops along rivers provide a look at the stratigraphy underlying the vast cover of Amazonian vegetation.

The stratigraphy along the Río Yurúa described by Campbell et al. (2004) follows the typical pattern in lowland Amazonia. Below the upper Miocene–lower Pliocene Madre de Dios Formation, which is unusual among Amazonian formations in that it does have a readily recognizable stratigraphy (Campbell et al., 2000), are exposed, moderately consolidated, massive red clays and mudstones with thin horizons of less consolidated fine to coarse sands. Thin conglomeratic lenses are also common, consisting of calcareous concretions, clay balls, fragments of bone, silicified wood, and coarse sand with a matrix of clay. It was the latter type of deposit that contained the fossil vertebrates recorded at Santa Rosa, Peru.

Identification of the Paleocene–Eocene Yahuarango Formation as the fossil-bearing unit at Santa Rosa was based on the presumed Eocene age of the fossils, which in turn was based on the stage of evolution of the most abundant mammals in the local fauna. As noted by Campbell et al. (2004), however, there are possible problems with this formational assignment, and additional stratigraphic data are required before it can be confirmed. More detailed stratigraphic studies along the Río Yurúa

---

[1] Vertebrate Zoology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007. Email: kcampbel@nhm.org

Science Series, Number 40, pp. 155–163
Natural History Museum of Los Angeles County, 2004

might provide these critical data, but it is possible that the formation producing the Santa Rosa local fauna will remain in question until a strong means of correlation between the Santa Rosa local fauna and other faunas still to be found in areas where the stratigraphic sequence can be determined with confidence.

MARSUPIALS

As a measure of the uniqueness of the marsupial paleofauna from Santa Rosa, it should be noted that Goin and Candela (2004) recognize eleven new species in ten genera (eight new), with all major lineages of South American marsupials represented. In and of itself, finding so many new species in a region previously unrepresented in the paleontological record is not surprising. In this case, however, only two of the new species are referable to previously described genera, two new genera could not be referred to known families, and an additional two genera were only tentatively referred to known families. Furthermore, two new genera could not be referred to any known family or order, which is rather exceptional for South American marsupials. With no other tropical, low-latitude Paleogene faunas available, however, it is not possible at this time to assign a level of significance to the uniqueness of this paleofauna. That is, there is a question as to whether the Santa Rosan marsupial paleofauna is representative of Paleogene marsupial faunas of Amazonia that were dramatically different from contemporary paleofaunas of higher latitudes, or whether it represents only a temporal or geographic anomaly.

Goin and Candela (2004) describe two factors that have limited our knowledge about South American marsupials, and Paleogene marsupials in particular. One is the biased geographic distribution of Paleogene faunas of South America, as noted above. The other is that most living marsupials are of small to very small size, an attribute that presumably pertained to most extinct members of the Marsupialia in South America. Indeed, most of the marsupial specimens from Santa Rosa are very tiny specimens. With the recent application of screen-washing techniques, such as those employed at Santa Rosa to fossil-bearing sediments in South America, an increasingly large number of new taxa of microvertebrates are being recovered. Although the fossils recovered in this manner are often primarily isolated teeth, these specimens still provide a wealth of new information about the species represented.

The Santa Rosan marsupials are quite informative regarding the early phases of several marsupial lineages. For example, in their discussion of the "opossum-like" marsupial *Rumiodon inti,* Goin and Candela (2004) identify and describe in detail a series of characters that separate the herpetotheriids (Herpetotheriidae) from didelphoids (Didelphidae). Their analysis supports the concept of temporally separate radiations for the two groups (early Tertiary for herpetotheriids; Neogene for didelphoids).

Among the polydolopimorphians are what appear to be very early representatives of that group. *Incadolops ucayali* is the most generalized prepidolopid (Polydolopimorphia, Prepidolopidae) currently known. *Hondonadia pittmanae* is one of the two polydolopimorphian taxa that cannot be placed to family, but it appears to be related at the generic level to marsupials of southern South America. It is placed in a new taxon, the superfamily Bonapartherioidea, family indeterminate. *Wamradolops tsullodon,* also a polydolopimorphian, is a possible early representative of the lineage leading to groeberiids (Groeberiidae), the origin of which remains a mystery. It is enigmatic in sharing derived features with several lineages of polydolopimorphians, and it is interpreted as suggesting monophyletic group status for a variety of polydolopimorphians. Goin and Candela (2004) describe how *W. tsullodon,* on the one hand, and the paucituberculatans *Perulestes cardichi, P. fraileyi,* and *Sasawatsu mahaynaq,* on the other, reveal the details of acquisition of the upper molar pattern in the two major lineages of South American "pseudodiprotodont" marsupials, the Polydolopimorphia and Paucituberculata, respectively. *Perulestes* cannot be assigned with confidence to a known family of Paucituberculata because most of its dental features are so generalized, although it is tentatively referred to the family Caenolestidae. *Sasawatsu* can only be referred to the Palaeothentidae even more tentatively.

