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BOLETÍN Nº 23
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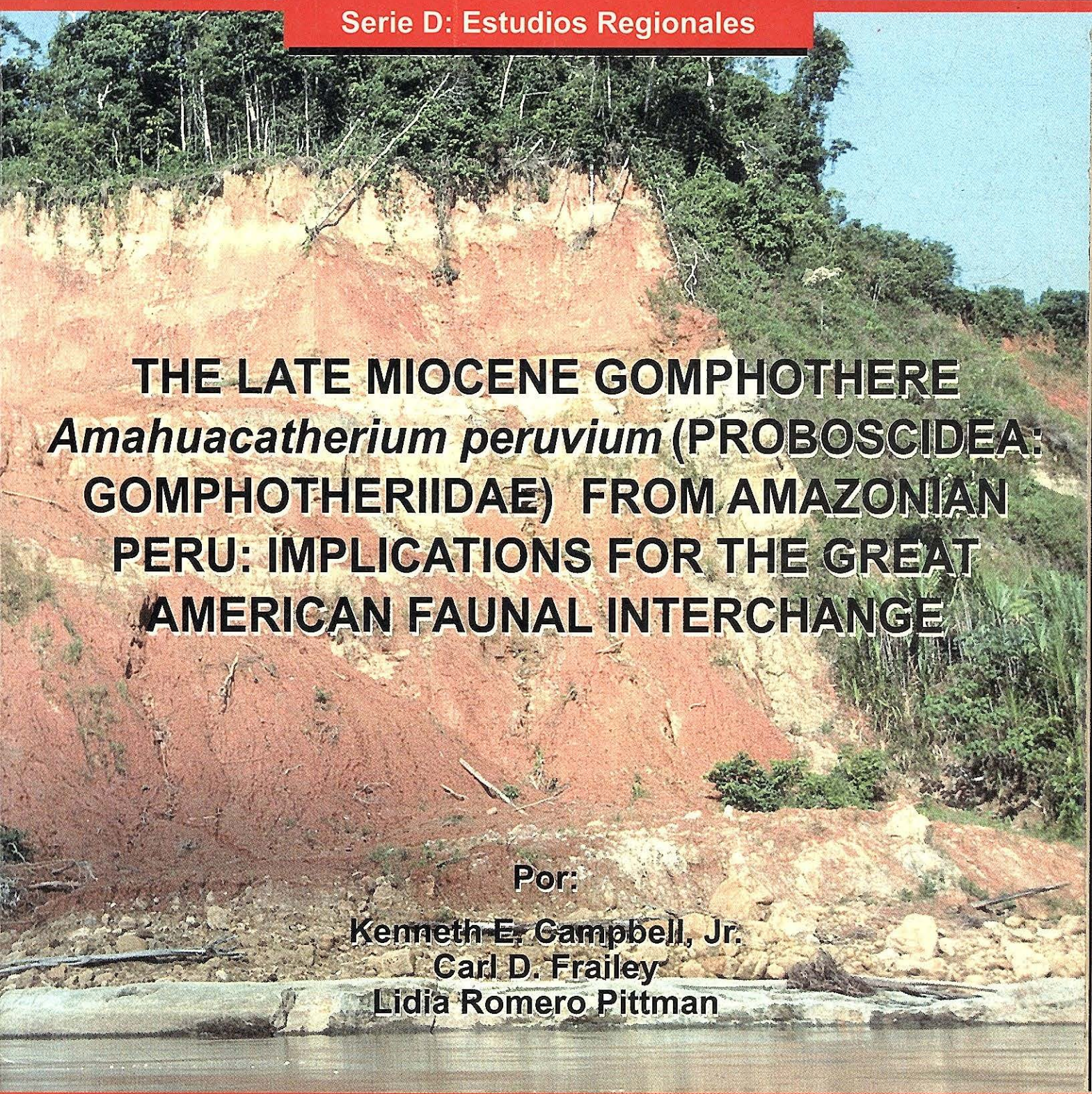

THE LATE MIOCENE GOMPHOTHERE *Amahuacatherium peruvium* (PROBOSCIDEA: GOMPHOTHERIIDAE) FROM AMAZONIAN PERU: IMPLICATIONS FOR THE GREAT AMERICAN FAUNAL INTERCHANGE

Por:

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INGEMMET
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By
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ABSTRACT

Osteological characters of the recently described proboscidean *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) are presented in detail. This proboscidean was recovered from Upper Miocene (Chasicoan) deposits exposed along the Río Madre de Dios in the Amazonian lowlands of southeastern Peru. It was a tetrabelodont, brevirostrine gomphothere with highly derived lower jaws that retained tusks and molars with a moderately complex enamel pattern. The taxon is interpreted as representing an early lineage of brevirostrine gomphotheres of the subfamily Cuvieroniinae that was derived from the rhynchorostrine complex, although it is possible that this lineage arose independently from that of *Gomphotherium* without being part of the rhynchorostrine complex.

Amahuacatherium peruvium came from below the basin-wide Ucayali Unconformity, which formed during a period of basin-wide erosion that occurred during the early late Miocene global sea level lowstand initiated at ~12.0 Ma. This taxon represents the earliest occurrence of proboscideans, or of any North American mammal, in South America. It also represents the earliest occurrence in both North America and South America of any participant in the Great American Faunal Interchange. Some North American proboscidean taxa may be derived from lineages that arose in South America during the late Miocene or Pliocene.

A review of the geology of western Amazonia places the specimen in the context of the geologic history of the region and establishes the probable age of the specimen as at least ~9.5 Ma, and possibly significantly older. The age of the specimen, which is well supported by a $^{40}Ar/^{39}Ar$ of 9.01±0.28 Ma date on a stratigraphically higher volcanic ash, and the southern position of its locality suggests that movement of proboscideans into South America may have occurred significantly earlier, or during the early late Miocene sea level lowstand initiated at ~12.0 Ma. We propose that proboscideans dispersed from North America to South America following a route through Panama via the Serranías de San Blas-Darién that connected to the Baudo Arch of the allochthonus Choco Terrane

and ended at the Istmina Hills of Colombia. This route bypassed the Bolivar Trough, which did not close until much later. It appears that peccaries, camelids, and tapirs were other North American groups that dispersed to South America in the late Miocene.

A review of the current understanding of the timing and physical nature of the connection between Central America and South America provides new insights into a more complex Great American Faunal Interchange than previously appreciated. We propose that extensive faunal interchange began much earlier than the 2.7-2.5 Ma date currently recognized and that most of the taxa crossing the isthmus early were eurytrophic or tropical forest dwellers. The determining factors as to which taxa participated in the early phases of the interchange were related more to individual size, swimming ability, and habitat preferences of any given taxon than they were to global climatic shifts or glacially induced sea level fluctuations. Taxa inhabiting the tropical forests probably played a dominant role in the interchange, a role that is only now being recorded. The final terrestrial link between North America and South America was established in the early Pliocene as accretion of the allochthonous Choco Terrane to western Colombia was completed, although marine incursions across the Central American isthmus to the north may have temporarily interrupted this link. The participation of savanna-adapted taxa in the interchange may have been only a late feature of the GAFI, occurring when global cooling and Plio/ Pleistocene sea level lowstands facilitated the establishment of temporary coastal plains or interior savannas on the Central American isthmus and in northern South America.

RESUMEN

Se presentan en detalle los caracteres osteológicos del proboscideo *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) descrito recientemente. Este proboscideo fue recuperado de los depósitos del Mioceno (Chasicoan) expuestos a lo largo del río Madre de Dios en las tierras bajas al sudeste del Perú. Este proboscideo fue un gomphothere tetrabelodonte y brevirostrino con mandíbulas inferiores que conservan los incisivos y molares con un patrón de esmalte ligeramente complicado. El taxón es interpretado como el representante de un linaje antiguo de gomphotheres brevirostrinos de la subfamilia Cuvieroniinae que se derivó del complejo rhynchorostrino, aunque es posible que este linaje se haya originado independiente de aquellos de *Gomphotherium* sin ser parte del complejo rhynchorostrino.

El *Amahuacatherium peruvium* proviene de la parte baja de la discordancia que se formó durante un período de gran erosión en toda la cuenca del Amazonas al comienzo del Mioceno tardío, cuando el nivel del mar comenzó a descender globalmente hace 12.0 Ma. Este taxón representa la ocurrencia más temprana de proboscideos, o de cualquier mamífero norteamericano en América del Sur, también representa la ocurrencia más temprana en América del Norte y en América del Sur de cualquier participante en el Gran Intercambio Faunal Americano. Algunos taxa de proboscideos norteamericanos pueden derivarse de linajes que se originaron en América del Sur durante el Mioceno tardío o Plioceno.

Una revisión de la geología de la Amazonía pone al espécimen en el contexto de la historia geológica de la región y establece la edad probable del espécimen por lo menos de 9.5 Ma y posiblemente más antiguo. La edad del especimen es sustentada por una datación de $^{40}Ar/^{39}Ar$ de 9.01 ± 0.28 Ma, edad de una muestra de ceniza volcánica estratigráficamente más alta, situada al sur de esta localidad, lo que sugiere que el movimiento de proboscideos en América del Sur pudo haber ocurrido significativamente más temprano o durante el Mioceno cuando el nivel del mar empezó a descender hace 12 Ma.

Nosotros proponemos que los proboscideos de América del Norte dispersados en América del Sur siguieron una ruta a través de Panamá vía las serranías de San Blas-Darién que conectó al arco de Baudo y el Terreno alóctono de Chocó y finalizó en las colinas Istmina de Colombia. Esta ruta desvió el Bolívar Trough, que no se cerró hasta mucho más tarde. Parece que los sajinos, camélidos y tapires fueron otros grupos norteamericanos que se dispersaron a América del sur en el Mioceno tardío.

Una revisión del actual conocimiento del tiempo y naturaleza física de la conexión entre América Central y América del Sur proporciona nuevas visiones dentro de un más complicado Gran Intercambio Faunal Americano que previamente apreciáramos.

Nosotros proponemos que ese extenso intercambio faunal empezó mucho más temprano que 2.7 – 2.5 Ma, datación actualmente reconocida y que la mayoría de los taxa que cruzaron temprano el istmo fueron euritróficos o habitantes del bosque tropical. Los factores determinantes acerca de la participación de los taxas en las fases tempranas del intercambio estaban relacionados más al tamaño individual, habilidad de nadar y preferencia del hábitat de cualquier taxón, dado que ellos fueron hacia un cambio climático global o glacialmente inducido a fluctuaciones del nivel del mar. Taxas que habitaron los bosques tropicales probablemente jugaron un rol dominante en el intercambio, un rol que solo está siendo ahora indicado. El vínculo final entre América del Norte y América del Sur se estableció en el Plioceno temprano y como acreción del Terreno alóctono de Chocó en Colombia occidental fue completada, aunque las incursiones marinas que atraviesan el istmo de América Central hacia el Norte pudo haber interrumpido este vinculo temporalmente.

La participación de los taxas de sabana adaptados en el intercambio pudo haber sido solo un rasgo tardío del Gran Intercambio Faunal Américano, ocurrido cuando el enfriamiento global y la baja del nivel del mar facilitaron en el Plio-Pleistoceno el establecimiento de llanuras costeras temporales o sabanas en el interior del istmo centroamericano y al norte de América del Sur.

INTRODUCTION

As movements of the earth's crust gradually connected North and South America at the close of the Tertiary, land animals expanded their ranges northward and southward in what is known as the Great American Faunal Interchange (GAFI). The sequence of range extensions, or dispersals, of different taxonomic groups between continents, the survival and diversification of dispersing taxa, and the effect of new competition on indigenous species have been subjects of interest to paleontologists and neontologists alike for more than a century. Accordingly, a tremendous literature has built up concerning the events surrounding the GAFI, a literature that has had a profound effect on how we view the evolutionary history of the faunas of the Americas. A very partial listing of the more notable works includes the following: Wallace, 1876; Scott, 1937; Simpson, 1940, 1950, 1980; Patterson and Pascual, 1972; Webb, 1976, 1978, 1985, 1991; Marshall, 1979, 1985, 1988; Marshall et al., 1982; and Webb and Marshall, 1982.

From the more recent literature on the GAFI [e.g., Stehli and Webb (1985), Marshall and Sempere (1993), MacFadden et al. (1993), Webb and Rancy (1996), Webb (1997, 1998)], one could easily conclude that the major features of the GAFI are well known and that all that remains is to fill in the details. In reality, the rarity of fossils from Central America and northern South America, and particularly the Amazon Basin, has hindered a full understanding of this event. The subject of this paper, a recently described fossil proboscidean from the lowlands of the Peruvian Amazon, radically alters the perceived involvement of one group of mammals in the GAFI and raises major questions about the accuracy of the current GAFI paradigm. We take this opportunity to review various aspects of the current GAFI paradigm and present new hypotheses relating to the dynamic history of the GAFI.

Heretofore, South American proboscideans have been relegated to relatively minor status in the scheme of faunal shifting between the Americas, and paleontological interest in them was limited to questions of relatedness and habitat preferences among these presumed

late arrivals from the north (e.g., Casamiquela et al., 1996). Curiously, all known South American proboscideans were gomphotheres. In North America, the gomphotheres had been dominant among late Miocene and Pliocene proboscideans, but on that continent their diversity and numbers declined in the Pleistocene while seeming to proliferate in South America. Two (Lambert, 1996), and perhaps three (Dudley, 1996), of the four gomphothere genera that occurred in South America in the Pleistocene were present in North America in the Pliocene (Savage and Russell, 1983). The natural conclusion was that diversification of the group had preceded their entrance into South America (Simpson and Paula Couto, 1957). According to Savage (1955), a Pliocene arrival into South America, which was unsupported by direct fossil evidence, was necessary to connect the apparent ancestral group in North America with the continuation of gomphotheres in South America. With the discovery of *Amahuacatherium peruvium* in Upper Miocene strata in the Amazon Basin of eastern Peru, the entire existing scenario of diversification and dispersal of gomphotheres is challenged.

DEFINITIONS

The following abbreviations are used in the text and figures:

AMNH	American Museum of Natural History
F:AM	Frick Collection, American Museum of Natural History
FGS	Florida Geological Survey
GAFI	Great American Faunal Interchange
INGEMMET	Instituto Geológico, Minero y Metalúrgico
LACM	Natural History Museum of Los Angeles County
SALMA	South American Land Mammal Age
STFB	Sub-Andean Thrust and Fold Belt
UCMP	University of California, Museum of Paleontology

DISCUSSION OF *Amahuacatherium peruvium*

Systematics and Description

Class Mammalia
Family Gomphotheriidae Cabrera 1929
Subfamily Cuvieroniinae Cabrera 1929
Amahuacatherium Romero-Pittman 1996

Type Species. *Amahuacatherium peruvium* Romero-Pittman 1996.

Emended Diagnosis. Gomphotheriid with mandibles short (brevirostrine condition), very shallow below M_3, with total depth approximately two-thirds of width. Lower tusks present, rooted under and immediately medial to posterior portion of M_2, with roots with relatively large dorsal groove above longitudinal axes. M_3 with 5 lophids and a terminal cone (or half lophid), all lophids anteriorly convex, primary cones slender and inclined anteriad; and posttrite cones placed anterior to pretrite cones; separation of apexes of primary cones in each lophid equal to height of individual cones; accessory buttressing conules present on all pretrite cones; trefoiling on all pretrite cones with moderate wear, incipient trefoiling on some posttrite cones with moderate to extreme wear; multiple small conules in lingual valleys; anterior and labial cingulae, but no lingual cingulum. M_2 with posterior lophid with pretrite trefoiling, no posttrite trefoiling, multiple small conules, and no lingual or labial cingulae. Upper third molars with multiple small conules.

Etymology. From *Amahuaca*, name of a tribe of Amerindians indigenous to eastern Peru; and *-therium*, from Greek *-therion*, beast, animal.

Amahuacatherium peruvium Romero-Pittman 1996

Holotype. Mandibles with dentition, lacking ascending rami and symphysis; partial M^3's, and postcranial fragments, INGEMMET No. 2801, Paleontology Collections of the Instituto Geológico, Minero, y Metalúrgico of Peru. Material is highly fragmented;

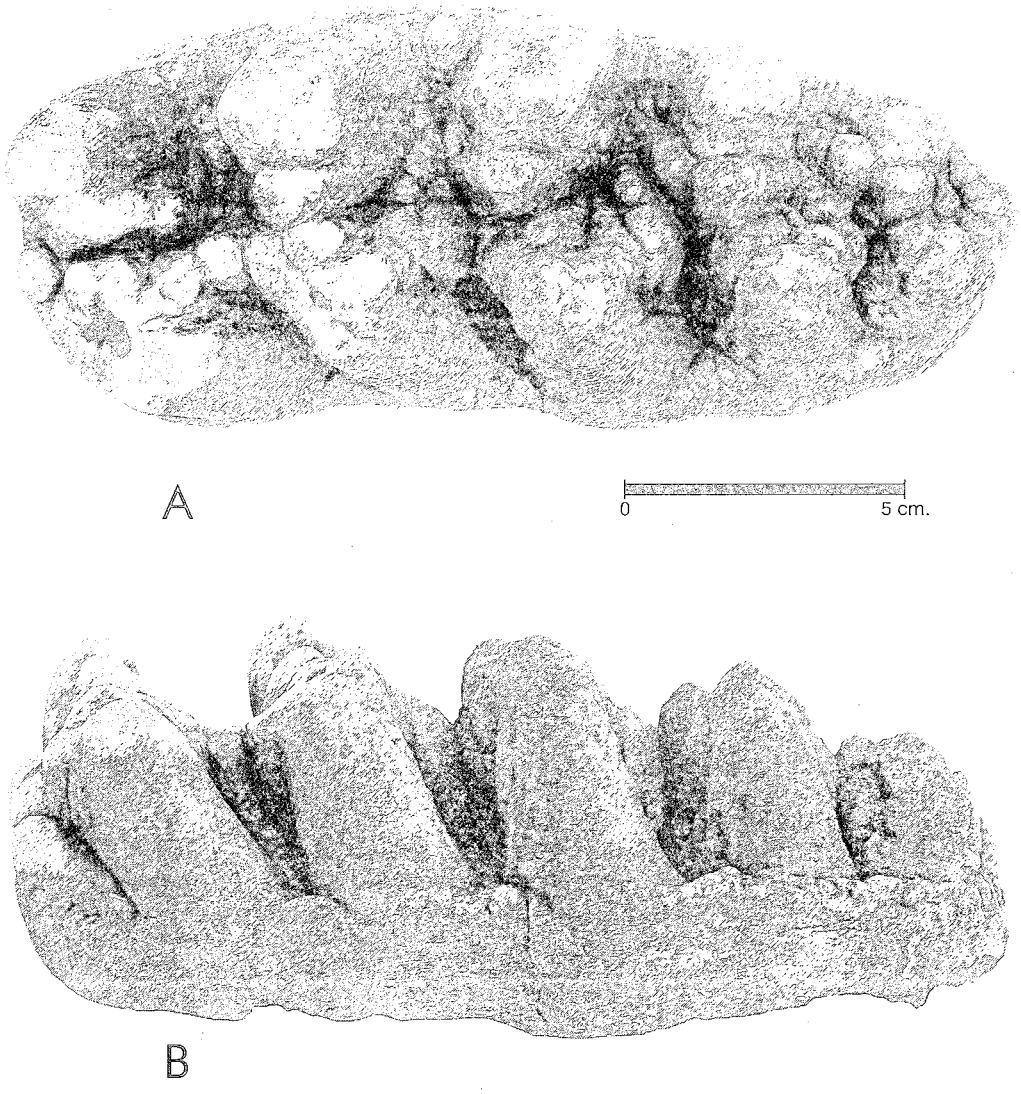
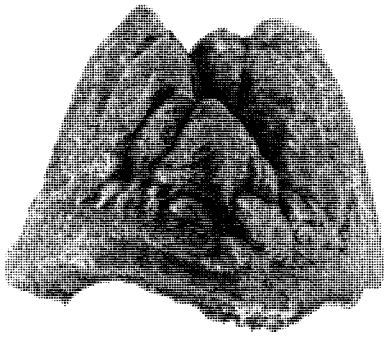


Figure 1. Holotypical left M_3 of *Amahuacatherium peruvium*, in A, occlusal; B, labial; C, lingual; and D, distal view. Note the open, U-shaped valleys, the many small conules filling the lingual valleys, the slender cones without swollen bases inclined anteriad, the minimal mediad inclination of the pretrite primary cones, and the accessory buttressing conules on the pretrite cones that would produce trefoiling with wear. Comparable accessory buttressing conules are absent adjacent to the second and third posttrite cones, but the remaining posttrite cones would show incipient trefoiling with moderate to extreme wear. Photograph from a cast, LACM 140398. Scale bar = 5 cm.

C



D

Figure 1. Continued

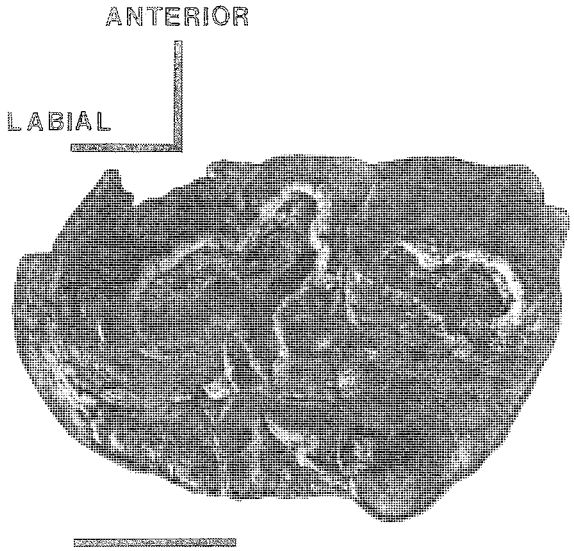


Figure 2. Holotypical M_2 of *Amahuacatherium peruvium*, in occlusal view. Scale bar = 2 cm.