Incorporating the new evidence from the Santa Rosan marsupials with that from new research on high-latitude marsupials, Goin and Candela (2004) propose and argue for a new classification of the Polydolopimorphia. This will surely stimulate new avenues of research into South American marsupials. It should also focus attention on the need for additional Paleogene faunas from Amazonia to complement those of higher latitudes.

There are many highlights, in addition to the systematic contributions, in Goin and Candela's (2004) paper on the Santa Rosan marsupials. They found, for example, that a strikingly large proportion of the marsupials were frugivorous or frugivorous–insectivorous. This interpretation was based on structural features of the teeth, such as molars with low cusps, heterodonty, thick enamel, and a reduction of shearing crests, among other characters. The size of these marsupials and their inferred diet is suggestive of arboreal locomotion, although this remains to be tested with currently unavailable cranial and postcranial material. Interestingly, one taxon of unknown ordinal affiliation, *Wirunodon chanku* is so small its possible feeding habits are difficult to interpret. Although the teeth of this species share features with opossums of carnivorous feeding habits, its very small size must have limited it to small insects or worms. The tiny opossum *Ki-*

ruwamaq chisu might also have been limited to feeding on small insects (Goin and Candela, 2004).

Wamradolops tsullodon was the most abundant marsupial taxon, making up about 42 percent of the total marsupial specimens. Features of the teeth of this species, plus its small size, suggested to Goin and Candela (2004) that it was probably mainly frugivorous. This species shares several of its most derived characters with groeberiids, which have been interpreted as extremely specialized toward frugivory, especially food items that are hard to process dentally (Simpson, 1970). This might well be true, but it might be useful to note that one of the most abundant types of insects in tropical forests are beetles, which have a characteristically hard carapace. As pointed out by Simpson (1970), the groeberiids are very limited in their temporal and spatial distribution, which suggested to him that their isolated occurrence, at the time of his writing, in the fossil record at Divisadero Largo, Argentina (Divisaderan SALMA, early Oligocene) resulted from a brief interval when their preferred(?) tropical habitat expanded briefly into higher latitudes.

At the other end of the spectrum is the complete absence of polydolopines (Polydolopimorphia, Polydolopidae), which are the best represented marsupial taxa in Paleogene levels in Patagonia. This is considered significant because it appears that the distribution of these multituberculate-like marsupials was also governed by the distribution of their preferred habitat. In this case, however, it was temperate, not tropical, habitats that were key to their distribution. The polydolopines appear to have been restricted to South American and Antarctic forests where beech trees, which prefer cool, humid climates, were dominant and podocarps and araucarian conifers were common.

The Santa Rosan marsupial paleofauna is also very intriguing for information pertaining to paleobiogeographic reconstructions. For example, if confirmed as a didelphimorphian, *R. inti* might be one of the first South American records of the family Herpetotheriidae, although work in progress by Goin and colleagues suggests that marsupials of this family were present in central Patagonia and eastern Brazil in the Paleocene (Goin and Candela, 2004). Herpetotheriids were previously known from lower Tertiary levels in North America, Europe, and northern Africa. They are thought to be related to North American and European peradectids.

Hypotheses of paleobiogeographic reconstructions also must include *Wirunodon chanku,* order and family indeterminate, although it might share characters with both peradectians and early didelphimorphians. This species appears closest to the early Eocene *Kasserionotherium tunisiense* Crochet, 1986, a ?peradectian of Tunisia. Goin and Candela (2004) suggest that this relationship, if confirmed, could be evidence of a biogeographic relationship between South America and Africa in the early Paleogene.

RODENTS

The rodents of the Santa Rosa local fauna represent the earliest known South American rodents. As noted by Frailey and Campbell (2004), they are fundamentally similar to each other, sharing a common pattern of four principal cusps connected by low crests. Available partial mandibles indicate that the species they represent were hystricognathous. Differences between the described genera are subtle, but consistent, and they allow the genera to be placed into three families: Erethizontidae, Agoutidae, and Echimyidae. In several cases, it is possible to identify trends that relate genera from Santa Rosa to younger South American taxa. Were it not for these identifiable trends, it might have been difficult to justify placing the Santa Rosan rodents into more than a single family.