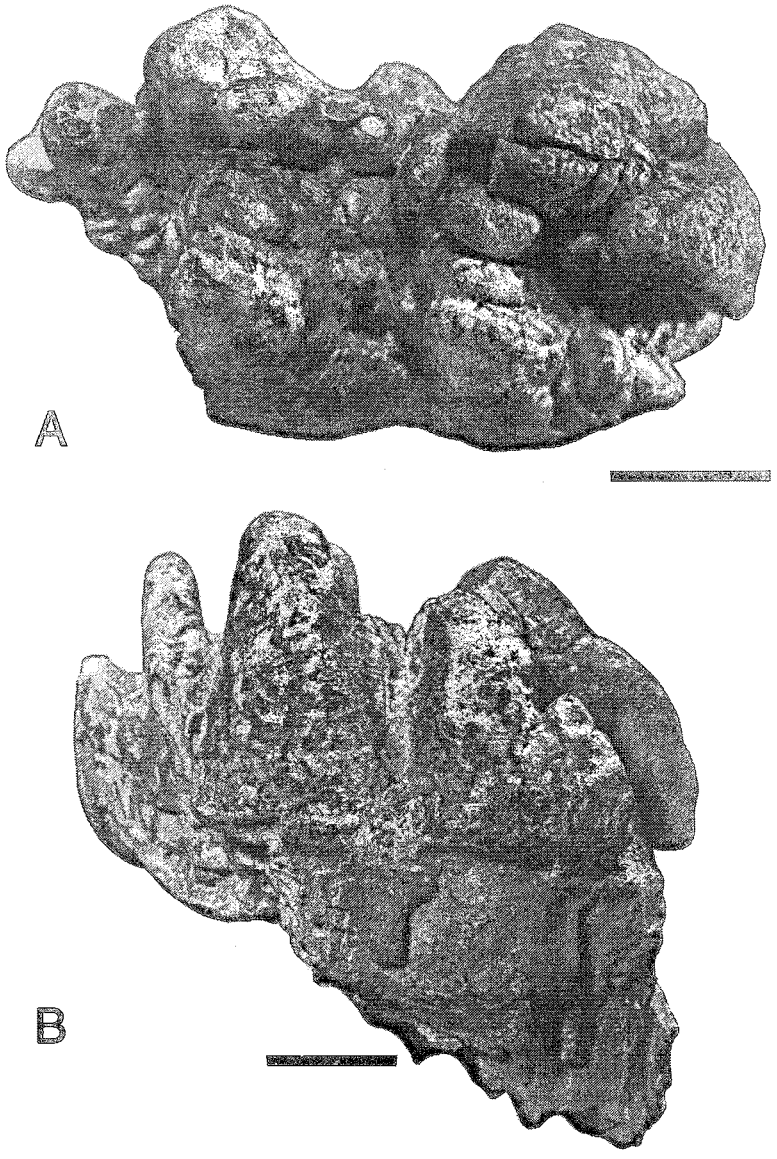


Figure 3. Posterior portion of the holotypical left M^3 of *Amahuacatherium peruvium*, in A, occlusal and B, lingual view. Anterior to left. Note the many small conules and the tall, slender cones without swollen bases. Scale bars = 2 cm.

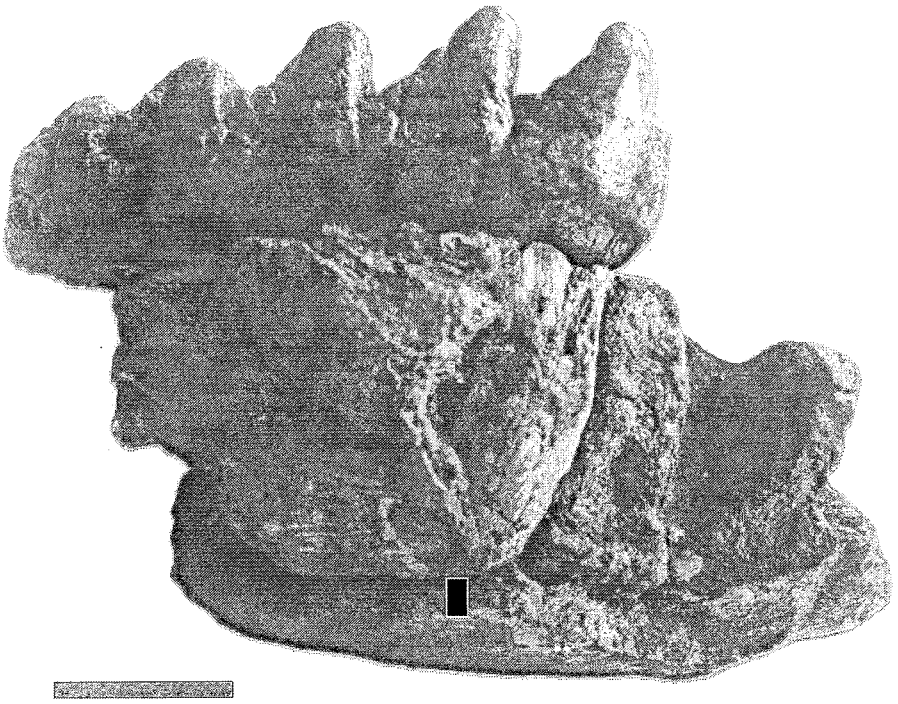


Figure 4. Medial view of partial left mandibular ramus of *Amahuacatherium peruvium*, with M_3 in place. The crown of the tooth was broken from its root and later reattached, resulting in the apparent line between the two parts. Anterior to the M_3 is the alveolus for the posterior root of the M_2. The M_2 and M_3 are shown together in Fig. 5. The specimen is resting slightly on its side in this view, giving an oblique view that exposes part of the ventral surface of the ramus. The vertical bar under the root of the M_3 indicates the approximate actual thickness of the ramus at that point. The posterior end of the root of the lower tusk was positioned anterior to the root of the M_3, just under the medial portion of the posterior root of the M_2. Scale bar = 5 cm.

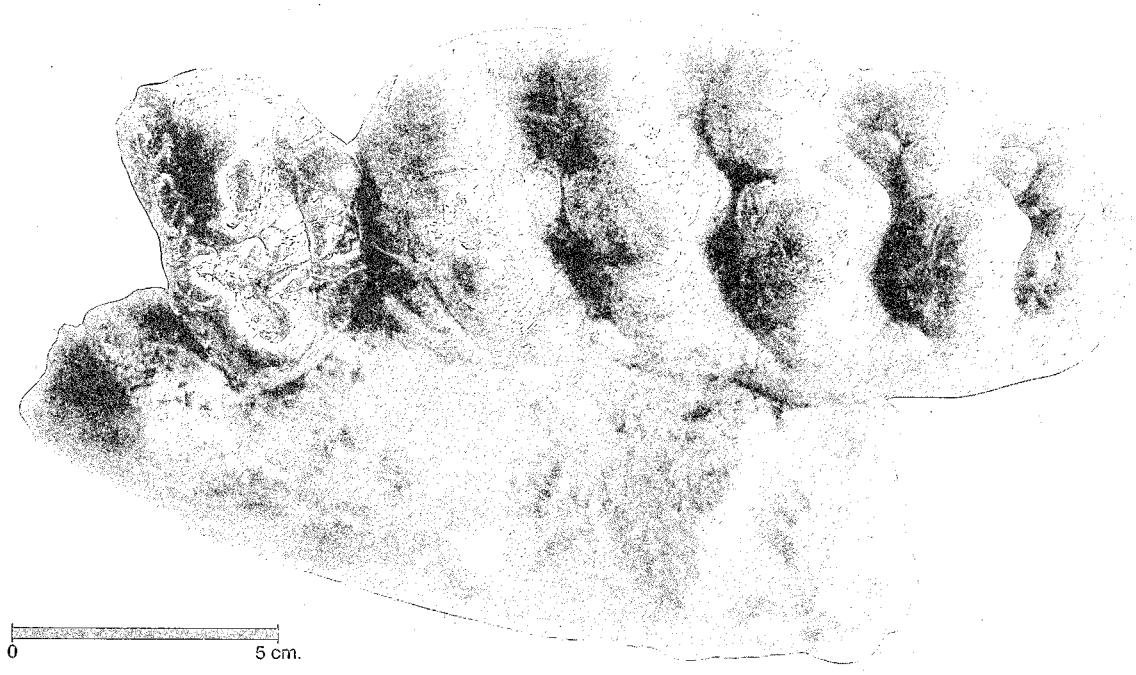


Figure 5. Occusal view of the M_2 and M_3 of *Amahuacatherium peruvium* in place in a portion of the left mandibular ramus, anterior to left. Note the broad lateral expansion of the ramus at the M_3; the alveolus for an anterior root of the M_2, which appears as a large excavation seen in the lateral side of the anterior end of the ramus; and the curvature of the lateral edge of the ramus. Scale bar = 5 cm.

only portions of the mandibles are intact, but these include left and right third molars, posterior lophids of both M_2's, and roots of the tusks. The M^3's lost pieces to erosion and were broken in removal. None of the remaining material can be identified with certainty. Casts of the left M_3, both partial M_2's, and the partial left M^3 are in the Vertebrate Paleontology Collections of the Natural History Museum of Los Angeles County, LACM 140398.

Emended Diagnosis. As for genus.

Measurements: See Table 1. See Fig. 6 for explanation of measurements.

Type Locality. Left bank of the Madre de Dios river at Aurinsa, provincia Tambopata, departamento de Madre de Dios, Peru; Latitude 12° 34' 26" S; longitude 70° 06' 25" W. LACM Locality 6258; elevation ~300 m amsl; Fig. 7.

Horizon and Age. From deposits at the top of the Contamana Group (Kummel, 1948) [Solimões Formation in Brazil (Moraes Rego, 1930; Caputo et al., 1971)], immediately below the Ucayali Unconformity separating the Contamana Group from the overlying Madre de Dios Formation (Oppenheim, 1946; Campbell and Romero-P., 1989). During the annual dry season, when the river is at its lowest, the formational contact is right at or just below the water line of the river (Fig. 8), thus it is difficult to determine with certainty the specific nature of the fossil-producing horizon, e.g., whether or not it might be a channel deposit and what its relationship to the underlying strata might be. The absence of data pertaining to the older Tertiary strata underlying the Ucayali Unconformity in this region precludes an unquestionable assignment of the horizon in question to a specific formation within the Contamana Group, although it is most probable that it lies within the Ipururo Formation (Kummel, 1948; Guizado, 1975; Pardo and Zuñiga, 1976). Palacios-M. et al. (1996) refer to these beds as part of the Ipururo Group, citing Kummel (1948) as the source for the denomination. However, Kummel (1948) referred only to an "Ipururo Formation" within the Contamana Group.

The minimum age for the specimen is postulated to be at least ~9.5 Ma, or late Miocene (Chasicoan SALMA; 12-9 Ma). This is based on the fact that the specimen comes from below the Ucayali Unconformity; a $^{40}Ar/^{39}Ar$ date on a volcanic ash, the Cocama ash, from above the Ucayali Unconformity is 9.01±0.28 Ma (Campbell et al., in press). This ash date corroborates the prior interpretation that the faunas derived from above the Ucayali Unconformity were late Miocene in age based on characteristic Huayquerian taxa (Frailey, 1986). Others, however, have suggested that these faunas

Table 1. Measurements (mm) of *Amahuacatherium peruvium.*

A. Mandibular ramus below M_3: Height 94.5, width 145.0

B. Height of specimen measured through combined ramus and M_3 at lophid 2: 163.0

C. M_3:

Length: 187.0

Width:

At lophid 1:	76.0
At lophid 2:	78.0
At lophid 3:	83.0
At lophid 4:	72.0
At lophid 5:	54.0

Unworn crown height

Labially (measured from the cingulum or valley floors)

	Parallel to external surface	Vertical Height
Cone 1	x	x
Cone 2	x	x
Cone 3	51.0	37.0
Cone 4	44.0	38.0
Cone 5	31.0	28.0

Lingually (measured from a line drawn along the valley floors)

Cone 1	41.0		35.0
Cone 2	41.0		34.0
Cone 3	39.0		33.0
Cone 4	32.0		27.0
Cone 5	27.0		23.0
Cone 6	19.0	(posterior cone)	16.0

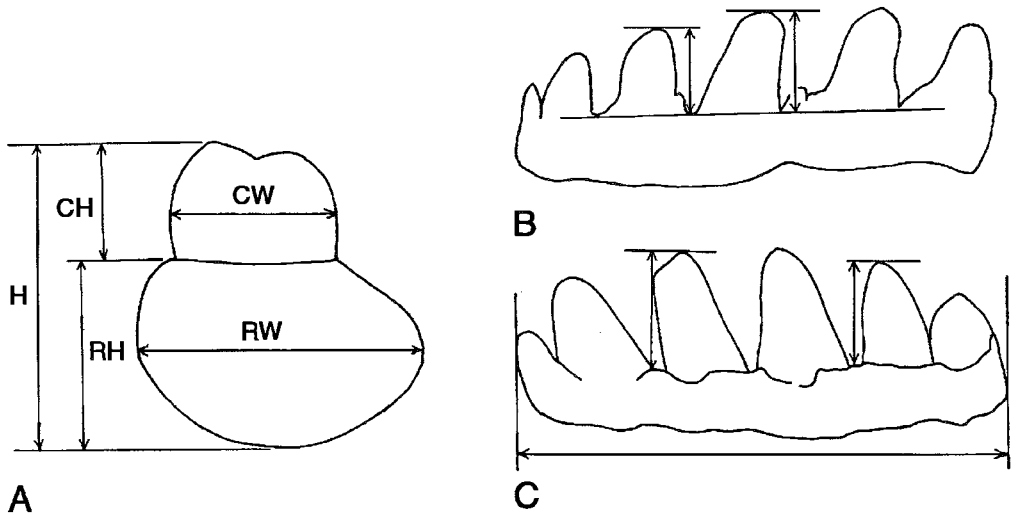


Figure 6. Illustrations showing how measurements of *Amahuacatherium peruvium* were taken. **A,** Section through mandibular ramus at M_3; **B,** lingual view of left M_3, anterior to right, showing how height of posttrite primary cones was measured; and **C,** labial view of left M_3, anterior to left, showing how height of pretrite primary cones was measured. CH = crown height, CW = crown width; H = height, RH = ramus height, RW = ramus width.

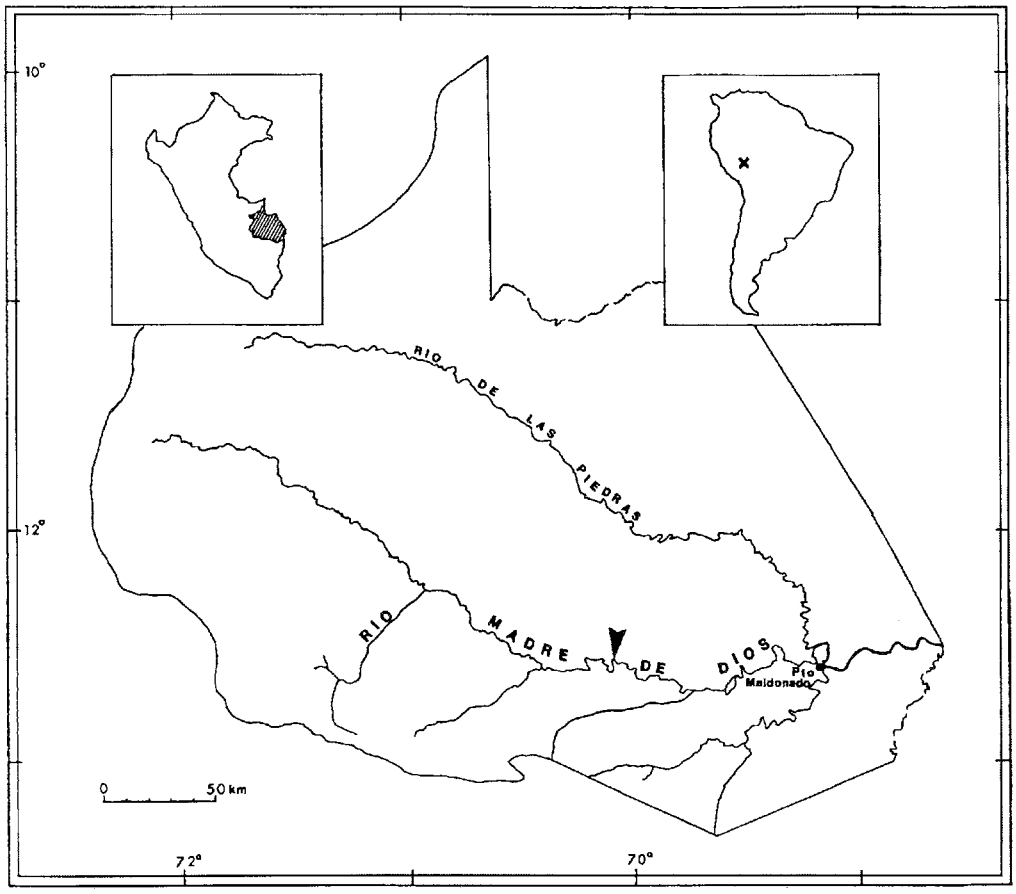


Figure 7. Map of southeastern Peru showing holotypical locality LACM 6258, Aurinsa (at tip of arrow), from which came *Amahuacatherium peruvium*.

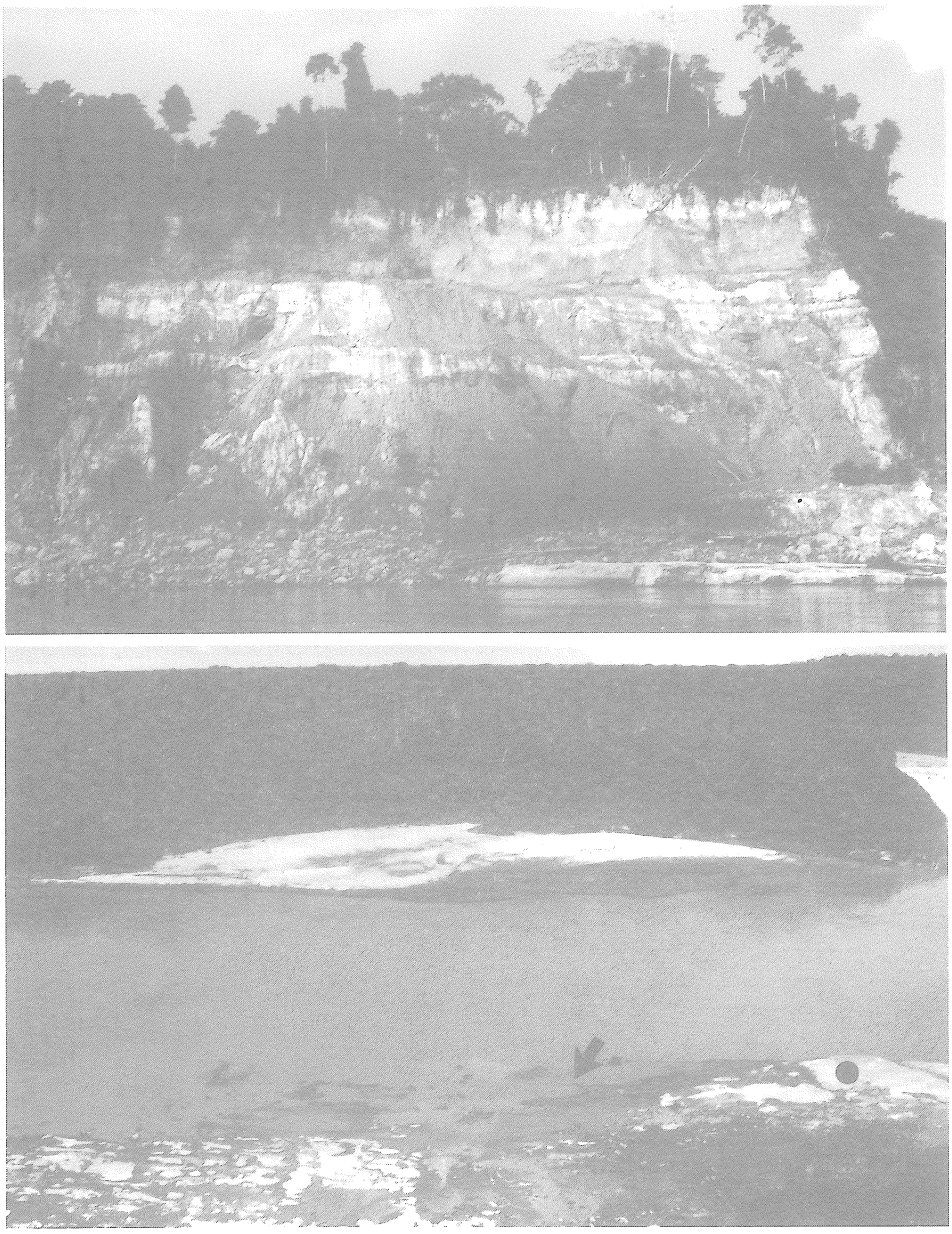


Figure 8. View of Aurinsa, locality LACM 6258. **Above**: The gomphothere specimen came from a low shelf that comprises the top of the Contamana Group at this locality. The shelf is shown here just emerging above the water line at the right side of the photograph. The top of the shelf is the surface referred to as the Ucayali Peneplane, which is to a large extent covered by slump blocks at the base of this outcrop. The overlying Madre de Dios Formation is approximately 70 m thick at this outcrop. **Below:** From the top of the cliff shown above, the shelf that produced *Amahuacatherium peruvium* can be seen to extend into the river channel. The specimen came from approximately the position on the shelf indicated by the arrow. The site was under water at the time this photograph was taken, which was several years prior to the discovery of the specimen. The dot indicates that portion of shelf seen protruding from river in the upper view.

might be older (e.g., Broin et al., 1993; Webb, 1995). The date for the Cocama ash indicates that these faunas are truly borderline as to whether they are Chasicoan or Huayquerian in age, but we conclude that they will probably prove to be latest Chasicoan. The presence of the same taxa both above and below the Ucayali Unconformity suggests that there might not be a huge time difference between faunas above and below the unconformity in all instances, although this might certainly be true in some instances. A more detailed discussion of the age of the fauna is presented below (see Geology).

Collector. The specimen was collected in 1991 by a joint field party from the Instituto Geológico, Minero y Metalúrgico (INGEMMET) of Peru and the University of Turku, Turku, Finland. Parts of the specimen were clearly articulated when discovered (Figs. 9, 10). The two M^3's were lying on their labial sides, in their appropriate places one to the other. No obvious cranial bone was present. Both mandibles, with their dentitions but missing the symphysis, and various postcranial skeletal elements were present. After partial excavation preparatory to removal, a sudden, disastrous night-time rise in the level of the river caused the loss of most of the bony parts of the specimen and fragmentation of what was saved.

Etymology. From Peru, the country of origin.

Description. Of the mandibles, only short, undeformed sections at M_2 and M_3 survived collection and transport intact and remain complete ventrally. These show a shallow ramus that is expanded laterally such that in cross-section the transverse diameter greatly exceeds the depth (Figs. 5, 11). The depth and width of the ramus below M_3 are 94.5 x 145.0 mm, respectively. The ramus is not crushed, thus its small size and minimal depth below M_3 (Fig. 4) are a natural condition, a condition unique among gomphotheres. Further, the depth of the mandibular ramus does not increase anteriorly, i.e., the occlusal surface of the molars and he ventral surface of the rami remain parallel. Although one might question how such a small and, particularly, shallow ramus could support a "normal-sized" tooth, the fact that it did cannot be questioned because the wear on the M_3 indicates that the specimen represents an adult animal.

Apparently, the mandibles were reduced in length and had achieved a brevirostrine condition (Fig. 12). This is indicated by several features. First, the mandibular rami have their lateral sides curving sharply mediad at their anterior ends (Figs. 5, 12). Further, as the M_3 erupts, the M_2 is pushed not only anteriad, but also laterad toward the side of the ramus. An anterior alveolus for roots of the M_2 is clearly seen as an opening in the side of

Figure 9. Anterior view of the lower jaws and dentition of *Amahuacatherium peruvium in situ*, prior to any excavation. The lower tusks (= T), with their dorsal groove, can be seen in this view in place under the M_2's. A clump of light gray clay lies within the alveolus for the anterior root of the left M_2. More of the left mandibular ramus is in position here than appears in the earlier figures, and the anterior curvature of the ramus can be noted. The symphysis and ascending rami are missing. The two partial M^3's appear as isolated teeth to the right of the knife.

Figure 10. Posterior view of *Amahuacatherium peruvium* as it was being excavated. The lower dentition is seen in the upper center, whereas the two partial M^{3}'s are visible to the left. Other parts of the specimen are in the lower left corner of the photograph.

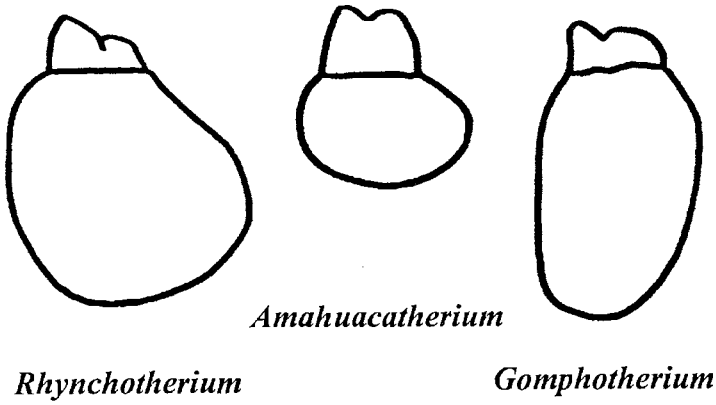


Figure 11. Cross-sectional outlines of the mandibular rami at M_3 of three genera of gomphotheres. Drawings not to scale; sizes adjusted to uniform width of M_3. Outlines of *Gomphotherium* and *Rhynchotherium* from Tobien (1973). The size and shape of the cross-sectional outline of the mandible seen in *Amahuacatherium peruvium* (INGEMMET 2801) is the natural, uncrushed, condition. The small size of the mandible, and particularly its shallow depth, relative to the "normal-sized" M_3 is unique among known gomphotheres. Both *Amahuacatherium* and *Rhynchotherium* have lateral (to the right) "bulges" of the mandibular ramus, whereas in *Gomphotherium* the tooth is centrally placed in a ramus of nearly uniform thickness.

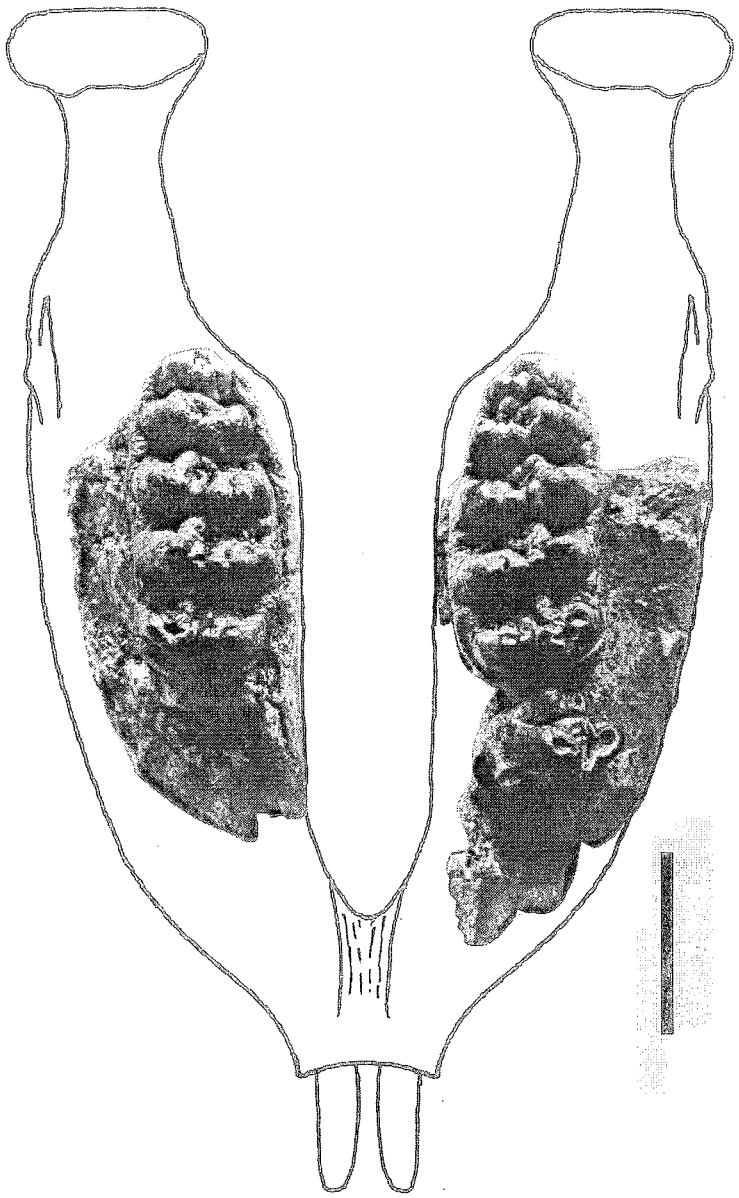


Figure 12. Reconstruction of the mandibles of *Amahuacatherium peruvium*, using the partial mandibular rami as the basis. Although we assume the lower tusks were functional, their small size is interpreted as indicating that they did not protrude far beyond the end of the symphysis or they would have been subjected to breakage. Scale bar = 10 cm.

the left ramus (Figs. 5, 9). Both M_2's of the specimen are broken just anterior to the posterior lophid. The anterior portions of the M_2's appear to have been broken away and lost prior to the death of the animal because in each tooth the broken surface is worn, which is what one would expect from wear or erosion, as opposed to crisp edges created by breakage during excavation. The anterior portions of these teeth do not appear in the field photographs. The positions of the anterior alveoli indicate that the M_2's were being forced from the tooth row on an arc that continued the curvature of M_3. The M_2's are not heavily worn, and their apparently rapid replacement may be a consequence of the extreme shortening of the mandible.

The conclusion that the brevirostrine condition was present is also supported by the fact that the rami do not increase in depth anteriorly, in contrast to the condition seen in longirostrines or even in some brevirostrines that have a deep, gutter-like symphysis. The increase in anterior depth in longirostrine forms provided vertical strength, or support, for an elongated symphysis. In the brevirostrines with a deep, gutter-like symphysis the increase in depth may simply have been a means of accommodating the tongue and resisting stress on the symphysis. In the shorter, stout jaw of *Amahuacatherium*, the stresses on this part of the mandibles were apparently less severe and managed by the more rounded (in cross section) rami.

In this specimen there is no indication of a symphysis posterior to the anterior end of the preserved portion of the left ramus (Figs. 9, 12), thus it is not possible to know what form it may have taken. However, based on the curvature of the rami and the fact that their depth does not increase anteriorly as in longirostrine gomphotheres we can infer that the symphysis did not extend too much farther forward than the preserved portions of the mandibles and that it was not deeply guttered (Fig. 12).

Small mandibular tusks are present. The roots are straight, and approximately 25 mm in diameter at the most anterior point preserved. In a field photograph taken prior to excavation (Fig. 9), a relatively large groove can be seen in the dorsal midline of each tusk. These grooves are similar to those illustrated for "*Aybelodon hondurensis*" Frick 1933 (Frick, 1933, fig. 5; figure reproduced in Tobien, 1973, fig. 11). From this specimen it is not possible to know how far anteriad this groove extended. The presence or absence of enamel on the lower tusks could not be determined from this specimen.

The tusks lie near the ventral and medial margin of the rami, immediately below and internal to the posterior root of the M_2. We know of no other instance where the roots

of the lower tusks lie so far back in the jaws, i.e., to the point where the tusks underlie the molars. All illustrations seen [e.g., that for "*Aybelodon hondurensis*" (Frick, 1933)], show the posterior end of the root of the lower tusks lying within the symphysis, well anterior and away from the molars. Osborn (1936) illustrates the positioning of the roots of the lower tusks in several genera, all at a distance from the molars. It should be noted that the longitudinal curvature observed in the anterior portion of the M_3 carried the tooth along the path followed by the M_2, i.e., toward the side of the ramus. If the M_3 did not curve outward, its deep root, as seen in Fig. 4, would have left no room for the tusks and they would have been pushed out the front of the jaw. Even with the curvature of the M_3 of this specimen, it would seem that the roots of the lower tusks must have been affected in some way by the complete eruption of the M_3.

The right and left M_3's are intact, little worn, and in excellent condition. The dentine is exposed on only the anterior two pretrite (labial) cones. In general features, the M_3 curves labially anteriorly, and it narrows to a rounded point at its posterior margin. The lophids each consist of two primary cones connected by smaller conelets of nearly equal height. The primary cones are nearly vertical, with only a slight inclination toward the long axis of the tooth. The major posttrite (lingual) cones are placed anterior to the major pretrite cones, i.e., the lophids are oblique to the long axis of the tooth. The intervening conelets form a slight, anteriorly convex curve to the lophid.

Tall, buttressing (accessory) conules are present on each of the pretrite cones. With moderate wear, or approximately 25 percent of crown height, the trefoil or clover-leaf enamel pattern that is typical of gomphothere molars would form on the pretrite half of each lophid. Multiple small conules of varying height fill the lingual valleys, and some are large enough to approach the trefoil pattern on the lingual side of the tooth. With moderate to extreme wear (50%-75%), an incipient, or first stage, trefoil pattern would develop around the anterior (1st) and posterior two (4th and 5th) posttrite cones.

The last complete lophid, lophid 5, is about half the transverse width of the first three lophids. Two major, marginal (lingual and labial) cones are evident. Accessory conelets complete the lophid and connect the labial cone with a single, central posterior cone (the final half-lophid). The result is a nearly circular, or C-shaped, structure at the posterior terminus of the tooth. This structure is present in both M_3's.

A prominent cingulum is present on the anterior margin. A small, but continuous, crenulated cingulum begins at the postero-lateral base of the first pretrite cone, runs the

length of the tooth, wraps around the posterior margin, and continues anteriad to the base of the fifth posttrite cone. There is no lingual cingulum, except that at the base of the fifth lingual cone.

The other teeth preserved, i.e., both of the highly fragmented M^3's and posterior parts of both M_2's, display the same abundance of conules seen in the M_3's. In the M^3's (Fig. 3) the valleys are even more obscured by the conules than in the lower molars. The posterior terminus of M^3 is a rounded end of the ovate occlusal outline, just as it is in M_3. Other characters that can be discerned in these fragments are that the posterior lophid of M_2 has pretrite trefoiling, no posttrite trefoiling, multiple small conules, and no lingual or labial cingulae. A comparable structure to the curious C-shaped posterior half-lophid at the distal terminus of the M_3's is also seen at the distal terminus of the M_2's (Fig. 2), where it appears as a diagonal crest composed of conules that extends postero-mediad from the pretrite cone of the posterior lophid. This crest provides a continuous set of valley conules between the last lophid of the M_2 and the first lophid of the M_3 when the two teeth are in contact.

Comparisons With Other Genera. In the comparisons with other genera, primary emphasis is placed on the characters of the mandibles and the M_3. Although some features of the M^3 and M_2 can be discerned, as noted above, their fragmentary nature does not permit direct, detailed comparison with other genera.

Based on the assumption that the South American gomphotheres are derived from North American gomphotheres, and the fact that all North American middle Miocene gomphotheres were longirostrine (long-jawed), it may be inferred that the South American gomphotheres are probable descendants of Miocene longirostrine (long-jawed) gomphotheres of North America. Because of a shortened mandible relative to earlier gomphotheres, the Hemphillian and Blancan genus *Rhynchotherium* Falconer 1868 (subfamily Rhynchotheriinae) has been considered representative of the probable antecedent lineage of the South American group (Tobien, 1973:239), all of which are brevirostrine. *Rhynchotherium* developed from stock of the Barstovian to Hemphillian genus *Gomphotherium* Burmeister 1837 (subfamily Gomphotheriinae) (Tobien, 1973), and from molar features alone the two genera are difficult if not impossible to separate (Savage, 1955). However, *Amahuacatherium*, which was contemporaneous with late Clarendonian forms of *Gomphotherium* but preceded the Hemphillian forms of *Rhynchotherium*, may be separated from both of those genera on the basis of its brevirostrine condition, dental features, and the cross-sectional size and shape of the

mandibular ramus. Further, these three genera can be separated from the four known genera of South American gomphotheres on the basis of dental features. Dental features also provide a means of separating most of the latter from each other. The highly derived mandibles of *Amahuacatherium* suggest that this lineage did not give rise to any of the later South American gomphotheres. It is more probable that this lineage represents an early entrance of gomphotheres into South America that did not diversify and eventually became extinct (see below).

The lower third molars of *Rhynchotherium* and *Gomphotherium* are similar to those of *Amahuacatherium* in their major features. The degree of trefoil development of the pretrite cones is similar among *Gomphotherium*, *Rhynchotherium*, and *Amahuacatherium*. The anterior and posterior buttressing conules that wear into the characteristic gomphothere trefoil pattern form a nearly continuous ridge that closes the labial valleys in all three genera. The most striking difference among the molars that sets *Amahuacatherium* apart is the large number of conules (= cuspules of some authors) that fill the lingual valleys. In some instances, e.g., the first, fourth and fifth lophids, these are sufficiently large to demonstrate incipient trefoiling on the posttrite (lingual) cones (= secondary trefoiling). Trefoiling on the posttrite cones in *Gomphotherium* and *Rhynchotherium* is absent or incipient, with both Tobien (1973) and Miller (1990) referring to secondary trefoiling in some specimens of *Rhynchotherium*. Although minor conules are present in some specimens of *Gomphotherium* and *Rhynchotherium*, they are never as numerous nor as large as those seen in *Amahuacatherium*.

Additional differences between the M_3's of *Amahuacatherium*, on the one hand, and those of *Gomphotherium* and *Rhynchotherium* on the other, lie in the shape and position of the major cones. In *Gomphotherium* and *Rhynchotherium* the lophids form fairly straight transverse crests, and the pretrite cones are noticeably inclined toward the medial axis of the tooth, significantly decreasing the distance between the apexes of the primary cones of each lophid (Fig. 13). In *Amahuacatherium* the inclination of the pretrite cones toward the medial axis of the tooth is slight, thus the apexes of the cones are set far apart. This character is, of course, most noticable in specimens that show little wear. Further, in *Gomphotherium* and *Rhynchotherium* the major cones are larger at their bases, i.e., they are swollen in appearance rather than slender like the cones of *Amahuacatherium*. As a result, the labial and lingual views of the valleys tend to be more V-shaped in *Gomphotherium* and *Rhynchotherium*, rather than U-shaped as seen in *Amahuacatherium*. The U-shape is particularly evident on the labial side in *Amahuacatherium*.

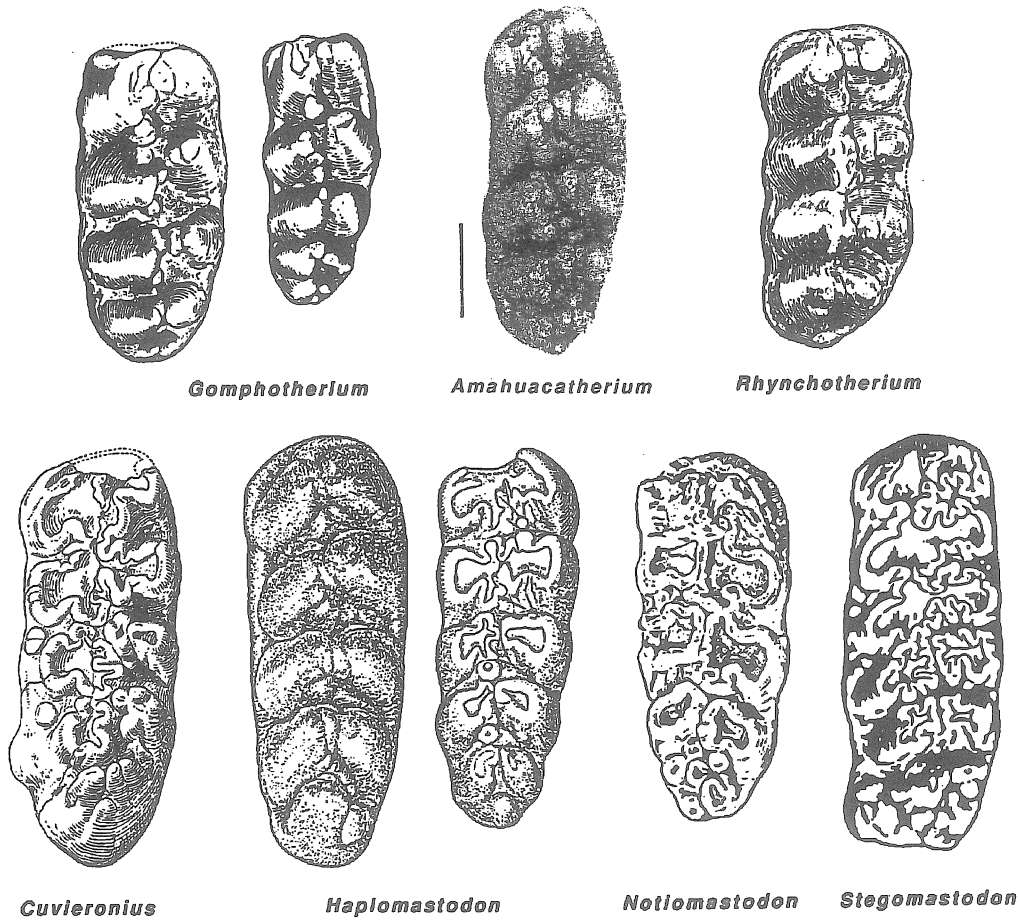


Figure 13. Sketches of left M_3's for genera discussed in text. Scale bar beside *Amahuacatherium* M_3 is 5 cm; all specimens are to this scale. Note the convexity of the lingual surface and the point of maximum width of the M_3 of *Amahuacatherium* in comparison to that seen in the other genera. Note also the greater width between the apexes of the primary cones of each lophid in *Amahuacatherium* in comparison to the other genera, which is primarily a reflection of the fact that the pretrite cones of *Amahuacatherium* are not inclined mediad as dramatically as in the other genera. Sources for drawings: *Gomphotherium*, F:AM 21287 (reversed) and 21273 (reversed), Frick (1933; fig. 25); *Rhynchotherium*, F:AM 18255, Frick (1933; fig. 23); *Cuvieronius*, Museo de La Plata 8-407, Osborn (1936; fig. 561); *Haplomastodon*, Simpson and Paula Couto (1957; fig. 3); *Notiomastodon*, Pascual et al. (1966; pl. 89); *Stegomastodon*, AMNH 18240 (reversed), Osborn (1924; fig. 2).

The South American gomphotheres were placed in the subfamily Notiomastodontinae Osborn 1936 by Tobien (1973), following the discussion of Simpson and Paula Couto (1957). In the present paper, we follow Shoshani and Tassy (1996b), who give priority to Cuvieroniinae Cabrera 1929. Four genera comprise this subfamily: *Cuvieronius* Osborn 1923, *Stegomastodon* Pohlig 1912, *Haplomastodon* Hoffstetter 1950, and *Notiomastodon* Cabrera 1929. These form a group of bunodont gomphotheres with trilophodont upper and lower second molars. All previously known representatives are brevirostrine and lack lower tusks, i.e., they have the dibelodont condition. The brevirostrine dibelodont condition is unusual in gomphotheres and, in the New World, unique to the Cuvieroniinae.

All known species of the early New World gomphotheres of the genus *Gomphotherium* and the later *Rhynchotherium* were longirostrine. The mandible of *Rhynchotherium* is shortened and down-curved, however, when compared to that of *Gomphotherium*, in a way that suggests an evolutionary trend toward the brevirostrine condition of the Cuvieroniinae. This, at least, has been the operational hypothesis as no alternative exists in the fossil record. Coincident with this mandibular shortening is a dorso-ventral thickening of the mandibular rami (Tobien, 1973), making them more "stout."

The mandibular ramus at M_3 of *Amahuacatherium* shows the lateral expansion characteristic of *Rhynchotherium* and later brevirostrine cuvieroniid gomphotheres, as opposed to the less laterally expansive condition seen in the larger rami of *Gomphotherium* (Fig. 11). The lateral expansion of the mandible of *Amahuacatherium* is similar to that seen in supposed transitional longirostrine/brevirostrine species such as *Rhynchotherium browni* Osborn 1936 or *Rhynchotherium falconeri* Osborn 1923 from upper Pliocene deposits of Mexico and Texas, respectively (Tobien, 1973). As far as the lateral expansion of its mandibular ramus is concerned, *Amahuacatherium* may possess a condition intermediate between that of *Gomphotherium* and *Rhynchotherium*, or between that of *Rhynchotherium* and the later brevirostrine South American gomphotheres. However, *Amahuacatherium* lacks the great mandibular depth of *Gomphotherium* and *Rhynchotherium* (Figs. 11, 14, 15), and, indeed, with its extremely thin lower margin below M_3, the mandible of *Amahuacatherium* is unique among all proboscideans. The ratio of mandibular width to depth of *Gomphotherium* is 0.67; the same ratio in *Rhynchotherium* is 1.0; but it is 1.5 in *Amahuacatherium*.