By coincidence, the number of new rodent taxa is the same as that for marsupials: eleven new species in eight new genera. However, the diversity of the rodents is greater because there are at least six possible additional species of rodents that were not named because the material available was not considered adequate for name-bearing types. Despite the many similarities among the rodents of Santa Rosa, this diversity is considered quite significant.

The Santa Rosan rodents make significant contributions to the debate as to whether the ancestral caviid tooth condition was tetralophodont or pentalophodont. In reference to this debate, Butler (1985:395) stated, "The problem [of the ancestral number of lophs] will be resolved only when the position of the metacone is established by the discovery of a primitive form that still has traces of cusps." Were it so simple, the cuspate Santa Rosan rodents would seem to settle the question in favor of the tetralophodont condition because all of the Santa Rosan rodents have a basic tetralophodont pattern, and in only one genus (*Eobranisamys*) is this basic pattern altered by the addition of an accessory loph, a neoloph, to form a pentalophodont condition. The neoloph appears to have formed by the linear confluence and stabilization of minor cuspules in the posterior part of the metaflexus, probably together with the development and elongation of crenulations on the anterior surface of the posteroloph (Frailey and Campbell, 2004). Other taxa also have similar cuspules in the metaflexus, but they are highly variable and do not appear to have stabilized as a crest. Also pertinent to this question is the fact that in the Santa Rosan rodents the lateral two cusps on the upper teeth (paracone and metacone) and the medial two cusps on the lower teeth (entoconid and metaconid are characteristically closer to each other than are the cusps on the opposite side of each cheek tooth (protocone and hypocone in uppers; protoconid and hypoconid in lowers). This cusp arrangement, which occurs in all Santa Rosan rodents and is different from that of other early rodents, was seemingly considered by Butler (1985:395) to be a hypothetical arrangement, and the lack of specimens showing such an arrangement was described as a “difficulty” in arguing for an ancestral tetralophodont condition in caviids. As an ancestral condition in South American rodents, however, this cusp arrangement would appear to establish the basis for interpreting an important point of evolutionary divergence in early rodents.

The flattened, scissorslike cutting surface of Neogene and Recent caviids was not yet developed in the Santa Rosan rodents. Rather, the primary (i.e., temporally the longest functional) wear surface appears to have been terraced, but with no gross indication of labiolingual movement during chewing. Chewing motion appears to have been propalinal, as in modern caviids, but with elevated labial (upper molars) and lingual (lower molars) cusps until a late wear stage. Although this may represent an interesting type of early chewing pattern, detailed analysis of wear striae is required before any definitive statement about chewing motion in Santa Rosan rodents can be made (Frailey and Campbell, 2004).

The similarity of all of the Santa Rosan caviid rodents to each other, as well as to the erethizontids, suggested to Frailey and Campbell (2004) that the hypothesis of Wood (1949) and Wood and Patterson (1959), wherein the Acaremyinae (family Octodontidae) were considered to be the possible structural ancestors of caviid rodents, was doubtful. Frailey and Campbell (2004) placed no Santa Rosan rodents in the Acaremyinae, suggesting that the latter were already more specialized than the former. In this case, the Octodontidae, rather than representing the lineage that gave rise to the rest of the caviids, was a group that split off fairly early from the main group that gave rise to the rest of the caviids, as did the erethizontids. If so, then the erethizontid dental pattern would be closer to the ancestral caviid pattern than that of the acaremyines.

Although an ?Eocene age for the paleofauna is supported by available evidence (see “Age of the Santa Rosa Local Fauna”), the lack of an accurate age assignment hinders discussion of the origins and relationships of the South American rodents. The Santa Rosan rodent fauna is as diverse as the most diverse Deseadan SALMA (late Oligocene) localities known, which suggests that the origin and radiation of South American rodents must have occurred in the early Eocene, or before. Although principal previous hypotheses of South American rodent origins have focused on possible links to North American or African lineages, the ?Eocene Santa Rosan rodents would seem to raise objections to both of those possibilities (Frailey and Campbell, 2004).

An alternative hypothesis, that is, that the South American rodents are an autochthonous South American group of mammals derived from an ancestral Gondwanan lineage, has also been proposed by various authors, but it has not received much attention, primarily because of the lack of early Tertiary fossil evidence (see review of evidence in Frailey and Campbell, 2004). The Santa Rosan rodents seem to provide some of this missing evidence, and this alternative hypothesis is favored by Frailey and Campbell (2004). Clearly, however, additional, and older, fossil evidence is required before there can be said to be strong support for this alternative hypothesis.

Martin (2004) demonstrates that all three subtypes of multiserial Hunter–Schreger bands (HSB) present in Oligocene and younger “caviomorphs” were already present in rodents from Santa Rosa, including what is considered to be the most derived type of HSB. He did not discover anything atypical for “caviomorph” rodents in the six isolated incisors he examined, or anything more primitive than what is seen in Deseadan SALMA or later South American rodents.

To account for the diversity of incisor schmelzmuster in the rodents from Santa Rosa, Martin (2004) suggests two possibilities. One is that a dispersal event from African ancestors occurred in the early or middle Eocene. A difficulty with this is that the oldest African records of rodents with multiserial HSB are from the late Eocene (Jaeger et al., 1985; Martin, 1992), which would be contemporaneous with the Santa Rosan rodents as currently dated. The second possibility Martin (2004) suggests is that there were waves of dispersal of African ancestors carrying the different types of incisor schmelzmuster to South America shortly before the time of Santa Rosa. In that event, however, one might expect to find rodents in Africa that are much more similar in dental features to those of Santa Rosa than are actually known from late Eocene sites in Africa.

NOTOUNGULATES

The several specimens of notoungulates, representing at least three and possibly as many as six species, are the first Paleogene records of this group from lowland Amazonia (Shockey et al., 2004). Although a variety of notoungulates have been recorded from the Neogene of Amazonia, the interatheriid from Santa Rosa is the first record of any age for that family in Amazonia. The notoungulate specimens cannot be referred to any known genera or species, and placement even to family is uncertain in instances. The naming of new taxa was deferred until better material is available. With so few specimens and so few taxa, however, and no other lowland tropical Paleogene fauna for comparison, the notoungulates can offer few hints regarding their overall diversity and the importance of the group to the Amazonian mammalian fauna.

OTHER MAMMALS

The only possible specimen of a bat from Santa Rosa can only questionably be referred to the Chiroptera because it is damaged (Czaplewski and

Campbell, 2004). This specimen is important, however, because, if it is a bat, it represents only the third Paleogene record of a bat from South America and, if its age were indeed Eocene, it would be the oldest bat known from South America. The specimen would be equally important should additional specimens from the Santa Rosa locality show that it is not a bat because, in that case, it would represent an order of mammals previously unknown in the Paleogene of South America.

An unusual mammalian specimen from the Santa Rosa local fauna described by Goin et al. (2004) defied all attempts to relate it to any known group of mammals. This single, multicuspate molariform tooth seemed to lack enamel on its external surface, but it could not be determined whether this was natural or a result of taphonomic processes. Microstructure analysis was suggestive, but not conclusive, for mammalian enamel structure. Goin et al. (2004) concluded that this specimen might be best allocated to Gondwanatheria (family Ferugliotheriidae), but they admit that the tooth is quite baffling.

AGE OF THE SANTA ROSA LOCAL FAUNA

In their description of the geology of the Santa Rosa locality, Campbell et al. (2004) pointed out that there were no available stratigraphic data that could be of use in deriving the age of the Santa Rosa local fauna. The outcrop at the locality is so limited in extent and unremarkable in its lithic characteristics that it offers few clues to its formational context. Although Campbell et al. (2004) tentatively refer the fossiliferous deposit to the Paleocene–Eocene Yahuarango Formation, this is based on the age of the fossils derived from the faunal studies, not on stratigraphic data.

From their study of the marsupials, Goin and Candela (2004) concluded that the Santa Rosa local fauna was middle Paleogene in age but that there were insufficient data to assign it to any currently recognized SALMA. They considered it most likely that the paleofauna was middle to late Eocene in age, but there remained a slight possibility that it was of early Oligocene age. The older age is suggested by the perceived similarities of the Santa Rosan marsupials to early Tertiary South American marsupials, and even to early Tertiary North American, European, or African taxa. The majority of the eleven new taxa described appear to be related most closely to Paleocene or Eocene taxa, a few seem similar to early Oligocene taxa, and the others are so unique they provide no age-relevant information. Precise assignment of an age to the marsupials of the Santa Rosa paleofauna through correlation with paleofaunas of known ages is, therefore, difficult.