The M_3's of *Amahuacatherium* have many features that distinguish them from those of the four previously recognized genera of the Cuvieroniinae. The M_3's are widest

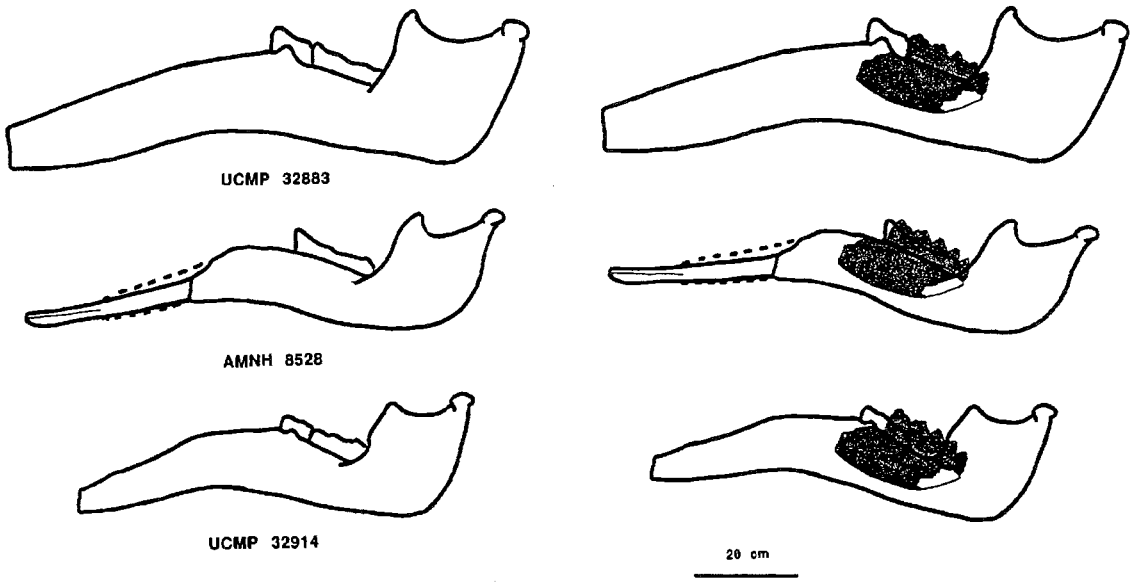


Figure 14. Mandibular rami of *Gomphotherium* compared to the holotypical mandibular fragment of *Amahuacatherium*, which is shown here on the right in dark shading superimposed upon the drawings of *Gomphotherium*. Sources for drawings of *Gomphotherium*: UCMP 32883, 32914 (Tobien, 1973; fig. 10); AMNH 8528 (Mebrate, 1987; fig. 42, after Osborn, 1936; fig. 462).

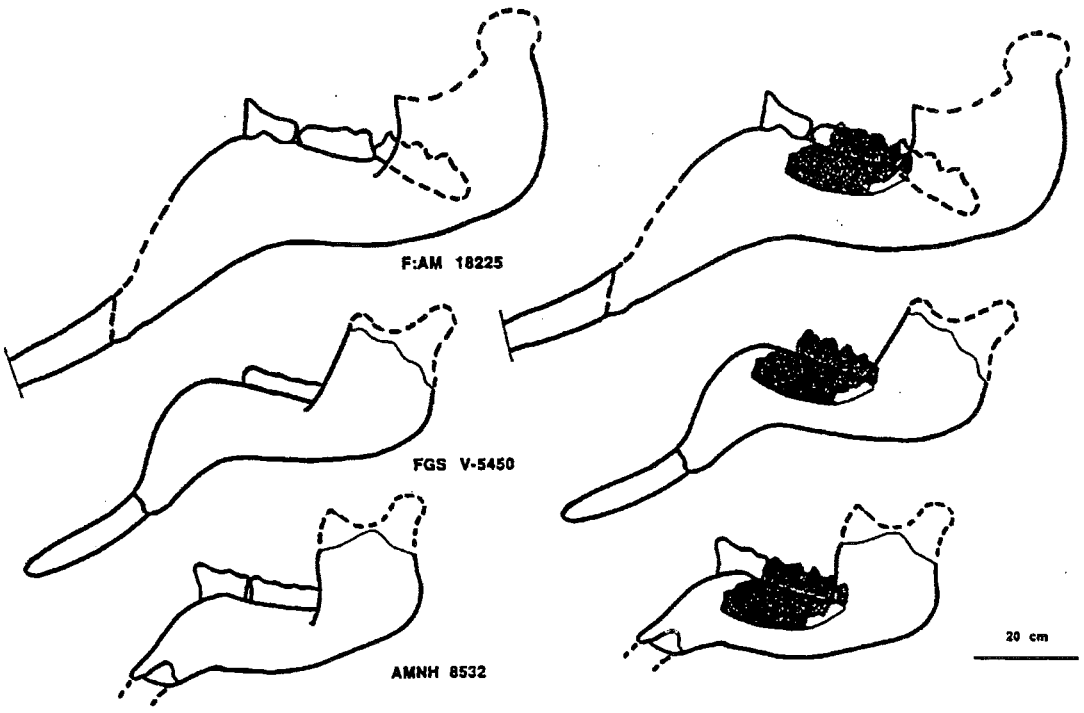


Figure 15. Mandibular rami of *Rhynchotherium* compared to the holotypical mandibular fragment of *Amahuacatherium*, which is shown here on the right in dark shading superimposed upon the drawings of *Rhynchotherium*. Sources for drawings of *Rhynchotherium*: F:AM 18225 (Frick, 1933; fig. 23); FGS V-5450 (Olsen, 1957; fig. 1); AMNH 8532 (Mebrate, 1987; fig. 65, after Osborn, 1936; fig. 468).

at the second and third lophids, instead of the more typically elongate cuvieroniid M_3 that is uniform in width or slowly narrows toward the posterior (Fig. 13). The cones are slender, rather than swollen, and tilt toward the anterior. In no M_3 of known cuvieroniids is the last lophid connected with the last half-lophid to form the distinctive C-shape seen in *Amahuacatherium*. Although this portion of the tooth is variable in gomphotheres, this feature is interpreted to be a well-formed and distinctive character of the M_3 in *Amahuacatherium*. It is seen in both M_3's of the holotype.

Among the cuvieroniids, *Stegomastodon* and *Notiomastodon* have complex enamel patterns with tall, buttressing conules present on both labial and lingual cones. With moderate wear, the characteristic packed trefoil pattern develops on both sides of the molars and creates a flat occlusal surface. The complexity of the M_3 in these two genera exceeds that seen in *Amahuacatherium*, in which posttrite trefoiling is incomplete even with extreme wear. The M_3 of *Notiomastodon* is broad in comparison to that of *Amahuacatherium*, and the valleys are reduced in size because of enlarged cones and conules.

Stegomastodon has a rectangular M_3 compared to that of *Amahuacatherium*. The complexity of the enamel pattern at moderate wear is extreme, although enlargement of the numerous buttressing and valley conules in *Amahuacatherium* would lead to a matching of this complexity. Valleys are constricted in *Stegomastodon* because of the enlarged conelets. Labial valleys are almost absent, unlike the open labial valleys in *Amahuacatherium*. Thick cement in the valleys is a feature of *Stegomastodon* not seen in *Amahuacatherium*.

The molar enamel patterns in *Haplomastodon* and *Cuvieronius* are comparatively simple and very similar, leading Simpson and Paula Couto (1957) to conclude that isolated teeth of these may be difficult to distinguish. They further concluded, however, that the resemblances between the molars of the two genera were "...mainly in primitive characters... (Simpson and Paula Couto, 1957:168)." *Haplomastodon* has the least complex dental pattern of all the cuvieroniids. The trefoil pattern is well formed only on the pretrite cones of the M_3, and few valley conules are present. Furthermore, the M_3 of *Haplomastodon* differs from that of *Amahuacatherium* in that the lophids are more nearly transverse, contrasting with the anteriorly placed posttrite cones seen in *Amahuacatherium*. The apexes of the cones are particularly close together in *Haplomastodon*, in contrast to the more open crown of this tooth in *Amahuacatherium*. A single, isolated prominent posterior cone appears to be a fairly constant feature of the M_3 of *Haplomastodon* (see figures

in Simpson and Paula Couto, 1957, for many examples), in contrast to the multiple conelets and large posterior cone (half lophid) that are connected to the small fifth lophid in *Amahuacatherium*.

The M_3 of *Cuvieronius* is more elongate than that of *Amahuacatherium* and it lacks the numerous valley conules. In other respects the two genera are similar, including crenulated walls of the cones and an anterolateral curvature (in dorsal view). Although this curvature is generally less in *Cuvieronius*, isolated M_3's from Mexico in the LACM vertebrate paleontology collections referred to *Cuvieronius* (LACM 1135/1891 and LACM(CIT) 163/2009) display a similar degree of curvature to that seen in *Amahuacatherium*. Some specimens of *Haplomastodon* M_3's also have some curvature (Simpson and Paula Couto, 1957). Thus, the degree of curvature seen in M_3's seems to be subject to some variation in cuvieroniids. The observed curvature in the holotypical M_3's of *Amahuacatherium* is consistent with the extreme brevity of the mandible and the hypothesized curved path of dental replacement. As such, the curvature of this tooth in the holotypical specimen of *Amahuacatherium* is unlikely to be a simple variant within a population in which the teeth are typically straight.

Measurements of the left mandible and M_3 are given in Table 1. Dentally, *Amahuacatherium* is equivalent in size to any of the genera under discussion. Size comparisons between the M_3's of *Amahuacatherium* and *Haplomastodon* and between *Amahuacatherium* and *Gomphotherium* are given in Fig. 16, although, because size is not a generic character, no relationships can be inferred from these plots. In its overall combination of features, including small lower tusks; short, shallow, and wide mandibles; and a more derived molar structure, *Amahuacatherium* is clearly unique in comparison to *Gomphotherium* and *Rhynchotherium*. The presence of lower tusks and the unique mandibular shape also serve to distinguish *Amahuacatherium* from all previously known genera of the Cuvieroniinae. This distinction is reinforced by the complexity of the molar structure in *Amahuacatherium*, which is quite different from both the least and most derived of the genera placed in this subfamily (Fig. 13).

Analysis of Relationships

Amahuacatherium is temporally and geographically situated to be derived from the "rhynchorostrine complex" of Savage (1955) and to be an early representative of the Cuvieroniinae. The operational hypothesis of gomphotheriid evolution in the New World

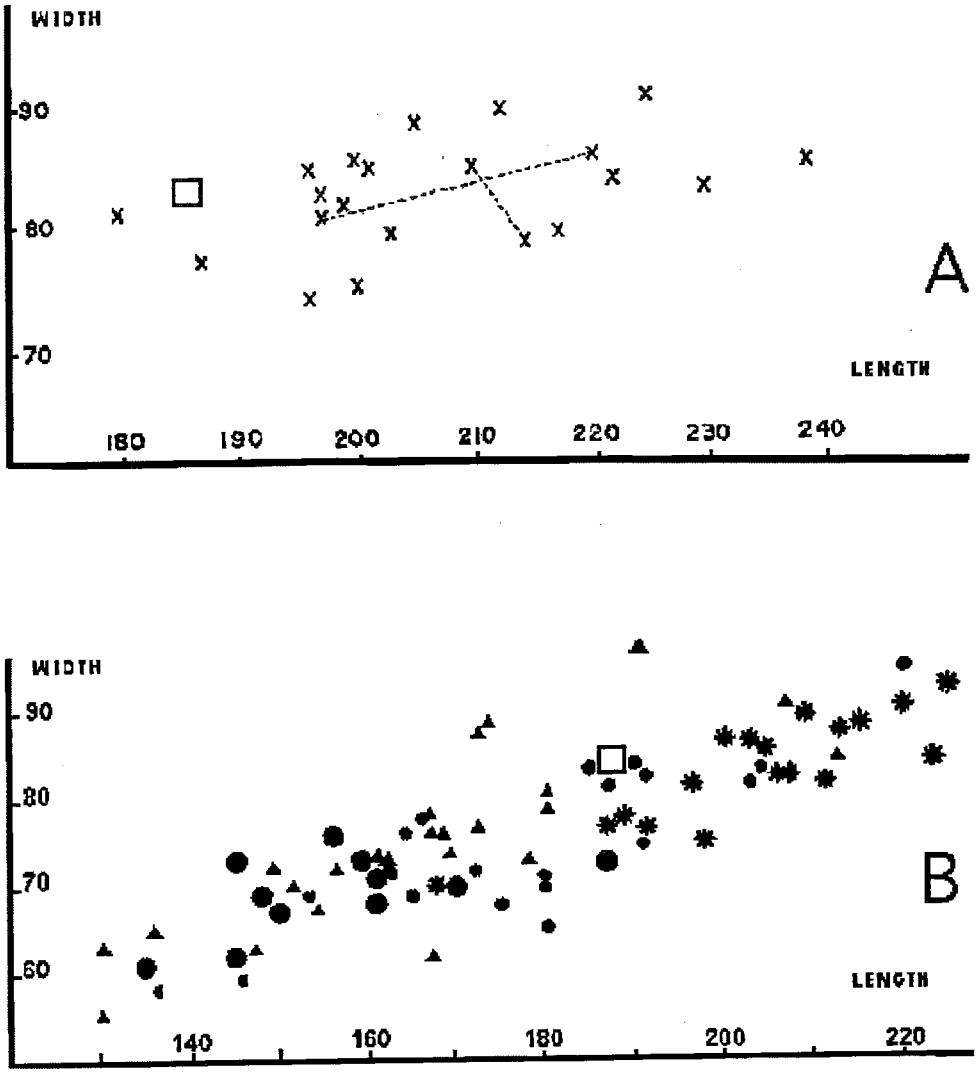


Figure 16. **A,** Size comparison between M_3's of *Amahuacatherium* (square) and *Haplomastodon* (from Simpson and Paula Couto (1957, fig. 5). Dotted lines connect teeth of same individual. **B,** The same comparison between *Amahuacatherium* (square) and species of *Gomphotherium* (from Tobien, 1973, fig. 9). Although these charts show that *Amahuacatherium* overlaps both *Gomphotherium* and *Haplomastodon* in size, because size is not a generic character these comparisons do not reveal any phylogenetic relationships.

has been that from the bunodont, trilophodont, tetrabelodont, longirostrine (or, b-3-4-1, *sensu* Tobien, 1973; fig. 2) gomphotheres, a reduction of the lower mandibular symphysis and tusks led, through the *Rhynchotherium* lineage, to the Cuvieroniinae, of which the four previously known genera are bunodont, trilophodont, dibelodont, and brevirostrine (or, b-3-2-b, *sensu* Tobien, 1973; fig. 2) (see, e.g., Savage, 1955; Tobien, 1973).

We have not attempted a phenetic cladistic analysis of the relationships among all of the genera placed in the family Gomphotheriidae because this paper is not intended as a review of that family. Further, we see little value in applying this methodology, as currently practiced, to fossil material, or even to many modern groups, where gaps in the data field may be enormous and choice and interpretation of characters remain subjective. Although seldom mentioned, it must be recognized that an analysis as performed by a computer program is the only objective aspect of this methodology. Some might argue that cladistic methodology is only an inference procedure, and that choice and interpretation of characters have nothing to do with cladistics. Theoretically, this may be true. In practice, however, they are usually inseparable (e.g., Tassy, 1996b). As a consequence, results are often meaningless because of the subjective nature of data sets analyzed. The problems associated with choice and interpretation of characters stand out in the most recent attempts at cladistic relationships within the Proboscidea, those of Shoshani (1996) and Tassy (1996b; which closely follows Tassy, 1990). A few examples of some of the problems with these cladistic analyses as they relate to the subject of this paper are noted in the discussion below. It was encouraging to see the frank and candid discussion of the difficulties of applying cladistic methodology to proboscidians by Shoshani (1996), which demonstrated that he, at least, recognized the problems inherent in the methodology.

Despite the above, we recognize that cladograms are useful and informative tools for representing data available for taxa under discussion. Thus, we have attempted herein to portray the relationships among the various genera using explicit summaries, or character cladograms (Nelson and Platnick, 1981), of the available data. The data we discuss are from published sources as cited and our own analysis.

The most recent treatment of relationships among genera of gomphotheres is that of Shoshani (1996), part of which is presented here as Cladogram A (Fig. 17A). As part of a more comprehensive work, the genera listed in this figure were not treated in detail by Shoshani (1996), and the analysis of relatedness as presented is based on very few characters. The characters used by Shoshani are given in Table 2. While demonstrating

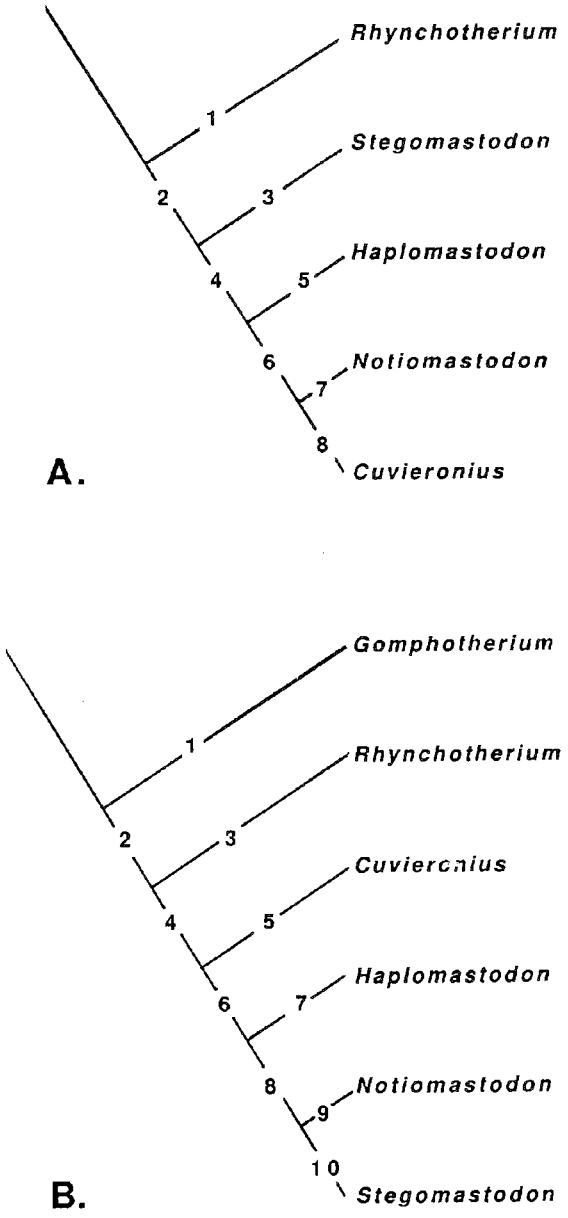
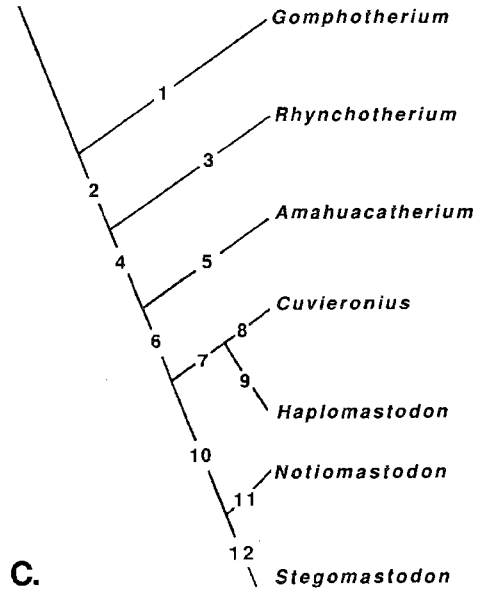
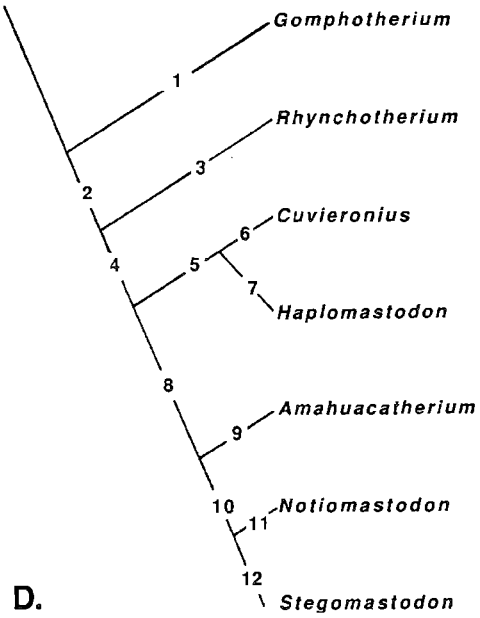


Figure 17 Cladistic arrangements of *Gomphotherium*, *Rhynchotherium*, and genera of the Cuvieroniinae. **A,** As presented in Shoshani (1996). **B,** Arrangement of previous authors (Savage, 1955; Tobien, 1973). **C,** Inclusion of *Amahuacatherium* as sister taxon to Cuvieroniinae. **D,** Inclusion of *Amahuacatherium* as sister taxon to *Notiomastodon/Stegomastodon*. See text for details.



C.



D.

Figure 17 Continued

Table 2. Characters used in the construction of Cladogram A (= fig. 16.5 of Shoshani, 1996). Numbers in brackets refer to Shoshani's (1996, App. 16.1) characters. This cladogram is constructed using taxa under discussion in the present paper.

1. helicoidal upper tusks [8], absence of premolars 2-3 [27], M^{1-3} central conules enlarged [37], tetralophodont M^3 [34], molars with trefoiling on pretrite lophids [55], mandibular symphysis long [94]
2. absence of premolars 2-4 [27], pentalophodont, or more, M^3 [34, unknown for *Notiomastodon*], molars with trefoiling on pretrite and posttrite lophids [55], mandibular symphysis short and spout-like [94]
3. upper tusks straight when viewed laterally [7], tusk enamel always absent [10], crown of molars with abundant cement [63] (*Stegomastodon*)
4. upper tusks curve dorsally when viewed laterally [7] (unknown in *Notiomastodon*), little cement on molars [63]
5. little or no upper tusk enamel [10] (*Haplomastodon*)
6. longitudinal band of upper tusk enamel [10]
7. upper tusk enamel band straight (*Notiomastodon*) (Tobien, 1973)
8. upper tusk enamel band spiraled (*Cuvieronius*) (Tobien, 1973)

Table 3. Characters used in the construction of Cladogram B (using characters noted by previous authors; see text).

1. bunodont, trilophodont, tetrabelodont, longirostrine (b-3-4-l of Tobien, 1973)
2. reduced mandibular symphysis and lower tusks, laterally expanded mandibular ramus
3. downcurved mandibular symphysis; molars with trefoiling on pretrite lophids and rarely on posttrite lophids; lower tusks slightly upcurved, with or without enamel band (*Rhynchotherium*)
4. bunodont, trilophodont, dibelodont, brevirostrine (b-3-2-b of Tobien, 1973)
5. spiral enamel band on upper tusks (*Cuvieronius*)
6. (no characters)
7. enamel band on upper tusks lost (*Haplomastodon*)
8. cement on molars, complicated molar pattern with full pretrite and full or nearly full posttrite trefoiling, flat occlusal surface
9. straight enamel band on upper tusks (*Notiomastodon*)
10. no enamel band on upper tusks, thick cement on molars (*Stegomastodon*)

Table 4. Characters used in the construction of Cladogram C [using characters noted by previous authors and features of the holotypic specimen of *Amahuacatherium* (see text)].

1. bunolophodont; trilophodont; tetrabelodont; longirostrine; molars with pretrite trefoiling; cones inclined to central axis of tooth; large, broad-based cones; V-shaped valleys
2. reduced mandibular symphysis, lateral expansion of mandibular ramus at M_3
3. downcurved mandibular symphysis; molars with pretrite trefoiling and rarely posttrite trefoiling; lower tusks slightly upcurved, with or without enamel band (*Rhynchotherium*)
4. brevirostrine condition, pretrite plus some posttrite trefoiling, presence of small valley conules unrelated to trefoil pattern
5. M_3 with slender-based cones and U-shaped valleys; great obliquity of transverse lophids; M_3 ovoid in outline with strong anterolateral curve; mandible short, shallow, laterally expanded in cross-section at M_3, lower tusks reduced (*Amahuacatherium*)
6. lower tusks lost; mandibular symphysis short and spout-like; elongate M_3, with broad-based cones and V-shaped valleys
7. molar enamel wear pattern simplified, with few or no valley conules; posttrite trefoils poorly or not developed
8. M_3 with open valleys, anterolateral curvature variable; large, isolated valley conules present on margins; spiral enamel band on upper tusks (*Cuvieronius*)
9. oblique transverse lophids; strong tendency for inclination of cones to midline of tooth; loss of upper tusk enamel in adults (*Haplomastodon*)
10. M_3 with moderate obliquity of transverse lophids; choerodont, with full pretrite and full or nearly full posttrite trefoiling; cement present on molars; flat occlusal surface with moderate wear
11. straight enamel band present on upper tusks; numerous valley conules not associated with cones; trefoil pattern unclear toward posterior of M_3 (*Notiomastodon*)
12. no enamel band on upper tusks; thick cement on molars; elongate, rectangular M_3 (*Stegomastodon*)

Table 5. Characters used in the construction of Cladogram D [using characters noted by previous authors and features of the holotypic specimen of *Amahuacatherium* (see text)].

1. bunolophodont; trilophodont; tetrabelodont; longirostrine; molars with pretrite trefoiling; cones inclined to central axis of tooth; large, broad-based cones; V-shaped valleys
2. reduced mandibular symphysis and associated lateral expansion of mandibular ramus at M_3
3. downcurved mandibular symphysis; molars with pretrite trefoiling and rarely posttrite trefoiling; lower tusks slightly upcurved, with or without enamel band (*Rhynchotherium*)
4. brevirostrine condition, lower tusks reduced; well developed conelets between half-lophids
5. lower tusks lost, abbreviated spout-like symphysis, molars with no or only incipient posttrite trefoiling, elongate and rectangular M_3
6. M_3 with open valleys, anterolateral curvature variable; large, isolated valley conules present on margins; spiral enamel band on upper tusks (*Cuvieronius*)
7. oblique transverse lophids; strong tendency for inclination of cones to midline of tooth; loss of enamel band on upper tusks in adults (*Haplomastodon*)
8. valleys between cones filled with conules on both labial and lingual sides of M_3; molars with posttrite trefoiling on some lophids; incipient choerodonty; cones near vertical, with no midline inclination
9. M_3 with slender-based cones and U-shaped valleys; great obliquity of transverse lophids; M_3 ovoid in outline with strong anterolateral curve; mandible short, shallow, laterally expanded in cross-section at M_3 (*Amahuacatherium*)
10. lower tusks lost, abbreviated spout-like symphysis, M_3 with moderate obliquity of transverse lophids; choerodont with full pretrite and nearly full posttrite trefoiling; cement present on molars; flat occlusal surface with moderate wear
11. straight enamel band present on upper tusks; numerous valley conules not associated with cones; trefoil pattern unclear toward posterior of M_3 (*Notiomastodon*)
12. no enamel band on upper tusks; thick cement on molars; elongate, rectangular M_3 (*Stegomastodon*)

the close relationship of the genera that comprise the Cuvieroniinae [and corroborating earlier work, principally that of Tobien (1973)], Shoshani (1996:174) states that "...the exact relationship within the South American complex is not entirely clear, ..." This is true, and yet Shoshani's presentation is substantially at odds with that of other authors who used more characters to create what may be said to be the more conventional view (Savage, 1955; Tobien, 1973), which is presented here as Cladogram B (Fig. 17B). Characters for this cladogram are listed in Table 3. In this view, i.e., Cladogram B, *Cuvieronius* separated early from the group from which came the other genera. It is the earliest occurring genus of the Cuvieroniinae, appearing in the Hemphillian of North America (Savage and Russell, 1983). Continuing in this presentation, the trends within the Cuvieroniinae are toward greater complexity in molar enamel pattern with loss of upper tusk enamel having occurred twice (in *Haplomastodon* and *Stegomastodon*).

The introduction of *Amahuacatherium* permits a re-evaluation of the subfamily Cuvieroniinae. It should be noted that although a reduced mandibular symphysis could not be conclusively demonstrated in *Amahuacatherium*, such is inferred for that genus and in our analysis we assume *Amahuacatherium* was brevirostrine.

When *Amahuacatherium* is included among the genera of gomphotheres, it may take one of two possible positions. The first is that seen in Cladogram C (Fig. 17C), which reflects an overall similarity between *Amahuacatherium* and *Gomphotherium/ Rhynchotherium*, i.e., relative primitiveness. Characters used in the construction of this cladogram are listed in Table 4. The order of acquisition of these characters reflects the hypothetical placement of *Amahuacatherium* in an early position relative to the later evolution of the four genera of brevirostrine gomphotheres. *Haplomastodon* and *Cuvieronius* are placed as sister-taxa in that they share a comparatively simple molar pattern, in contrast to that of *Amahuacatherium*, *Stegomastodon*, and *Notiomastodon*. This simplification, therefore, becomes a derived character for *Haplomastodon* and *Cuvieronius*. Dentally, *Haplomastodon* and *Cuvieronius* are so similar that Simpson and Paula Couto (1957) stated that they could not be separated by teeth alone. Although they are very similar, we offer some observations that may prove useful when dealing with isolated molars (Table 4). For the sake of the current discussion, these two genera may be treated as one group without altering the major elements of the analysis.

In the second cladogram that includes *Amahuacatherium*, Cladogram D (Fig. 17D) and the characters listed in Table 5, what appears to be the initial stage of enamel complexity (incipient choerodonty) in *Amahuacatherium* is interpreted as a derived feature

in common with the other known genera that have complexly folded enamel, i.e., *Stegomastodon* and *Notiomastodon*. In this view, *Cuvieronius* and *Haplomastodon* are yet linked by those features that previously allied them with *Stegomastodon* and *Notiomastodon*. This presentation requires no character reversals, unlike the molar simplification that unites *Cuvieronius* and *Haplomastodon* in Cladogram C (Fig. 11C). It does, however, require the loss of lower tusks and the development of an abbreviated, spout-like symphysis in two separate lineages of the cuvieroniids, once at node 5 and once at node 10. These two characters are undoubtedly linked, i.e., a spout-like symphysis is not possible unless the lower tusks are lost, so such a sequence is plausible.

Thus, *Amahuacatherium* could be placed in sister-group status to the other genera of the Cuvieroniinae (Cladogram C) on the basis that it is brevirostrine, but that it still retains reduced lower tusks. On the basis of molar enamel complexity, the genus could be assigned sister-group status to *Stegomastodon* and *Notiomastodon* only (Cladogram D).

A third possibility is that the *Amahuacatherium* line arose directly from the *Gomphotherium* lineage before the appearance of *Rhynchotherium*. With the oldest *Rhynchotherium* being from upper Miocene deposits of Honduras (Webb and Perrigo, 1984), and approximately the same age as *Amahuacatherium*, this possibility warrants serious consideration. This would require that *Amahuacatherium* be placed into a new subfamily, as a sister-group to *Rhynchotherium* and the later cuvieroniids. Additional fossil material is required before a more precise resolution of how *Amahuacatherium* fits into the scheme of gomphotherian evolution can be achieved.

It is instructive at this point to examine in detail some of the results of the studies of Shoshani (1996) and Tassy (1996b), the most recent attempts to provide cladistic analyses of proboscideans. We focus solely on some aspects of those papers that pertain to this study.

Tassy's (1996b) paper was a phylogenetic reconstruction of all taxa within the Proboscidea. As a modification of a prior study (Tassy, 1990), the paper was presented as a "'state of the art' (Tassy, 1996b:39)" summary of proboscidean relationships. In this study, the gomphotheres, stegodontids, and elephantids were considered a monophyletic group, although the monophyly was supported by only two traits. One trait was a higher cranial vault (character 37, state 2 of Tassy, 1996b), specifically, "cerebral part of cranium inflated vertically." The intent of this character is fairly clear in that state (0) "not inflated,"

and state (1), "inflated with sagittal crest lost," in combination with state (2), trace the progressive vertical development of the cranium. The problem with this character is that it is highly subjective and within the New World gomphotheres of the subfamily Cuvieroniinae there is a significant difference between the vertical inflation seen in the cranium of *Stegomastodon* and that seen in *Cuvieronius*, as was clearly discussed and illustrated by Simpson and Paula Couto (1957; pl. 1). The vertical inflation in *Stegomastodon* may be almost twice what is seen in *Cuvieronius*. It can easily be argued that "state 2" of this character does not apply to all genera of the subfamily Cuvieroniiae, so the suggestion that it supports the monophyly of three families, one of which includes this subfamily, is questionable.

This character is also used by Shoshani (1996:165) in his cladistic analysis, although it is considerably modified. Shoshani's terminology is 73) cranium: state (0), "swelling absent (sagittal crest present);" state (1), "swelling present with loss of sagittal crest;" and state (2), "wide cerebral area." It is inferred that the three states of this character are comparable to those of Tassy's (1990) character 37 (which is the same in Tassy, 1996b). The very subjective nature of the third state remains, however. Further, we submit that there is a fundamental difference between the two authors in that being "inflated vertically" is not the same as having a "wide cerebral area." Shoshani (1996; app. 16.2) also does not recognize the substantial differences in the degree of inflation of the cranium seen among the members of the subfamily Cuvieroniinae.

The second character used by Tassy (1996b) to establish the monophyly of the gomphotheres, stegodontids, and elephantids is his character 74, state (1). This character is "lower tusks: transverse section flat (0), piriform (1), or circular (2)." Tassy (1996b:46) wrote, "According to Tobien (1973a) [herein, Tobien, 1973] the latter character [i.e., piriform cross-section of lower tusks] is the best for the group." What is meant by "the group" in that sentence is unclear because Tobien (1973) did not discuss stegodontids or elephantids except in passing. It must be strictly in reference to gomphotheres. But, in fact, there is no such statement, explicit or implicit, in Tobien (1973). What Tobien (1973:221) does say is, "As has been mentioned several times before, **the peg form of the lower incisors** is a typical structural element of the Old World *Gomphotherium angustidens* and the North American small gomphotheres as well." [emphasis ours] And later (Tobien, 1973:266), "The *Gomphotherium* ("*Trilophodon*") group is characterized by strong upper incisors and a long mandibular symphysis provided with incisors of pyriform **or rounded** transverse section ("peg incisors")." [emphasis ours] Indeed, the great cross-sectional variation seen in lower tusks of *Gomphotherium* is illustrated by Tobien (1973;

figs. 3, 8) and Mazo (1996: 139). With such a great variability of this character seen within the gomphotheres alone, the character state of "pyriform cross-section" of lower tusks cannot be used to support the monophyly of gomphotheres, stegodontids, and elephantids. And, of course, several genera in these three groups do not have lower incisors at all, which makes the contribution of the character state even more questionable. Inexplicably, with all of the data to the contrary, Shoshani (1996:174) also says that *Gomphotherium* has pyriform lower tusks, as opposed to "roundish."

Tassy's analysis becomes even more confusing as far as the gomphotheres are concerned when he divides the gomphotheres into Old World trilophodont gomphotheres (= gomphotheres1), all within the genus *Gomphotherium*, and the New World gomphotheres (= gomphotheres2). Within the latter he includes all the autochthonous genera of New World gomphotheres and the Old World *Sinomastodon* Tobien, Chen, and Li 1986, but excludes the New World members of the genus *Gomphotherium*. He then goes on to say, "New World gomphotheres appear to be more closely related to tetralophodont gomphotheres (node 11) than to trilophodont gomphotheres from Eurasia, due to the presence of lower tusks with rounder cross-sections (74 (state 2))" (Tassy, 1996b:47). In fact, only one (*Rhynchotherium*) of the six genera that he places in his New World gomphothere group is known to have lower tusks, although in his data matrix (Tassy, 1996b:42) he scores his New World gomphotheres as if lower tusks were present in all. This defies the purpose of analysis based on character states. He certainly cannot support his claim that the genera of New World gomphotheres are united by the shape of the lower tusks when only one out of six genera has them.

Shoshani's (1996) characters related to the lower tusks are also confusing. As his character 2 (Shoshani, 1996:162) he has "I_1: (0) present or (1) absent." He implies that this is equivalent to Tassy's (1990 [1996b]) combined character 70, "lower tusks: present (0), or absent (1)" and character 82, "lower incisors: all present (0), or at least one pair is missing (1)." He scores all genera of proboscideans for which data are available as having state (1), or to be lacking I_1's. Luckett (1996) discusses upper incisor homologies in proboscideans and concludes that the I^2 forms the upper tusks in these animals. If the assumption is made that the lower incisor homologies correspond to those of the upper incisors, then the I_2, rather than the I_1, forms the lower tusks. In that case, equating Shoshani's character 2 with Tassy's character 70 is inappropriate. That Shoshani (1996:153,174) makes the assumption that the I_2 forms the lower tusks is clear. Thus, Shoshani (1996) has no character comparable to Tassy's character 70.

The absence of lower tusks, of course, has been one of the long recognized, shared derived characters of the cuvieroniids, an important character that was apparently left out of Shoshani's analysis.

As a third example of the subjective state of character analysis in these papers on proboscideans, we cite secondary (=posttrite) trefoiling in the molars of gomphotheres. Shoshani (1996:164) lists as his character 55) Molars: trefoils: state (0) = none; state (1) = on pretrite plus quasi posttrite; state (2) = on pretrite and posttrite. What is meant by "quasi posttrite" is not explained, but perhaps the term is equal to "incipient secondary trefoiling" used by other authors. He codes *Gomphotherium* as "0," *Rhynchotherium* as "1," and all of the cuvieroniids as "2." He implies that this character is the same as Tassy's (1990) character 113, "posttrite conules absent (0), or present, at least outlined (1). Tassy (1996a:24) defines "posttrite conule" as "posttrite enamel pillar," which is equal to "posttrite central conule." The posttrite central conule is the conule on the anterior and posterior walls of each lingual half-lophid of the lower molars. Wear of the posttrite central conules leads to posttrite trefoiling. Tassy (1996b:42) codes both his "gomphotheres1" (= *Gomphotherium*) and "gomphotheres2" (=New World gomphotheres exclusive of *Gomphotherium*) as "0," thereby denoting that posttrite trefoiling is absent in all. This, of course, is in direct contradiction to Shoshani (1996), and, also, simply incorrect.

Tobien (1973) characterized *Gomphotherium* as having no or only incipient secondary trefoils, and he characterized molars of species of *Rhynchotherium* as having the simple *Gomphotherium* structure, i.e., without secondary trefoils. Webb and Perrigo (1984) stated that *Rhynchotherium* did not have posttrite trefoils, but Miller (1990:64) described a specimen of that genus that showed "incipient to modest development" of posttrite trefoils. Simpson and Paula Couto (1957) described both *Gomphotherium* and *Rhynchotherium* as having no, not even incipient, posttrite trefoils. In these two genera, then, there is considerable difference of opinion as to presence of secondary trefoiling. Whether these are temporal or populational differences is not knowable at this time. But, as noted by Savage (1955), these two genera are difficult if not impossible to separate on molar features alone, so they should at least be coded the same.

In the cuvieroniids, secondary trefoiling is widely recognized as well advanced in *Stegomastodon* and *Notiomastodon*, but this is not true for *Cuvieronius* or *Haplomastodon*. Tobien (1973:243) refers to the latter two genera as having molars "structurally more simple with secondary trefoils" than the former two genera. Simpson

and Paula Couto (1957:182) refer to both *Cuvieronius* and *Haplomastodon* as having poorly developed, or "variably incipient double trefoils," as opposed to the "double trefoils" seen in *Stegomastodon* and *Notiomastodon*. To suggest that all four of these genera have the same degree of posttrite trefoiling, as does Shoshani (1996), or that posttrite trefoiling is absent in all of these genera, as does Tassy (1996), is not an accurate description of the state of this character in the genera of New World gomphotheres.

Further on in Shoshani's analysis (1996:174), he finds state (2) of his character 94, ["Mandibular symphysis: (0) reduced symphysis; (1) long symphysis; (2) short, spout-like"] to be a synapomorphy for the Cuvieroniinae, even though it is homoplastic within Proboscidea as a whole. If *Amahuacatherium* is placed within the Cuvieroniinae this synapomorphy breaks down because *Amahuacatherium*, while brevirostrine, still has tusks, the positioning of which essentially precludes a spout-like symphysis. Tassy (1996b:42), on the other hand, having lumped the autochthonous New World longirostrine (2) and brevirostrine (4) genera into a single group for his analysis, codes all as having a long mandibular symphysis. The absence of lower tusks, while also homoplastic within Proboscidea as a whole, would probably also have appeared as a synapomorphy for the Cuvieroniinae in Shoshani's analysis had this character been included in his data base. Again, however, the placement of *Amahuacatherium* within the Cuvieroniinae removes that character as a synapomorphy.

Although Tassy (1996b) placed *Sinomastodon* within his "New World gomphothere" group, he did not place it in a subfamily. Shoshani (1996) also declined to place *Sinomastodon* into a New World subfamily of gomphotheres, although he commented that he tested and corroborated the hypothesis of Tobien et al. (1986) that *Sinomastodon* is closely related to the cuvieroniids. But this was true only if a limited number of carefully chosen characters for *Sinomastodon* were used in the analysis. McKenna and Bell (1997) place *Sinomastodon* in the Rhynchotheriinae.

From this brief look at the cladistic analyses of Shoshani (1996) and Tassy (1990, 1996b), it is apparent that the identification and description of characters, as well as correlation of characters among studies, leaves much to be desired. A thorough analysis of all the characters used in these two studies would undoubtedly yield many more examples of problems comparable to those cited above, an effort that is beyond the scope of this study. It is not surprising that the results of the cladistic analyses of Tassy (1996b) and Shoshani (1996) are not in agreement. The study of proboscidean relationships would benefit greatly from a rededication to the pursuit of precise data gathering and presentation.

That, along with new discoveries and the new data those discoveries will provide, will go further toward resolving proboscidean relationships than any number of analyses, cladistic or otherwise, based on imprecise data and poorly defined characters.

Zoogeographic Significance

Prior to the discovery of *Amahuacatherium peruvium*, it was thought that South American gomphotheres developed from North American gomphotheres that entered South America during the late Pliocene/early Pleistocene. No unequivocal pre-Pleistocene gomphotheres were known in South America. However, specimens of *Haplomastodon* were recovered from one locality in western Amazonia, Pedra Preta on the Rio Alto Juruá (Simpson and Paula Couto, 1981), along with material that has been referred to the late Miocene rodent *Phoberomys* Kraglievich 1926 (Paula Couto, 1978). The fossiliferous deposits at the Pedra Preta locality lie above the Ucayali Unconformity, thus these specimens of *Haplomastodon* are younger than *Amahuacatherium*. The incongruity of finding a supposedly late Pliocene/Pleistocene gomphothere in the same deposit as a late Miocene rodent was explained as a consequence of re-working of fossils from different levels with final deposition at Pedra Preta, although Simpson (in Simpson and Paula Couto, 1981) argued that the fossiliferous deposits along the Rio Alto Juruá and their contained fossils were essentially unified as to age. If so, then these fossils are all late Miocene in age based on the date of 9.01±0.28 Ma for the stratigraphically higher Cocama ash. Our own field observations support the suggestion that the fauna of Pedra Preta is a natural association and that a number of North American immigrants reached South America prior to the Pleistocene (Campbell and Frailey, 1995; 1996; see below). *Stegomastodon* and *Cuvieronius*, present in the Pliocene of North America, were thought to have developed in North America before their first appearance in South America (Simpson and Paula Couto, 1957). With gomphotheres added to the late Miocene fauna of South America, it can no longer be assumed that any of the Pleistocene gomphotheres of South America evolved in North America and entered South America at the close of the Pliocene.

Although the specimen of *Amahuacatherium* does not preserve an abundance of the data necessary to relate it precisely to other taxa of gomphotheres, its presence in South America in the early late Miocene poses some very different, intriguing possibilities for proboscidean evolution and dispersal between continents. The following discussion is, of necessity, speculative, but it is useful for understanding the potentially complex interrelationships among North American and South American proboscideans.

The scenario presented in Fig. 18A is a depiction of phylogeny and dispersal as expressed by Savage (1955) and accepted as generally correct by later authors (e.g., Tobien, 1973; Webb and Perrigo, 1984; Webb, 1991; Webb and Rancy, 1996; Dudley, 1996; and Lambert, 1996). The most notable exception is the exclusion of *Stegomastodon* from South America in the writings of Webb and his co-authors. With *Cuvieronius* and *Stegomastodon* occurring in much earlier strata in North America than in South America, and conscious of the Holarctic origin of Proboscidea and the isolation of South America in the Tertiary, it seemed probable to these authors that the major evolutionary events within the Cuvieroniinae had occurred in North America, with dispersal to South America being a late and relatively insignificant conclusion to the story. *Haplomastodon* may also have been a part of the North American Blancan, but there is some doubt that these attributions were correct (Simpson and Paula Couto, 1957:179-80; Tobien, 1973:243). In Fig. 18A-E, the presence of *Haplomastodon* in North America is included, questionably, but its presence in North America during the Blancan would not radically alter the suggested relationship. In Fig. 18B-E, *Haplomastodon* is included in the late Miocene South American record (the Pedra Preta specimens). Again, relationships are not affected, but with this inclusion one must consider that the direction of dispersal of this genus could have been south to north, rather than the more conventional north to south movement. In Fig. 18D, no direction of dispersal for *Haplomastodon* is indicated as it is unknowable and unimportant to the figure. Temporal ranges for these diagrams are from Savage and Russell (1983) and Shoshani and Tassy (1996b), with modifications as noted.