The rodents from Santa Rosa are the oldest known South American rodents (Frailey and Campbell, 2004), and, as such, they cannot be used to derive an age for the Santa Rosa local fauna through correlation with taxa elsewhere. On the basis of the stage of evolution of their teeth, the Santa Rosan rodents are clearly more primitive than the Deseadan SALMA (late Oligocene) rodents of Bolivia and Argentina, previously the oldest known rodent faunas of South America. Key characters include the brachydont condition of the Santa Rosan rodents, as opposed to the significantly more hypsodont state of younger rodents, and the minimal degree of fusion of the anterior two lophids of the lower molars of the Santa Rosan rodents compared with the greater fusion in younger taxa. The Deseadan SALMA rodents also had developed a chewing surface much more similar to that of younger caviids. The Santa Rosan rodents are interpreted as being older than the single rodent from the Tinguiririca local fauna of Chile, which is dated to 31.5 Ma (early Oligocene; Wyss et al., 1994), for the first two reasons cited above. However, with only a single, well-worn specimen from the Tinguiririca local fauna it is necessary to be a bit cautious about carrying interpretations too far. Still, the abundant marsupial paleofauna from Santa Rosa would appear to support the interpretation that the Santa Rosan rodents are older than that from the Tinguiririca fauna.

Information as to the age of the Santa Rosa local fauna on the basis of evidence from the notoungulates is mixed, but the lower end of the estimated age range approaches that inferred from the marsupials and rodents. According to Shockey et al. (2004), the toxodont specimens are higher crowned than Mustersan SALMA species, but lower crowned than Deseadan SALMA species of Toxodontia. In general, although the notoungulate species represented cannot be referred to known taxonomic categories with confidence, they appear most similar to known taxa that date from the early Oligocene (“Tinguiririca” age) to the late Oligocene (Deseadan SALMA). Until better material is available, however, how to interpret these hints from the notoungulates regarding the age of the fauna remains problematic, as noted by Shockey et al. (2004).

The combined evidence from the marsupials and rodents appears to support an age assignment of late Eocene, although the age could be either older (if more weight were given to the marsupials) or younger (if more weight were given to the notoungulates). Following the redating of Eocene SALMAs by Kay et al. (1999), the best compromise appears to be to consider the Santa Rosa local fauna as dating to the Mustersan SALMA until better age-pertinent data are available.

ENVIRONMENT OF DEPOSITION AND PALEOECOLOGY

As noted by Campbell et al. (2004), the fossils were deposited in lenses of coarse-grained, mostly sand-sized sediment with a matrix of clay within massive beds of clay. These lenses are not particularly thick, ranging from just 1–2 cm to 30 cm in thickness, with abrupt transitions to fine-grained clay deposits above and below. The presence of some large (i.e., up to 8–10 cm) bone fragments indicates fairly swift water movement, at least on occasion, but there are no rock clasts above sand size. All of the lenses sampled at the Santa Rosa locality were fossiliferous, although similar appearing coarse-grained lenses in other outcrops that were sampled were not. That there were multiple depositional events, that is, episodes of fossiliferous lens formation, at the Santa Rosa site indicates a fairly stable surrounding habitat from which the fossils came, but shifting water currents probably deposited bed load in different areas at different times. It is possible that analysis of the fish fossils from the site will provide more information about the type of aquatic environment in which the paleofauna was deposited.

The reason for the rich accumulation of fossils at Santa Rosa is unclear. The largest mammals preserved, the notoungulates, reached the size of sheep, and there were a few large crocodilians that may have been able to seek them out as prey. Most of the fossils, however, are microvertebrates, and the vast majority of these are only a few millimeters in size. Both of the most abundant groups of mammals, the rodents and marsupials, are represented by older individuals, as indicated by extensive wear on the teeth, as well as extremely young individuals with no visible wear on the teeth. For the most abundant taxa, a continuum of wear stages indicates individuals from a wide range of ages. None of the marsupials show any evidence of having passed through a predator, as might be indicated by acid etching of the enamel (Goin and Candela, 2004), but there are numerous examples of etched rodent teeth.

Goin and Candela (2004) suggested that many of the marsupials might have been arboreal animals, and although we know nothing of the habits of the early rodents, it is probable that some of them were also arboreal, or at least scansorial. A wide sampling of arboreal taxa in the fossil record is relatively rare, and it is indeed fortunate that we have a good sample from the first Paleogene fauna of tropical Amazonia. The presence of a presumed bat and a few birds indicates that at least a small portion of the flying guild was sampled as well.