Although temporally and morphologically suited to be placed early within the lineage of the later Cuvieroniinae, unique features of *Amahuacatherium*, such as the size and unusual configuration of the mandible, suggest that this lineage may be unrelated to the later New World gomphotheres. As such, the consequences of its inclusion in the scenario depicted in Fig. 18B does not affect the positions and relationships of the other taxa. Beyond demonstrating the passage of a large mammal across a narrowing marine barrier in the late Tertiary, the inclusion of *Amahuacatherium* in the Miocene fauna of South America is an interesting event, but unimportant to the evolution of the later Cuvieroniinae.

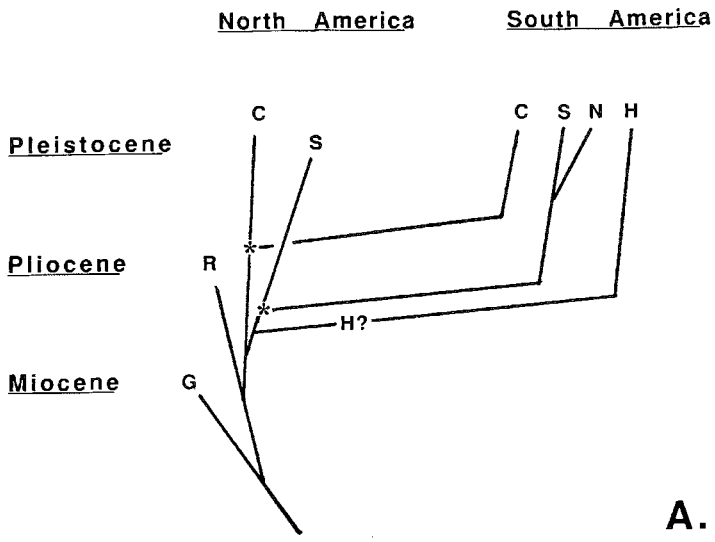
The hypothetical entrance into South America of the *Haplomastodon-Stegomastodon-Notiomastodon* contingent as shown in Fig. 18B, compared to the timing of events as presented in Fig. 18A, follows a re-interpretation of the age of the strata yielding fossils of *Haplomastodon* in the Amazon Basin (Campbell and Frailey, 1995, 1996; Frailey et al., 1996a, 1996b) (see below). A northward, rather than southward, dispersal of *Haplomastodon* becomes more viable in this scenario.

Figure 18C corresponds with Cladogram C (Fig. 17C). The position of *Amahuacatherium* in this scenario is that of an early sister-group to all later cuvieroniids. Here, the hypothetical position of *Amahuacatherium* is depicted in a situation in which the major evolutionary events within the Cuvieroniinae occurred in South America. Those genera that are found as fossils in North America would represent northward dispersals. This scenario is attractive in that *Cuvieronius* and *Stegomastodon*, which differ considerably from each other and the hypothetical ancestral rhynchorostrine stock, are not required to be closely related.

If the relationships among the five genera now placed in the Cuvieroniinae are as shown in Cladogram D (Fig. 17D), then a number of dispersal patterns are possible that affect *Cuvieronius* and *Haplomastodon*, but not *Amahuacatherium*, *Stegomastodon*, and *Notiomastodon*. Two of these are given in Figs. 18D and 18E. Figure 18D is a complicated scenario in that two lineages diverged immediately after evolution of the cuvieroniid line from basal rhynchorostrine stock. One lineage led to *Cuvieronius/ Haplomastodon* and a separate lineage led to *Amahuacatherium*, *Stegomastodon*, and *Notiomastodon*. It is possible that *Cuvieronius* may have evolved as a North American taxon that dispersed to South America in the late Pliocene/early Pleistocene, whereas the lineage leading to *Amahuacatherium*, *Stegomastodon*, and *Notiomastodon* dispersed to South America in the late Miocene. *Amahuacatherium* would then have been part of an early lineage within the radiation of South American gomphotheres. In this interpretation, the lineage leading to *Stegomastodon* would have dispersed into North America in the late Pliocene/early Pleistocene after originating in South America. This lineage became extinct in North America shortly thereafter, but survived in South America until the later Pleistocene. Continuing in this scenario, *Haplomastodon* was part of an early proboscidean dispersal into South America from North America, but *Cuvieronius* entered South America late. The known occurrences of *Cuvieronius* in South America would accurately reflect zoogeographic events. In Fig. 18E, both *Cuvieronius* and *Haplomastodon* have long, but for *Cuvieronius* unrecorded, histories in South America. Although the four taxa of South American gomphotheres in these last two scenarios form a monophyletic grouping, the Cuvieroniinae, it is entirely possible that the *Cuvieronius/Haplomastodon* lineage and the *Amahuacatherium/Stegomastodon/Notiomastodon* lineage arose independently from the ancestral rhynchorostrine stock and that the Cuvieroniinae as currently recognized is polyphyletic.

With the fossil record in tropical South America as poor as it is, particularly in the Amazon Basin, it is not surprising that multiple scenarios for the evolution and dispersal of

gomphotheres are possible. The resolution of major questions regarding gomphothere evolution must await the discovery of additional material. However, at this point in time it has become clear that the dispersal and evolution of gomphotheres in the New World was far more complex than has long been accepted. The scenarios presented above are offered only to demonstrate this complexity. The true story of gomphothere evolution may follow one of those scenarios, or it may involve yet another combination of events.



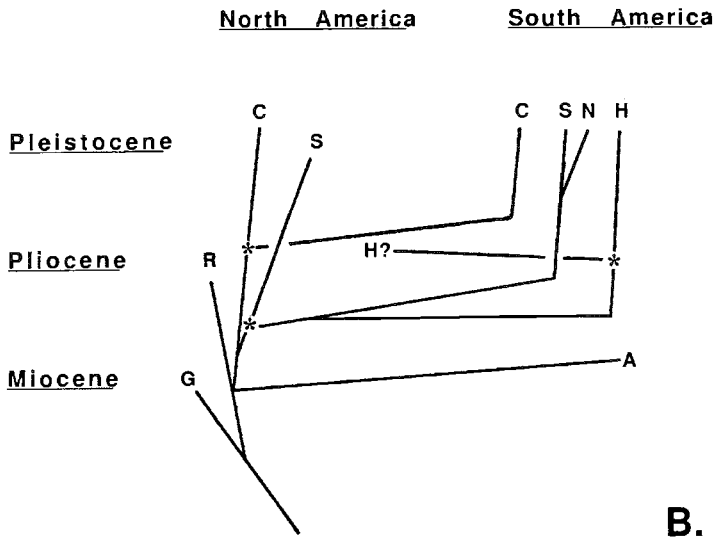
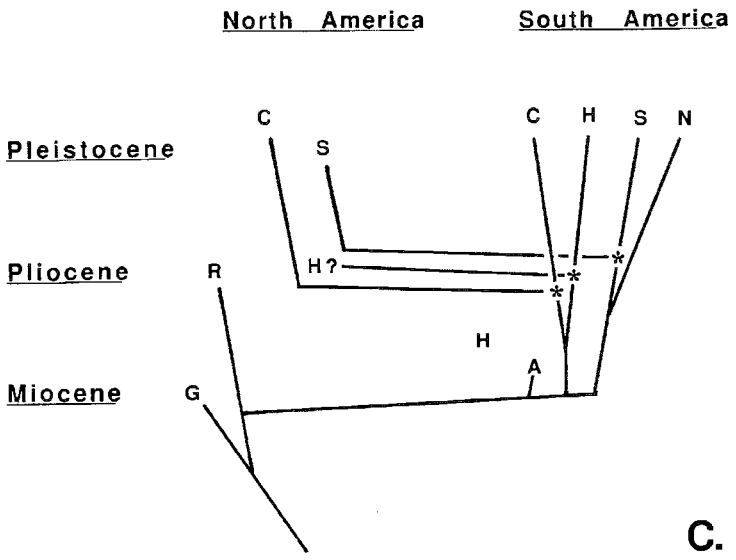
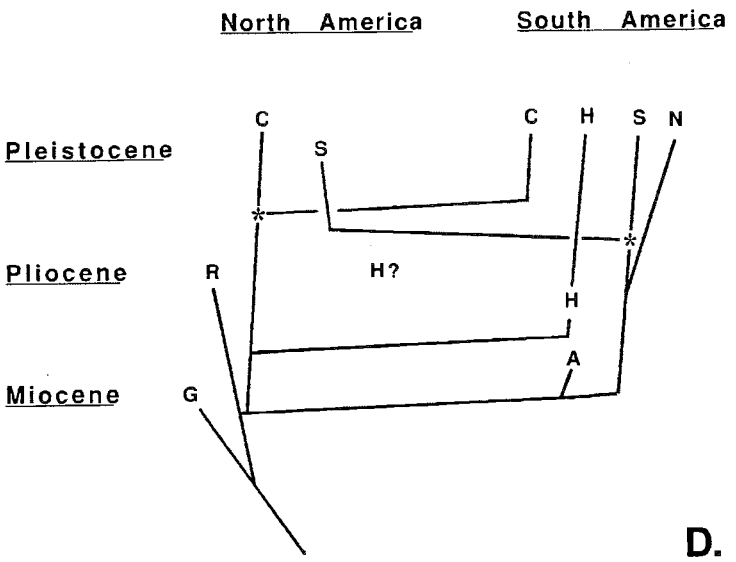


Figure 18 Five possible scenarios for the evolution and dispersal of the genera comprising the subfamily Cuvieroniinae, as discussed in the text. In the figures, **A** = *Amahuacatherium*; **C** = *Cuvieronius*; **G** = *Gomphotherium*; **H** = *Haplomastodon*; **N** = *Notiomastodon*; **R** = *Rhynchotherium*; **S** = *Stegomastodon*. Dispersal events denoted by asterisk.



C.



D.

Figure 18 Continued

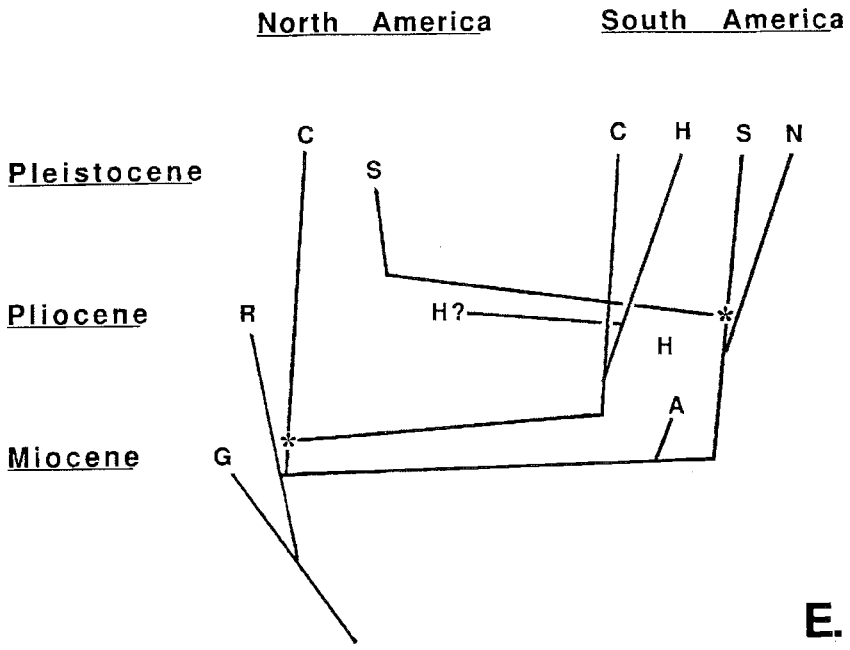


Figure 18 Continued

GEOLOGY

From a geological and paleontological standpoint, the tropical regions of the Americas remain among the least studied areas in the world. This is particularly true for the Amazon Basin, which covers an area of about 7 x 10^4 km^2, or about 40 percent of the entire South American continent, and within which few areas have been studied in detail. Several factors have contributed to limit our understanding of the geology of the Amazon Basin, the following of which are among the most significant. First, good outcrops are rare in Amazonia because of the almost complete cover of tropical vegetation. For the most part outcrops are found only in cutbanks of rivers and, except during dry seasons, only minimal exposures are accessible. Outcrops that reveal complete sections of the local stratigraphy are rarer still. This is because the uppermost (younger) levels are often missing from river cutbanks because of terracing in river valleys in the course of downcutting to current channel levels. Further, the bases of sections are often obscured by slumping or the accumulation of river-borne debris. Thus, it is difficult, but not impossible, to correlate strata in traditional ways over long distances within a river system or between river valleys.

Second, the complexity of the stratigraphic nomenclature that has developed over the past several decades has generated confusion as to exactly which strata may be under discussion. The complexity has come about because workers in the several countries having territorial interests in Amazonia have applied different names to the same geologic units. Or, in some instances, the same unit has received multiple names within the same country. This problem has been exacerbated by the fact that most of the geologic research of the past has occurred in the course of mineral or oil and gas exploration and is still proprietary information, or it is available only in rarely cited and hard-to-obtain internal company documents. Stratigraphic names proposed in these documents have often entered general usage, but they have no formal standing.

Third, the previous lack of any numerical age dates for western Amazonian strata has meant that the ages of the various strata could only be inferred through biostratigraphy

or other imprecise means. There is no precise chronology available for Amazonian strata, and only two $^{40}Ar/^{39}Ar$ dates provide chronologic anchors for interpreting the upper Cenozoic stratigraphic history of the Amazon Basin (Campbell et al., in press). The prior absence any numerical age dates for upper Cenozoic Amazonian strata has probably been the leading cause for many of the misinterpretations of the timing of events associated with the historical geology of Amazonia, including some aspects of our own work (e.g., Campbell and Frailey, 1984; Frailey et al., 1988; Campbell and Romero-P., 1989; Kay and Frailey, 1993). And, last to be noted here, the lack of an infrastructure makes the logistical problems of conducting field work in many places within Amazonia almost insurmountable.

Major efforts to describe the geology of lowland Amazonia were initiated by Brazil (see, e.g., RADAMBRASIL, 1977, and other issues in that series) and Colombia (PRORADAM, 1979). A comparable effort to describe the geology and natural resources of the Peruvian Amazon is currently underway (see, e.g., Placios-M., 1996). With these resources, many other individual publications, and our own field work, it is possible to piece together a general picture of the historical geology of the western Amazon Basin. Through the following brief review we present our current understanding of the late Tertiary geologic history of eastern Peru and westernmost Brazil and place *Amahuacatherium* within the context of that history in order to substantiate its late Miocene age assignment.

Tectonics of the Central Andes

The region under discussion lies between the Andes Mountains to the west and the ancient cratons of eastern South America, the Guiana Shield and the Brazilian Shield. The formation of the Andes has been a consequence of the ongoing subduction of oceanic lithosphere, i.e., the Nazca Plate, beneath continental lithosphere, i.e, the South American Plate. The timing of the large scale tectonic episodes that gave rise to the Andes can be used as a general, proxy guide to dating the geologic events that transpired in the adjacent Amazonian lowlands. The following summary of Andean tectonic episodes of Peru will assist in understanding the stratigraphic relationships described below.

The tectonic evolution of the Peruvian Andes began in the Cretaceous and encompassed six relatively short phases of compression when the subducting plate squeezed the continental crust against the shield rocks (Mégard, 1984, 1987; Sébrier and Soler, 1991). With each new phase of compression, the primary zones of compression at the active margin of the continent migrated eastward, in a southwest to northeast direction,

with the result that the Peruvian Andes are readily divisible into five longitudinal NW-SE trending, morphostructural zones. These are, from west to east: 1) the Coastal Zone; 2) the Western Cordillera; 3) the Altiplano; 4) the Eastern Cordillera; and 5) the Subandean Zone, which is also referred to as the sub-Andean thrust and fold belt (STFB) (Fig. 19). As would be expected, tectonic deformation within the most recently formed morphostructural zone, the STFB, has een greatest in the west, gradually diminishing to the east. East of the STFB, the sedimentary rocks underlying the llanos of Amazonia extend eastward as a thinning wedge, overlapping the western edge of the Brazilian Shield and forming the Amazonian Foreland Basin. Isolated deformation and uplift, some a consequence of the same compression episode that formed the STFB and some a consequence of the intrusion of volcanic plugs (Stewart, 1971) (Fig. 19), have also occurred within the llanos east of the STFB.

According to Mégard (1984, 1987), the post-Cretaceous compressive phases of uplift in the Peruvian Andes were the 1) Incaic (mid- to late Eocene); 2) Quechua I (early to mid-Miocene; not precisely known, but bracketed between 20 - 12.5 Ma); 3) Quechua II (late Miocene; 9.5-8.5 Ma); and 4) Quechua III (late Miocene/Pliocene; 6 Ma). The Quechua II phase is described by this author as differing from the other phases by having a north-south, as opposed to southwest-northeast, compressive stress direction. In this interpretation, during the Quechua II phase longitudinal faults (NW-SE) were reactivated, but few new structures were created.

Noble et al. (1990) recognized the following five post-Cretaceous periods of compressive deformation in northern Peru: Incaic I (Paleocene), Incaic II (44-39 Ma), Quechua I (25-17 Ma), Quechua II (12-8 Ma), and Quechua III (6-5 Ma).

In the southernmost Peruvian Andes, Ellison et al. (1989) recognized six post-Cretaceous deformation events. They described these as an Incaic event (late Eocene; ?40 Ma); and a series of five Quechuan events ("D" events in their usage): D1 (late early Oligocene, 32-30 Ma); D2 (earliest Miocene; 23-22 Ma); D3 (middle Miocene; ~15 Ma); and D4 and D5 (late Miocene; 8-7 Ma). They correlate their D4 event to the Quechua III phase of Mégard (1984).

Farther south in the central Andes (including parts of Peru, Bolivia, and Chile), Sébrier et al. (1988) and Sébrier and Soler (1991) recognized six post-Cretaceous compressional events, which are (following their designation): F1 (late Eocene; ca. 42 Ma); F2 (late Oligocene; ca. 26-28 Ma); F3 (middle Miocene; 15-17 Ma); F4 (early late

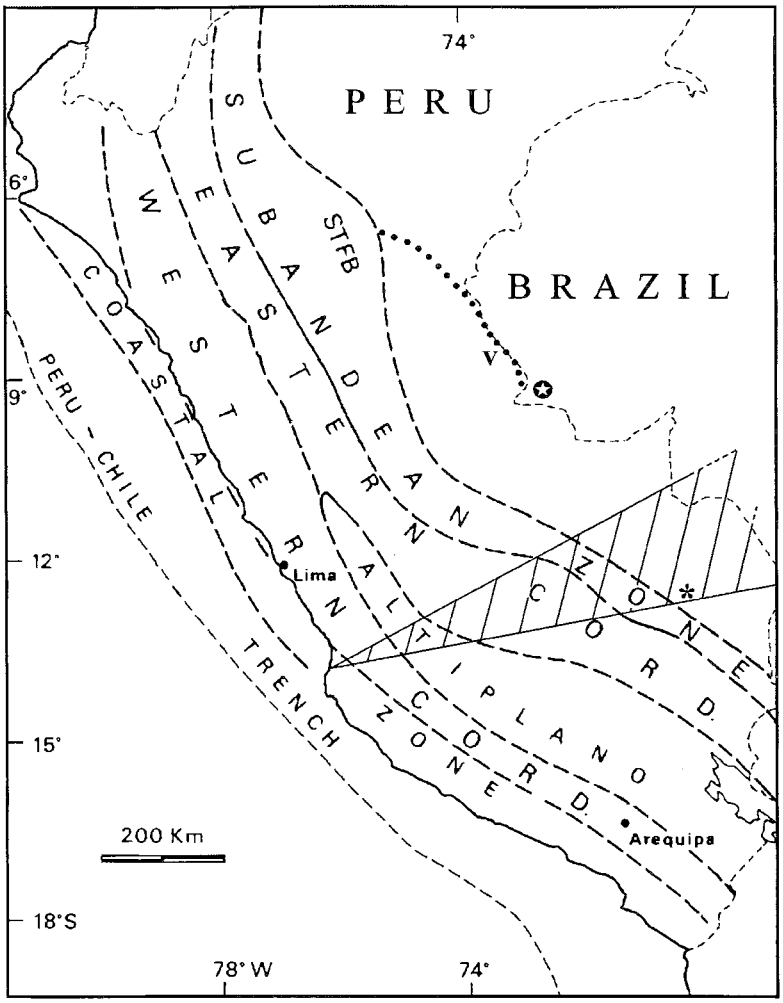


Figure 19. Map showing the five morphostructural zones of the Peruvian Andes. The Subandean Zone is also referred to as the sub-Andean thrust and fold belt (STFB). The dotted line indicates the approximate position of the anticlinal zone extending southeastward from the STFB, which includes the Contaya Arch and Serra do Divisor Arch. The location of the volcanic plugs dated by Stewart (1971) are indicated by "V." The hatched area is the Pisco-Abancay Deflection Zone, which is where the Pacific Plate changes from flat-slab subduction under the Andes to the north to dipping slab subduction to the south (after Mégard and Philip, 1976). The locality from which came *Amahuacatherium* (marked by asterisk) lies very near the southern limit of the deflection zone. The white star in black circle marks the location of the sections of Simpson and Paula Couto (1981) (Fig. 23) on the Alto Juruá River in Brazil. Base map modified from Mégard (1987).

Miocene; ca. 10 Ma); F5 (late Miocene; ca. 7 Ma); and F6 (late Pliocene-early Pleistocene; ca. 2 Ma).

Regardless of the differences in the specific timing recorded for these compressive events, there appears to be general agreement that there was a middle Miocene (Quechua I) event, an early late Miocene (Quechua II) event, and a late late Miocene (Quechua III) event. The differences in the number and timing of the compressive events described by these authors are not unexpected in that they were working in different areas of the Andes. It is also necessary to note that there is a change in this region from flat-slab subduction in northern and central Peru to dipping-slab (~30E) subduction in southern Peru, Bolivia, and northern Chile (Jordan et al., 1983). The transition between these two types of subduction is known as the Pisco-Abancay Deflexion Zone, as depicted by Mégard and Philip (1976) and Jordan et al. (1983). The site that produced *Amahuacatherium* lies within the transition zone, but very near its southern limit (Fig. 19), so it is not clear which of the above series of dates is most applicable to deformation in that region. The youngest phase (F6; ~2 Ma) recognized by Sébrier et al. (1988) and Sébrier and Soler (1991) has not yet been recognized in the Peruvian Andes, so it may have been of limited regional extent. See Fig. 20 for the relationship among these and other events discussed below.

The formation of the STFB has been linked to the Quechua III event (~7-6 Ma) (Pardo, 1982; Mégard, 1984; Ellison et al., 1989), which would suggest that the last major structural deformation located between the Eastern Cordillera and the Brazilian Shield occurred at this time. This would include the formation of the Contaya Arch and the Serra do Divisor Arch (also known as the Serra do Moa Arch), which are major anticlinal, partially thrust-bounded structures isolated within the llanos of eastern Peru. These arches extend in a curving line of variable width southeastward from the STFB (Fig. 19). The view that the formation of the STFB is tied to the Quechua III event is reinforced by the possibility that the Pliocene was a period of extensional deformation within the retroarc foreland (Sébrier and Soler, 1991). Near the beginning of this postulated period of extensional deformation, in the early Pliocene, there occurred an apparently isolated igneous event in the llanos of eastern Peru (Stewart, 1971) that resulted in the intrusion of three peralkaline volcanic plugs on the western flank of the Serra do Divisor Arch (Fig. 19). This event is dated to about 5 Ma based on two K:Ar dates (5.4 ± 0.2 Ma and 4.4 ± 0.2 Ma) from rocks taken from the volcanic plugs. As explained by Stewart (1971:2310), the above ages can only be described as minimum dates. The igneous plugs cut through upper Cretaceous rocks and domed and pierced the overlying Tertiary strata during emplacement. These strata were subsequently breached by erosion, exposing the intruded igneous rocks.

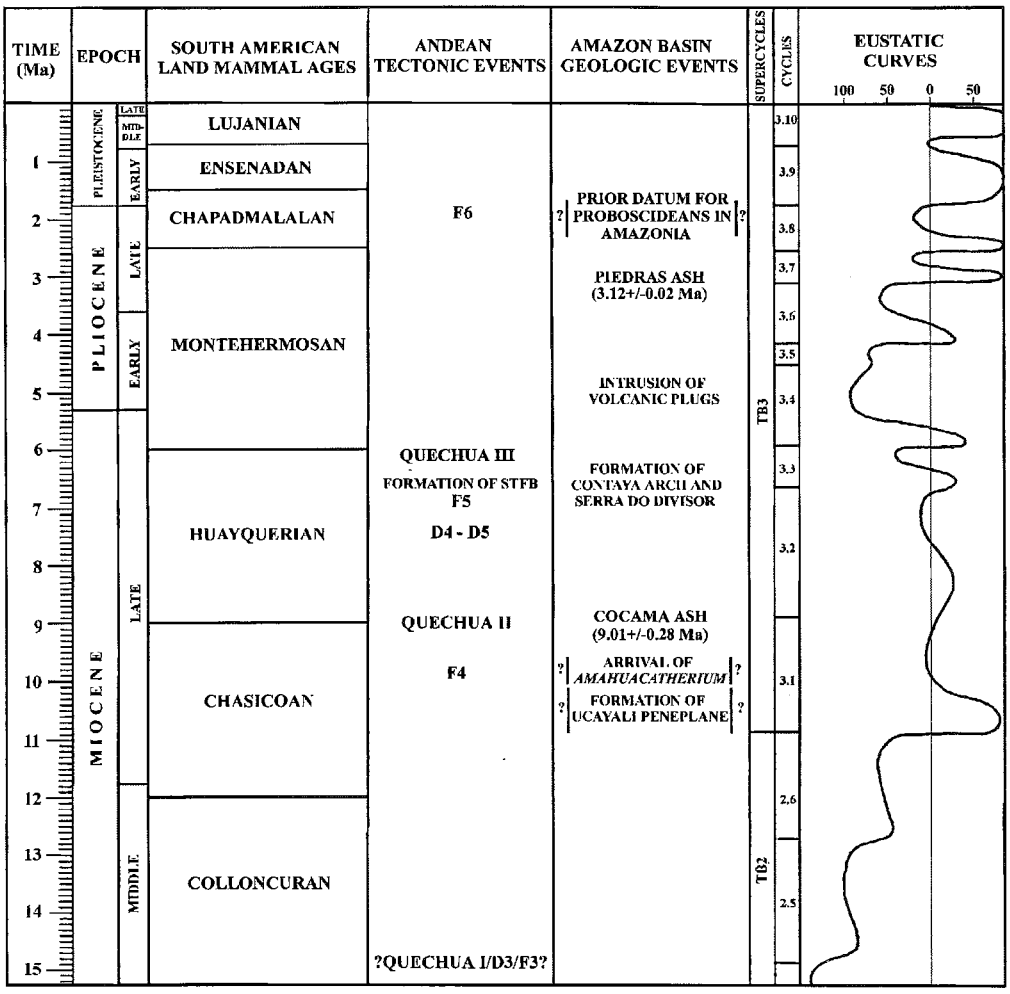


Figure 20. Chart relating geologic events of western Amazonia to Andean tectonic events, South American Land Mammal Ages, sea level fluctuations, and time. The geochronology is after Berggren et al. (1995), the land mammal ages are after Marshall and Sempere (1993), and the Andean tectonic events are after Mégard (1984, 1987), Ellison et al. (1989), Sébrier et al. (1988), and Sébrier and Soler (1991) (see text for details). The sea level curve is after Hardenbol et al. (1998). Events in Amazonia are as discussed in the text; all dates are approximate.

It was assumed that volcanic cones resulted from this igneous activity (Stewart, 1971:2310), but no phonolitic flows or pyroclastics that could be related to the plugs were identified. It was further assumed that the plugs postdate the formation of the Ucayali Peneplane (see below), an assumption supported by the obtained K:Ar dates. Unfortunately, there are no field data pertaining to the question of whether any portion of the younger Tertiary strata in the region, i.e., those overlying the Ucayali Peneplane and comprising the Madre de Dios Formation, were domed and pierced by the emplacing igneous plugs as were the strata of the older Contamana Group, or whether some beds of the Madre de Dios Formation may postdate this emplacement (see below).

It is possible that the younger strata in the lowlands of eastern Peru underwent further structural deformation as a consequence of the youngest Andean compressional phase (F6; ~2 Ma) recognized by Sébrier et al. (1988) and Sébrier and Soler (1991), but as yet there are no data to address this possibility.

Stratigraphy of Western Amazonia

The stratigraphy of the western Amazon Basin is fairly straight-forward in its general outline. Furthermore, the same general stratigraphic sequence of two distinct series of Cenozoic deposits can be observed from southeastern Colombia, southward through eastern Ecuador and Peru, western Brazil, and into northern Bolivia. Our interpretation of the stratigraphy of western Amazonia is not shared by all workers in the field, however, as will become clear below. The stratigraphic charts presented in Fig. 21 and the sections presented in Figs. 22 and 23 represent just some of the current interpretations of the stratigraphy of western Amazonia. The following discussion, and particularly that pertaining to the younger Tertiary deposits, is necessary to securely place *Amahuacatherium* within a stratigraphic context. With the two numerical age dates on the upper Cenozoic strata of Amazonia, the stratigraphy of Amazonia can be related to dated events of the Andes. First, however, there must be a clear understanding of that stratigraphy.

The Contamana Group: The lower, older series of deposits includes a Paleocene to Upper Miocene sequence, primarily clays, the strata of which are difficult to differentiate in much of lowland Amazonia where only well cores are available for study. However, distinct formations are more readily recognized, and they have been better described, in the foothills of the Andes and in the breached anticlinal ridges in the lowlands of eastern Peru and westernmost Brazil where more complete sections are available (e.g., Kummel, 1948; Guizado,

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COLUMNA ESTRATIGRAFICA COMPUESTA PARA EL ORIENTE PERUANO

ERA	SISTEMA	GRUPO	FORMACION	LITOLOGIA	POTENCIA METROS	DESCRIPCION-LITOLOGIA	AMBIENTE DEPOSICIONAL
CENOZOICA	CUATERNARIO					Grava; arenas y arcillas	Aluvial
	TERCIARIO		IPURURO		1000-1500	Areniscas, conglomerados y lodolitas marrones	Continental
			PEBAS		200-600	Lutitas y coquinas	Salobre
			CHAMBIRA		500-1500	Lodolita, limolitas y areniscas rojizas anhidr.	
			POZO		100-400	Lutitas grises, calisas grises y areniscas	Marino - lacustrino
			YAHUARANGO		100-1200	Lodolitas limolitas y areniscas abigarradas.	Continental
			CASA BLANCA			Arenisca blanca cuarzosas	Marino-deltaico

A. Generalized stratigraphic chart for all of eastern Peru. Modified from Guizado (1975).

			FAJA SUBANDINA			LLANO AMAZONICO		
			Marañon	Ucayali	Madre de Dios	Marañon	Ucayali	Madre de Dios
CENOZOICO	CUATERNARIO	Holoceno	No Diferenciado	Reciente	No Diferenciado	No Diferenciado	Reciente	NO DIFERENCIADO
		Pleistoceno		Ucayali			Ucayali	
	TERCIARIO SUPERIOR	Plioceno		Fm. Ipururo		Fm. Ipururo	Fm. Ipururo	
		Mioceno	Gpo. Chiriaco	Fm. Chambira	Capas Rojas no diferenciadas	Fm. Pebas / Fm. Chambira	Fm. Chambira	
		Oligoceno	Fm. Pozo	Fm. Pozo		Fm. Pozo	Fm. Pozo	
	TERCIARIO INFERIOR	Eoceno	Gpo. Huayabamba	Fm. Yahuarango / Fm. Casa Blanca		Fm. Yahuarango / Casa Blanca	Fm. Yahuarango / Casa Blanca	
		Paleoceno		Fm. Huchpayacu		Fm Huchpayacu	Fm Huchpayacu	

Fase Quichuana Discordancia Angular

B. Stratigraphic chart comparing the formations found in three subbasins of the sub-Andean region of Peru with those of the same three basins in the Amazonian region of Peru. See Fig. 24 for location of the sub-basins. Modified from Pardo and Zuñiga (1976).

Figure 21 Continued

PROJETO CARVÃO NO ALTO SOLIMÕES
COLUNA ESTRATIGRÁFICA

ERA	PERÍODO		ÉPOCA	UNIDADE ESTRATIGRÁFICA
CENOZÓICA	QUATERNÁRIO		HOLOCENO	ALUVIÕES E TERRAÇOS DE EROSÃO
			PLEISTOCENO	FORMAÇÃO IÇÁ
	TERCIÁRIO	NEOGENO	PLIOCENO	FORMAÇÃO SOLIMÕES
			MIOCENO	
		PALEOGENO	OLIGOCENO	
			EOCENO	FORMAÇÃO RAMON (?)
			PALEOCENO	

C. Stratigraphic chart of the western Amazon Basin of Brazil. Modified from Miai et al. (1977).

Figure 21 Three charts of the stratigraphy of western Amazonia reflect differing interpretations of the geology of the region. **A,** Stratigraphic chart of eastern Peru prepared by Petroleos del Peru (modified from Guizado, 1975). **B,** A second stratigraphic chart of eastern Peru (modified from Pardo and Zuñiga, 1976). **C,** Stratigraphic chart of western Brazil (modified from Maia et al., 1977). A very important congruence in these figures is the recognition of a major unconformity separating the Tertiary beds from those of the "Quaternary." This is the Ucayali Peneplane of Kummel (1948); see text. This unconformity is designated by the strong dashed line in "A," the hatched area in "B," and the wavy line in "C." The deposits above the unconformity are referred to the Quaternary by these authors, reflecting the widespread interpretation that these deposits are very young. We refer these deposits to the Madre de Dios Formation (see text; Fig. 16). We date the oldest beds of this formation, or Unit "A," to the late Miocene on the basis of the mammalian paleofauna and a $^{40}Ar/^{39}Ar$ date of 9.01±0.28 Ma on the Cocama ash deposit from within the lower portion of Unit "A." The Tertiary formations represented in these figures comprise the Contamana Group.

1975; Schobbenhaus et al., 1984). These Tertiary deposits are representative of a shallow sedimentary basin that filled with stratified, fine-grained sediments (Kummel, 1948; Rüegg, 1956; Maia et al., 1977; Nuttall, 1990; Hoorn, 1993, 1994a, 1994b). They have been folded and faulted, especially in the eastern foothills of the STFB, and similar structural deformation extends well to the east into the Amazonian lowlands of Peru and western Brazil as the Contaya Arch and Serra do Divisor Arch.

In eastern Peru these strata are generally referred to as the "Capas Rojas," or "Red Beds" (Rüegg, 1956), that comprise the Contamana Group (Kummel, 1948). The Contamana Group is best known in the Ucayali Basin because of the extensive field work and drilling accomplished there in association with the petroleum industry. The older portion of the Contamana Group contains the Paleogene Casa Blanca, Yahuarango, and Pozo Formations, listed in order of decreasing age (Fig. 21A). Some authors extend the Cretaceous Huchpayacu Formation into the Paleocene (Fig. 21B). In western Brazil, these older Cenozoic deposits are differentiated as the Ramon Formation (Fig. 21C), which is known only from outcrops in the Serra do Moa (Bouman, 1959) and subsurface well cores (Maia et al., 1977), and the younger Solimões Formation (Schobbenhaus et al., 1984).

The uppermost series of this group consists of the Paleogene/Neogene Chambira Formation and the Neogene Ipururo Formation (Fig. 21A,B); together they correspond, in part, to the Ramon Formation and, in part, to the Solimões Formation of Brazil (Fig. 21C). The well-known, fossiliferous Pebas beds of northeastern Peru are thought by some to lie between the Chambira Formation and the Ipururo Formation (e.g., Guizado, 1975) (Fig. 21A,B), and the Pebas beds are included in the Solimões Formation by Hoorn (1994b). The Pebas beds have been assigned to the Pliocene by some authors (e.g., Sheppard and Bate, 1980), but more recently they have been assigned to the Miocene by Nuttall (1990), based on molluscs, and to the middle to late Miocene by Hoorn (1994b), based on pollen studies. The Eocene Pozo Formation and the Miocene Pebas beds are the only unequivocal Cenozoic marine or estuarine deposits documented for western Amazonia.

The Ucayali Peneplane: The contact between the Contamana Group and the upper stratigraphic levels is a clear and obvious unconformity that marks a period of extensive erosion within lowland Amazonia (Kummel, 1948; Rüegg, 1956; Maia et al., 1977; Campbell et al., 1985) (see Fig. 21A-C). This period of rapid erosion formed the Ucayali Peneplane [as named by Kummel (1948)], and Kummel (1948:1260) expressed

the view that denudation during this time resulted in upwards of 5 km of sediment being removed from some areas of eastern Peru.

Unfortunately, although Kummel (1948:1260) clearly stated that the term Ucayali Peneplane was in reference to the unconformity between the Ipururo Formation of the Contamana Group and the overlying "Pliocene Ucayali Formation" (his designation), in a later reference in the same paper he referred to the broad, flat topography extending east of the Cordillera Oriental and surrounding the Contamana and Contaya Mountains as the Ucayali Peneplane (Kummel, 1948:1262). In the latter instance he must have been in reference to the Amazon planalto, which would be the surficial expression of his Ucayali Formation (Madre de Dios Formation in our usage; see below). The two surfaces are quite different in age (one being middle Miocene and other Plio/Pleistocene) and mode of formation (the older being an erosional surface and the younger a depositional surface). Koch (1959a, 1959b) later used the term Ucayali Peneplane in the second sense of Kummel (1948:1262), i.e., in reference to the planalto. The usage of Koch (1959a, 1959b) was later followed by Dumont et al. (1991), thus there has been confusion as to exactly what the term Ucayali Peneplane means. We use it here in the first sense of Kummel (1948:1260), i.e., the erosional surface that lies between the older Miocene strata of the Contamana Group and the overlying, nearly horizontal, upper Miocene-Plio/Pleistocene deposits of the Madre de Dios Formation. The Ucayali Peneplane as an erosional surface is then also an erosional unconformity, which may be referred to as the Ucayali Unconformity.

The fact that the Ucayali Peneplane is recognizable from southern Colombia (Khobzi et al., 1980; Hoorn et al., 1995), southward through Ecuador (Tschopp, 1953), eastern Peru (Kummel, 1948; Rüegg, 1952; Räsänen et al., 1992) and western Brazil (Simpson, 1961; Simpson and Paula Couto, 1981), to northern Bolivia (Campbell et al., 1985; Leyton-D. and Pacheco-Z., 1989), and hundreds of kilometers east of the Andes into Brazil (Maia et al., 1977; pers. obs.) suggests that a major Andean tectonic event or sea level change was involved in its formation. The possible timing of the formation of the Ucayali Unconformity is discussed below. Following this period of uplift and erosion, lowland Amazonia was again converted into a basin of deposition, which resulted in the accumulation of the upper stratigraphic sequence, the Madre de Dios Formation.

The Madre de Dios Formation: Overlying the marked angular unconformity formed by the Ucayali Peneplane there is a series of strata that comprises the upper Miocene-Plio/Pleistocene Madre de Dios Formation in Peru and Bolivia (Oppenheim, 1946; Campbell and Romero-P., 1989) and its lateral continuation in Brazil, the Içá

Formation (Maia et al., 1977). These beds have received many names in Peru, and for many years they were included in the Solimões Formation in Brazil (Caputo et al., 1971; Santos, 1974; Schobbenhaus et al., 1984). Although Kummel (1948) referred to the strata overlying the Ucayali Unconformity as the Ucayali Formation, the lateral equivalents of these beds to the south had earlier been named the Madre de Dios Formation by Oppenheim (1946). We follow the latter designation herein for reasons of priority. These deposits consist of heterogeneous beds of unconsolidated clays, silts, and fine sands, commonly with a fossiliferous basal conglomerate (e.g., Rüegg and Rosenzweig, 1949; Maia et al., 1977; RADAMBRASIL, 1977, 1978). The Madre de Dios Formation appears to be divisible into three members, informally designated Unit "A," Unit "B," and Unit "C," with Unit "A" being the oldest (Campbell et al., 1985) (Fig. 22). The three horizons are demarcated by abrupt changes in lithology across what may or may not be conformable boundaries. The basal conglomerate previously interpreted to underlie this series was named the Acre Conglomerate Member of the Madre de Dios Formation by Campbell et al. (1985), and it, or very similar deposits, have also been noted in western Amazonia (Simpson and Paula Couto, 1981; Dumont et al., 1988; Räsänen, 1991), central Amazonia (Maia et al., 1977), the Colombian Amazon (Galvis et al., 1979; Khobzi et al., 1980; Eden et al., 1982), and possibly in southeastern Amazonia (Viega, 1991). The Madre de Dios Formation shows no obvious evidence of folding (Khobzi et al., 1980; Eden et al., 1982; Maia et al., 1977; pers. obs.), although we have noted broad uplift in the Andean Foreland Basin in eastern Peru, and Koch (1959a, 1959b) and Dumont et al. (1991) have suggested that the surface of these beds is tilted away from the structural highs in the lowlands of eastern Peru. And, as noted above, localized doming of some horizons of the Madre de Dios Formation may have been caused by the Pliocene(?) intrusion of igneous plugs in the eastern Peruvian lowlands.

The above delineation of the Madre de Dios Formation into three horizons is comparable to that of Simpson and Paula Couto (1981) (Fig. 23). The informal terminology they used was different from ours, i.e., they used "Pleistocene Phase 1" for Unit "A," "Pleistocene Phase 2" for Unit "B," and "Recent" for Unit "C." Their dating of the beds to the Pleistocene was based on what they interpreted to be Pleistocene taxa in the fossil vertebrate fauna they recovered from the basal conglomerate of this formation. We will return to examine details of this point later.

For more detailed descriptions of the deposits of the Madre de Dios Formation, see Kummel, 1948; Guizado, 1975; Maia et al., 1977; Khobzi et al., 1980; Simpson and Paula Couto, 1981; Campbell et al., 1985; Leyton-D. and Pacheco-Z., 1989; Campbell

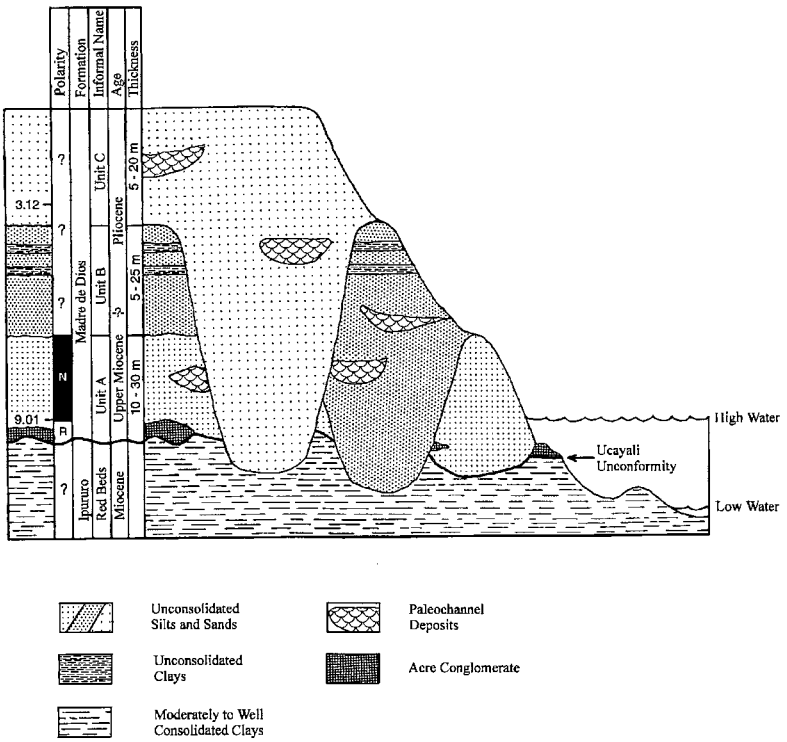

Figure 22. In outcrops in western Amazonia the oldest strata exposed during the dry season low water period belong to the Contamana Group, usually the Ipururo Formation (shown here) or Chambira Formation (both included in the Solimões Formation in Brazil). The Ucayali Peneplane appears as a marked unconformity, shown here as the dark line separating the Ipururo Formation from the overlying Madre de Dios Formation (= Içá Formation in Brazil). The Madre de Dios Formation is divisible into three horizons, the oldest being Unit "A," which dates to the late Miocene (Huayquerian) based on contained fossils and the $^{40}Ar/^{39}Ar$ date on the Cocama ash. The age of Unit "B" is unknown, but the basal portion of Unit "C" has been $^{40}Ar/^{39}Ar$ dated to 3.12±0.02 Ma. Unit "B" and Unit "C" can be found extending downward well into the underlying units, hypothetically as far as the Contamana Group, a consequence of deposition following riverine erosion of the underlying units. The extreme downcutting illustrated here has, however, never been observed in the field. The three units of the Madre de Dios Formation are primarily composed of horizontal beds of unconsolidated sands and silts, often with a high clay content. Fairly thick clay horizons may occur in all three units, but they are most common in Unit B (where they are depicted here). Isolated paleochannel deposits occur in all three units of the Madre de Dios Formation. The Acre Conglomerate (heavy cross-hatch pattern) usually occurs at the base of Unit "A," but may occasionally be found slightly higher in the section. Compare this figure with Fig. 23. From Campbell et al. (in press).