In their discussion of individual taxon abundance in Deseadan SALMA rodent faunas, Patterson and Wood (1982) pointed out that, within any given sample of rodents, whether fossil or Recent, one species seemed to be overwhelmingly dominant in terms of numbers. In the Santa Rosa local fauna, the same is true for both the marsupials and rodents, although more so for the former than the latter. For the marsupials, *Wamradolops tsullodon* represented almost 42 percent of the paleofauna, whereas for the rodents, *Eoespina woodi* represented almost 25 percent of the fauna. Two species qualified as the next most common rodent, with *Eoincamys pascuali* and *Eobranisamys romeropittmanae* each representing about 13 percent of the paleofauna.

If borne out, a Mustersan SALMA age for the Santa Rosa local fauna places it at a critical period of biotic change in South America. Following Kay et al. (1999), the Mustersan SALMA is now considered to range from approximately 35 to 32 Ma, or to straddle the Eocene–Oligocene boundary at 33.7 Ma (Berggren et al., 1995). As Pascual and Ortiz-Jaureguizar (1990), Woodburne and Swisher (1995), and Kay et al. (1999) point out, this period coincides with major compositional changes in mammalian communities in North America (the "Terminal Eocene Event"), Europe ("La Grande Coupure"), and Patagonia, South America. For Patagonia, where most Paleogene mammalian faunas of South America are found, Kay et al. (1999) describe the period from 34.5 to 28.5 Ma as one characterized by a transition from relatively warmer to cooler conditions. They describe this cooling as having the effect of decreasing mean annual precipitation and temperature, increasing seasonal temperature amplitude, and decreasing the mean temperature of the coldest month. A dramatic increase in the number of hypsodont taxa in southern South America was the most obvious result of these climatic effects. Hypsodonty appears to correlate with a more gritty diet, which can be brought on by an increase in available siliceous grasses or dust (Kay et al., 1999). An increase in hypsodonty could easily be tied to a decrease in tropical vegetation as cooling and a decrease in rainfall brought about a reduction in the distribution of tropical ecozones.

On a global scale, it would be expected that cooling in the high latitudes would lead to a greater heat gradient between the equatorial regions and the poles. This would lead, in turn, to a greater level of heat exchange between the tropics and the polar regions, which undoubtedly would have affected (i.e., strengthened) global wind patterns. How this might have affected the climate, and especially patterns of precipitation, in proto-Amazonia is unknown to me, but it would be unrealistic to expect the equatorial regions of South America to be unaffected by the dramatic changes in climate seen in the higher latitudes of that continent at the Eocene–Oligocene transition.

Although details of the Eocene paleoclimate of northern South America are not particularly well known, I think it is important to recognize the following facts. First, although the Santa Rosa site was a few degrees farther south in the late Eocene than it is today (possibly 2–5 degrees), it would still have been within existing climatic belts. Second, in the mid- to late Eocene, the Andes were experiencing their first (Mégard, 1984, 1987; Sébrier et al., 1988; Ellison et al., 1989; and Sébrier and Soler, 1991) or second (Noble et al., 1990) of up to six post-Cretaceous phases of uplift. The elevation of the mountain ranges raised at this time, and that of those produced by the preceding Cretaceous uplift events, is still unknown, but it can safely be assumed that these ranges did not begin to approach the heights reached by today's Andes. For example, an estimate by Jordan et al. (1997) was that Eocene uplift accounted for 25–50 percent of the elevation of the Western Cordillera of the Central Andes. And after reviewing available data pertaining to the uplift history of the Central Andes, several degrees of latitude south of the Santa Rosa locality, Gregory-Wodzicki (2000) concluded that the Western Cordillera in that region was no more than half of its modern elevation by 25–18 Ma (late Oligocene–early Miocene) and the Eastern Cordillera was at 25–30 percent of its modern elevation by 20 Ma (early Miocene). Widespread uplift of the Eastern Cordillera apparently did not begin until the Oligocene. Extrapolation from these conclusions to the uplift history of the Andes much farther north, that is, to the west of Santa Rosa, and to a period in the late Eocene is not yet justifiable, but this information does provide a general sense of the scale of the Andes in the late Eocene.

One consequence of a low Andean range is that orographic uplift, which is such a dominant feature of the climate of western Amazonia today and which produces so much of the precipitation in western Amazonia, probably would have been a small fraction of what is seen today. It would also have occurred farther to the west. In the absence of the high Andes, much of the moisture now trapped and recirculated within the Amazon Basin would have been carried westward over the Pacific coast of South America, producing a much drier proto-Amazonia.

Third, the Santa Rosa locality is today over 2400 km from the northeast coast of South America, the closest source for moisture-laden, tropical Atlantic winds, and this distance was probably similar in the Eocene. Depending on the seasonal strength of the prevailing trade winds and Eocene topography, precipitation from these winds over northeastern and eastern South America might have limited the amount of atmospheric water available to distant western Amazonia and increased seasonality in that region.

Furthermore, edaphic conditions might have promoted wide expanses of savanna vegetation in proto-Amazonia, much as they do today, even though today the region is probably under a climatic regime with much greater precipitation. With less rainfall, edaphic conditions might have contributed to even more widespread tropical savannas in South America.

Given the above facts, there is little reason to expect that the present vast expanse of tropical forest in Amazonia existed in the Paleogene. Indeed, it is perhaps more reasonable to speculate that the Santa Rosa local fauna represents a fauna from a riparian environment surrounded by savanna, a condition that would sustain brachydonty among the mammals of the forest (marsupials and rodents) and promote hypsodonty among the large mammals of the savanna (the notoungulates). Hypothetically, these environmental conditions might well have existed for some time prior to the Eocene–Oligocene transition, and they might also have been even more dominate prior to the first post-Cretaceous uplift of the Andes. If this were the case, using any type of "hypsodonty index" to estimate the age of the Santa Rosa local fauna could lead to significant error.

By itself, the Santa Rosa local fauna cannot be used to address questions of biotic change in the tropics at the Eocene–Oligocene transition, even if such had been occurring at the time of deposition, because it represents only a thin slice of time. Nonetheless, I consider it doubtful that Amazonia did not experience any affects from the climatic changes then occurring in higher latitudes. As with so many other questions raised by the Santa Rosa local fauna, that of how the Eocene–Oligocene climatic shift affected biotic communities in tropical Amazonia can only be answered by additional Paleogene faunas from the region.

ACKNOWLEDGMENTS

I thank all of the authors who contributed to our understanding of the Santa Rosa local fauna through their contributions to this volume. Their assistance and patience is much appreciated. I thank Nick Czaplewski, Carl Frailey, Francisco Goin, John Lundberg, and Thomas Martin for their comments that helped improve this summary.

LITERATURE CITED

Berggren, W.A., D.V. Kent, C.C. Swisher III, and M.-P. Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy. In *Geochronology time scales and global stratigraphic correlation,* ed. A. Berggren, D.V. Kent, and J. Hardenbol. Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication, 54:129–212.

Butler, P. 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. In *Evolutionary relationships among rodents. A multidisciplinary analysis,* ed. W.P. Luckett and J.-L. Hartenberger, 381–401. New York: Plenum Press.

Campbell, K.E., Jr., C.D. Frailey, and L. Romero-Pittman. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: Implications for the Great American Faunal Interchange. *Instituto Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín* 23:1–152.

———. 2004. The Paleogene Santa Rosa local fauna of Amazonian Perú: Geographic and geologic setting. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 3–14.

Crochet, J.-Y. 1986. *Kasserinotherium tunisiense* nov. gen., nov. sp., troisième marsupial decouvert en Afrique (Eocene inferieur de Tunisie). *Comptes Rendus de l'Académie des Sciences, Paris* 302(14):923–926.

Czaplewski, N.J., and K.E. Campbell, Jr. 2004. A possible bat (Mammalia: Chiroptera) from the ?Eocene of Amazonian Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 141–144.

Ellison, R.A., B.A. Klinck, and M.P. Hawkins. 1989. Deformation events in the Andean orogenic cycle in the Altiplano and Western Cordillera, southern Peru. *Journal of South American Earth Sciences* 2(3):263–276.

Flynn, J.J., and C.C. Swisher III. 1995. Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. In *Geochronology time scales and global stratigraphic correlation,* ed. A. Berggren, D.V. Kent, and J. Hardenbol, Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication, 54:317–333.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Río Acre region, western Amazonia. *Contributions in Science* 374:1–46.

Frailey, C.D., and K.E. Campbell, Jr. 2004. Paleogene rodents from Amazonian Peru: The Santa Rosa local fauna. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 71–130.

Goin, F., and A. Candela. 2004. New Paleogene marsupials from the Amazon Basin of eastern Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 15–60.

Goin, F.J., E.C. Vieytes, M.G. Vucetich, A.A. Carlini, and M. Bond. 2004. Enigmatic mammal from the Paleogene of Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 145–153.

Gregory-Wodzicki, K. 2000. Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin* 112:1091–1105.

Jaeger, J.-J., C. Denys, and B. Coiffait. 1985. New Phiomorpha and Anomaluridae from the late Eocene of north-west Africa: Phylogenetic implications. In *Evolutionary relationships among rodents,* ed. W.P. Luckett and J.-L. Hartenberger, 567–588. New York: Plenum Press.

Jordan, T.E., J.H. Reynolds III, and J.P. Erikson. 1997. Variability in age of initial shortening and uplift in the Central Andes, 16–33°30′ S. In *Tectonic uplift and climate change,* ed. W.F. Ruddiman, 41–61. New York: Plenum Press.

Kay, R.F., R.H. Madden, R.L. Cifelli, and J.J. Flynn (eds.). 1997. *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia.* Washington, D.C.: Smithsonian Institution Press, 592 pp.

Kay, R.F., R.H. Madden, M.G. Vucetich, A.A. Carlini, M.M. Mazzoni, G.H. Re, M. Heizler, and H. Sandeman. 1999. Revised age of the Casamayoran South American Land Mammal "Age"—Climatic and biotic implications. *Proceedings of the National Academy of Sciences, Washington* 96(23):13235–13240.

Marshall, L., and T. Sempere. 1993. Evolution of the Neotropical Cenozoic land mammal fauna in its geochronologic, stratigraphic, and tectonic context. In *Biological relationships between Africa and South America,* ed. P. Goldblatt, 328–392. New Haven and London: Yale University Press.

Martin, T. 1992. Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire,* 1–168.

———. 2004. Incisor enamel microstructure of South America's earliest rodents: Implications for caviomorph origin and diversification. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 131–140.

Mégard, F. 1984. The Andean orogenic period and its major structures in central and northern Peru. *Journal of the Geological Society of London* 141:893–900.

———. 1987. Structure and evolution of the Peruvian Andes. In *The anatomy of mountain ranges,* ed. J.-P. Schaer and J. Rodgers, 179–210. Princeton, New Jersey: Princeton University Press.

Noble, D.C., E.H. McKee, T. Mourier, and F. Mégard. 1990. Cenozoic stratigraphy, magmatic activity, compressive deformation, and uplift in northern Peru. *Geological Society of America Bulletin* 102:1105–1113.

Pascual, R., and E. Ortiz-Jaureguizar. 1990. Evolving climates and mammal faunas in Cenozoic South America. *Journal of Human Evolution* 19:23–60.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. In *Evolution, mammals, and southern continents,* ed. A. Keast, F.C. Erk, and B. Glass, 247–309. Albany: State University of New York.

Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149(7):371–543.

Rüegg, W. 1947. Estratigrafía Comparada del Oriente Peruano. *Boletín de la Sociedad Geológica del Perú* 20:57–100.

———. 1956. Geología y Petróleo en la Faja Subandina Peruana. *Simposio Sobre Yacimientos de Petróleo y Gas, XX Congreso Geológico International IV, Mexico,* 89–139.

Sébrier, M., A. Lavenu, M. Fornari, and J.-P. Soulas. 1988. Tectonics and uplift in Central Andes (Peru, Bolivia and northern Chile) from Eocene to Present. *Géodynamique* 3(1/2):85–106.

Sébrier, M., and P. Soler. 1991. Tectonics and magmatism in the Peruvian Andes from late Oligocene time to the Present. *Geological Society of America, Special Paper* 265:259–278.

Shockey, B., R. Hitz, and M. Bond. 2004. Paleogene notoungulates from the Amazon Basin of Peru. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru,* ed. K.E. Campbell, Jr. Natural History Museum of Los Angeles County, Science Series 40, 61–69.

Simpson, G.G. 1970. Addition to the knowledge of *Groeberia* (Mammalia, Marsupialia) from the mid-Cenozoic of Argentina. *Breviora* 362:1–17.

Wood, A.E. 1949. A new Oligocene rodent from Patagonia. *American Museum of Natural History, Novitates* 1435:1–54.

Wood, A.E., and B. Patterson. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120(3):279–428.

Woodburne, M., and C.C. Swisher III. 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. In *Geochronology time scales and global stratigraphic correlation,* ed. A. Berggren, D.V. Kent, and

J. Hardenbol. Society of Economic Paleontologists and Mineralogists (SEPM) Special Publication, vol. 54:335–364.

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 of Natural History, Novitates* 3098:1–31.

Received 2 July 2003; accepted 29 December 2003.

Natural
History
Museum
of Los Angeles County
900 Exposition Boulevard
Los Angeles, California 90007