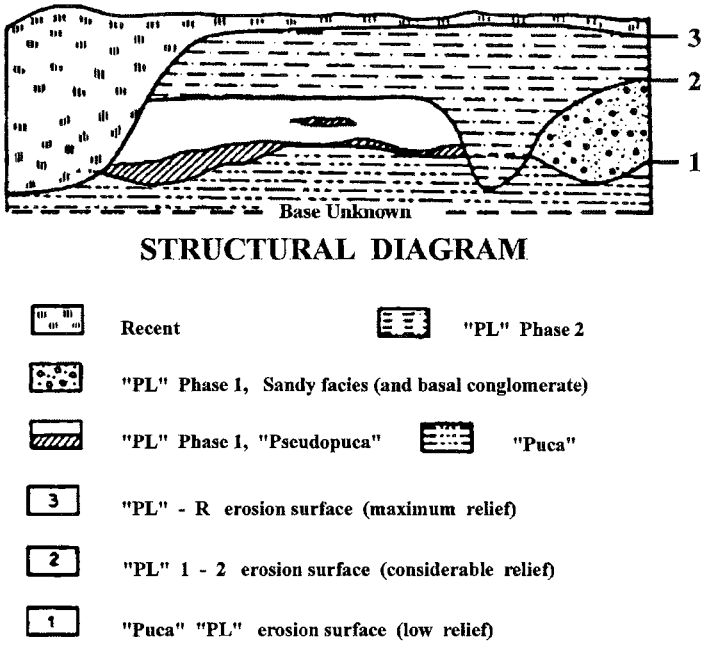

Figure 23. The interpretation of the stratigraphy of the Río Alto Juruá by Simpson and Paula Couto (1981) corresponds very closely to what we have observed throughout western Amazonia. Compare with Fig. 22. In this figure, "Recent" corresponds to Unit "C" of the Madre de Dios Formation, "PL" Phase 2 corresponds to Unit "B," and "PL" Phase 1 corresponds to Unit "A." "PL" stands for Pleistocene. "Puca" refers to the red beds of the Contamana Group, whereas "Pseudopuca" refers to clay deposits of Unit "A" that resemble those of the older red beds of the Contamana Group. The Ucayali Unconformity is here designated as the erosion surface "1," which separates the "Puca" from the "PL" Phase 1 deposits. Note the channeling of the upper units into the underlying units, occasionally to the beds of the Contamana Group. Modified from Simpson and Paula Couto (1981).

and Romero-P., 1989; and Räsänen et al., 1992. For opposing points of view and interpretations, see Santos and Silva (1976) and Silva (1988), who argue that the Madre de Dios Formation is not a separate formation but rather a continuation of the older depositional sequence.

The significance of the congruence between the interpretations of Simpson and Paula Couto (1981) and our own lies in the fact that these interpretations were arrived at independently and in separate regions of Amazonia. Simpson and Paula Couto's (1981) work was along the Río Juruá in Brazil, in the Acre sub-basin of Amazonia (Fig. 24), whereas our work was based in the Río Purus and Río Madre de Dios drainage basins, in the Madre de Dios-Beni sub-basin (Fig. 24) of Amazonia. This is taken as support for the hypothesis that deposition of the Madre de Dios Formation occurred contemporaneously throughout western Amazonia after the formation of the Ucayali Peneplane, as opposed to the model of non-synchronous deposition in each of the sub-basins of Amazonia proposed by Räsänen et al. (1990) (see below) and the continuous deposition model advocated by Santos and Silva (1976) and Silva (1988). The latter authors state that although they could recognize in outcrops the physical feature referred to as the Ucayali Unconformity, they interpreted it as a local cut and fill feature that varies widely in age depending upon where you might be in the basin. Were this the case it would be exceeding difficult, if not impossible, to correlate deposition in lowland Amazonia with mountain building episodes of the Andes or global sea level flucuations. However, this interpretation is in conflict with our field observations, and we reject it in favor of the hypothesis that the Ucayali Unconformity represents a single period of erosion within Amazonia.

With the single exception of Räsänen et al. (1995), who argued that the Madre de Dios Formation originated as tidal deposits during a late Miocene marine transgression, all authors agree that these deposits are of fluvial or fluvio-lacustrine origin. It should be noted, however, that in earlier papers Räsänen et al. (see, e.g., 1990; 1992) were in agreement with the latter, arguing that modern aggradational fluvial systems were the perfect analog for those that dominated at the time of deposition of the Madre de Dios Formation, even going so far as to postulate directions of fluvial transport. Their earlier interpretations differ from ours, however, in that they postulated the existence of several separate subsiding basins in western Amazonia that were active at different periods during the Tertiary, within which deposition occurred at different times (Fig. 24). We, on the other hand, see no evidence for separate, individual basins acting independently of each other, or independently of Andean tectonics, in the late Tertiary. Furthermore, there is no direct evidence that the structural arches that are claimed to be uplifting and separating subsiding basins in western

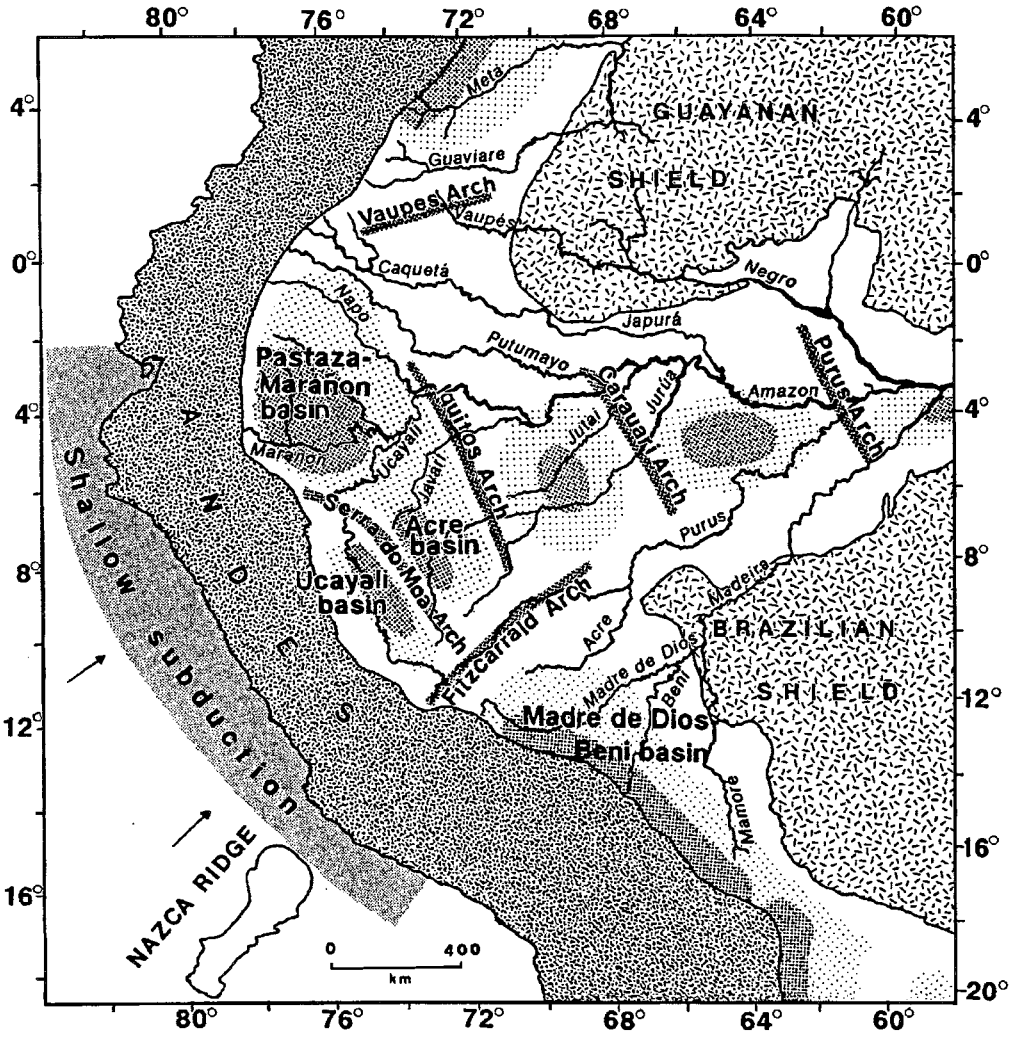

Figure 24. Some authors map the Amazon Basin as consisting of several depositional basins separated by structural arches. Although there are well core and seismic data that support the contention that these structures exist, there are only limited data that can be inferred to substantiate claims that any of these sub-basins and arches were active as separate structural entities during the late Tertiary. If these structural features had been independently active in the late Tertiary, the observed widespread uniformity of the Madre de Dios Formation could not exist. The Serra do Divisor (or Moa) Arch (which in this figure includes the Contaya Arch) and the Marañon Basin are the only structural features for which late Tertiary activity has been demonstrated, and the timing of that activity is not firmly dated. Map modified from Räsänen et al. (1990).

Amazonia (e.g., Dumont et al., 1988; Räsänen et al., 1990; Tuomisto et al., 1992) or affecting modern river transport (Mertes et al., 1996; Dunne et al., 1998) have been active at all in the late Cenozoic. In fact, one of these arches, the Iquitos Arch in western Brazil (Fig. 25), is overlain by several hundred meters of the Contamana Group (or Solimões Formation in Brazil), which is itself overlain by the Madre de Dios Formation (=Içá Formation in Brazil) (Miura, 1972; Maia et al., 1977). None of these strata appear to have been disturbed by uplift of the Iquitos Arch. Further, the section by Caputo (1991, fig. 3) illustrates the great depth of upper Cenozoic deposits resting upon the Iquitos Arch, deposits that thin toward the east (Fig. 26). If the Iquitos Arch had been uplifted in the Neogene it would be logical to expect a thinning of the upper Cenozoic deposits from east to west onto the Iquitos Arch, not the reverse. The only structural arch for which there is any evidence for movement in the late Cenozoic is the Serra do Divisor, which is thought to have formed as a consequence of the Andean Quechua III compressive event (see above). See Petri and Fúlfaro (1983) and Schobbenhaus et al. (1984) for additional discussions of these arches.

In a recent paper, Räsänen et al. (1998) discuss the geology and geomorphology in the region of Iquitos. In this paper they refer to certain stratigraphic units as "Unit A," "Unit B," and "Unit C." It should be clearly stated and understood that these units have absolutely no correlation to our Units "A," "B," and "C" of the Madre de Dios Formation. In fact, "Unit A" and "Unit B" of Räsänen et al. (1998) refer to beds of the Contamana Group lying below the Ucayali Unconformity, whereas "Unit C" of Räsänen et al. (1998) is clearly the same horizon as our Unit "A" of the Madre de Dios Formation. Räsänen et al. (1998) also describe what they refer to as separate stratigraphic units the "Iquitos sands" and "fluvial terrace deposits." Based on the data provided in their paper, including stratigraphic descriptions, sectins, and satellite imagery, it is clear that the "Iquitos sands" are a facies of our Unit "A" of the Madre de Dios Formation. The "fluvial terrace deposits" also represent Unit "A" of the Madre de Dios Formation, but possibly only in part; Unit "B" of the Madre de Dios Formation may also be represented in some of the "terrace deposits." Some of the confusion regarding the terrace deposits may be attributed to the fact that whereas Räsänen et al. (1998) interpret the river terraces along the river as depositional features, they are actually erosional features formed in the course of downcutting of the rivers to their current entrenched levels. Of course, there is probably a thin "skin" of more recent deposits covering the top of the terrace that accumulated as the terrace was being formed by erosion, but this is inconsequential in comparison with the remainder of the section.

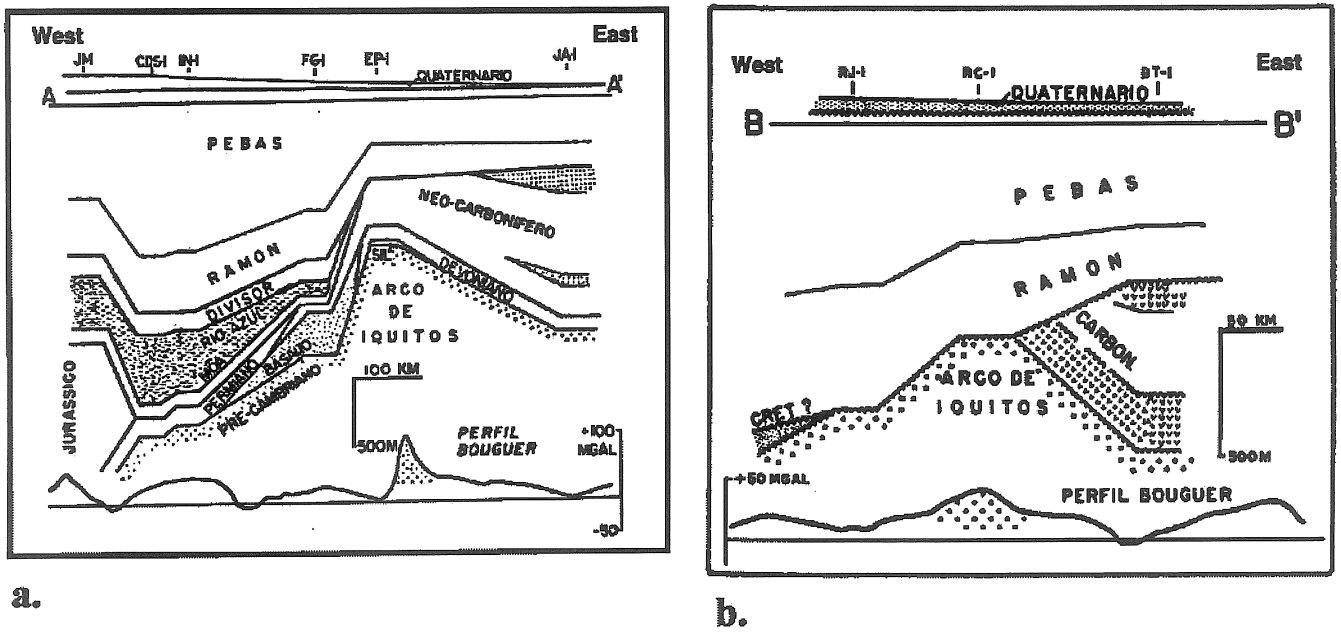

Figure 25. Two cross-sections through the Iquitos Arch, based on well-core data, reveal that several hundred meters of Tertiary sediments overlie this structural arch. The spacing of the wells that provided the core data is indicated at the top of the illustration. The "Quaternary" horizon in these profiles corresponds to the Madre de Dios Formation (= Içá Formation in Brazil). These data argue against hypotheses that the Iquitos Arch was active in the late Cenozoic, or that it has had any influence on modern river valley formation. Section A-A' is from approximately 8° 30' S, 73° 50' W to 6° 30' S, 70° 00' W, whereas section B-B' is from 4° 45' S, 72° 55' W to 4° 30' S, 70° 00' W. Modified from Miura (1972).

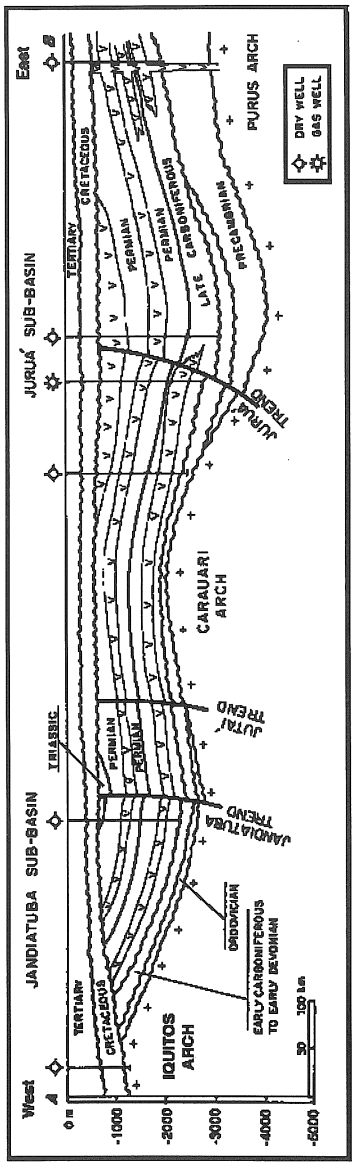

Figure 26. An east-west section through the Solimões basin shows that the Cretaceous and Tertiary beds overlying the Iquitos Arch thin considerably to the east. This is the opposite of what would be expected if the Iquitos Arch had been tectonically active, i.e., was being uplifted, in the Tertiary. Modified from Caputo (1991; fig. 3).

In summary, we are convinced by field observations and the available published data that western Amazonia acted as a single depositional basin in the late Cenozoic (with the possible exception of the Ucayali Basin, as explained below), that the Ucayali Unconformity formed as the consequence of a single erosional event occurring throughout western Amazonia, and that the Madre de Dios Formation covers western Amazonia as a single depositional sequence. This interpretation is supported by the sections presented in Figs. 21 and 23, which represent the conclusions of other, independent studies. Having established the broad regionalism of the geologic features and stratigraphy of western Amazonia, it is then possible to attempt to relate these features to dated geologic events.

Dating Geologic Events of Eastern Peru

The specimen of *Amahuacatherium* was excavated from a broad shelf at the base of a high cutbank of the Rio Madre de Dios in southeastern Peru (Fig. 8). Unfortunately, the contact between the strata of the Contamana Group and the overlying Madre de Dios Formation is poorly exposed at the site because of irregular slumping and the fact that an exceptionally low river water level is required for its exposure. However, the great contrast in lithology between the moderately consolidated older beds and the overlying loose, unconsolidated sands, silts, and clays supports the interpretation that the shelf from which came the gomphothere lies below the Ucayali Unconformity.

Deriving an age for the fossil-producing horizon is complicated by the difficulty in determining if the horizon belongs to within the Contamana Group, and, if so, where. Because it is right at the top of the older stratigraphic sequence there are two possibilities as to the age of the horizon. One is that it was a horizon buried within the stratigraphic sequence of the Contamana Group that was subsequently exposed by the erosion that brought about the peneplanation of those beds. In this case, the horizon bearing *Amahuacatherium* would predate the Ucayali Peneplane by an undetermined period of time. Alternatively, the deposit comprising the exposed shelf from which came *Amahuacatherium* formed at the time of formation of the Ucayali Peneplane and is therefore contemporaneous with that peneplane. In either case, deposition of the fossil predates the formation of the Madre de Dios Formation. At this site the entire section of the Madre de Dios Formation is exposed, i.e., there has been no terracing at the top of the section that might have removed the youngest strata, as clearly seen in radar and satellite imagery of the area. Neither is there any evidence of downcutting of the upper horizons through the underlying beds.

Age of the Madre de Dios Formation: A major advance in understanding the stratigraphy of Amazonia has been the discovery of two deposits of volcanic ash within the Madre de Dios Formation (Campbell et al., in press). These tuffs were dated using $^{40}Ar/^{39}Ar$ techniques. The older of the two deposits is a dense, fine-grained ash, approximately 1.5 m in thickness that crops out over a distance of ~15 m just upstream from the mouth of the Río Cocama, a small tributary of the Río Purus (Fig. 27) (10° 24' 55" S; 71° 10' 22" W). The base of this ash is ~4 m above the Ucayali Unconformity, which places it stratigraphically within the lower portion of Unit "A" of the Madre de Dios Formation. The outcrop is heavily vegetated, however, so it was not possible to observe directly its relationship to other horizons of Unit "A" exposed just upriver. A sample of this ash yielded a $^{40}Ar/^{39}Ar$ date of 9.01±0.28 Ma, which provides a minimum age for the beginning of deposition of the Madre de Dios Formation. We consider a good estimate for the initiation of deposition of the Madre de Dios Formation to be about 9.5 Ma because the Cocama ash is not at the base of Unit "A" and some time must be allotted for this basal interval. A possible source for this ash is the very large Macusani volcanic field of the Peruvian Eastern Cordillera, approximately 460 km due south, older deposits of which have been dated at 9.4 ±0.3 Ma (Noble et al., 1984). Appreciable volumes of ash flow material from this field are presumed to have entered the Amazon Basin.

This date is consistent with the magnetostratigraphy of the lower part of the Madre de Dios Formation at a locality on the Río Las Piedras 221 km south of the Cocama ash deposit (12° 03' 12" S; 69° 54' 06" W). A series of 11 sample sites that began ~2 m above the Ucayali Unconformity and extended through 19 m of section, or all of Unit "A," were analyzed. The lower two sample sites had reversed magnetic polarity, whereas the remainder were of normal magnetic polarity (Campbell et al., in press). Reversed Chron C4Ar.1r extends from 9.025-9.230 Ma (Berggren et al., 1995), which lies within the degree of error of the $^{40}Ar/^{39}Ar$ date of 9.01± 0.28 Ma. Whether the ash falls within the zone of reversed polarity or lies just above it is unknown.

Another test for the presence of remnant paleomagnetism in Amazonian sediments was run on samples from a cut bank of the Río Purus at São Francisco, Brazil (7° 35' 65" S; 65° 33' 55" W), about 640 km east northeast. These samples were taken from nine sites spaced 3.5 m apart, vertically, which covered the entire thickness of the exposure at this outcrop. All of the samples, except the highest, were collected in plastic containers because of the unconsolidated nature of the sediments. The highest, and youngest, set of three samples was taken as blocks from a moderately indurated horizon of Unit "B." This sequence of samples revealed a zone of reversed polarity basal in Unit "A" and another in

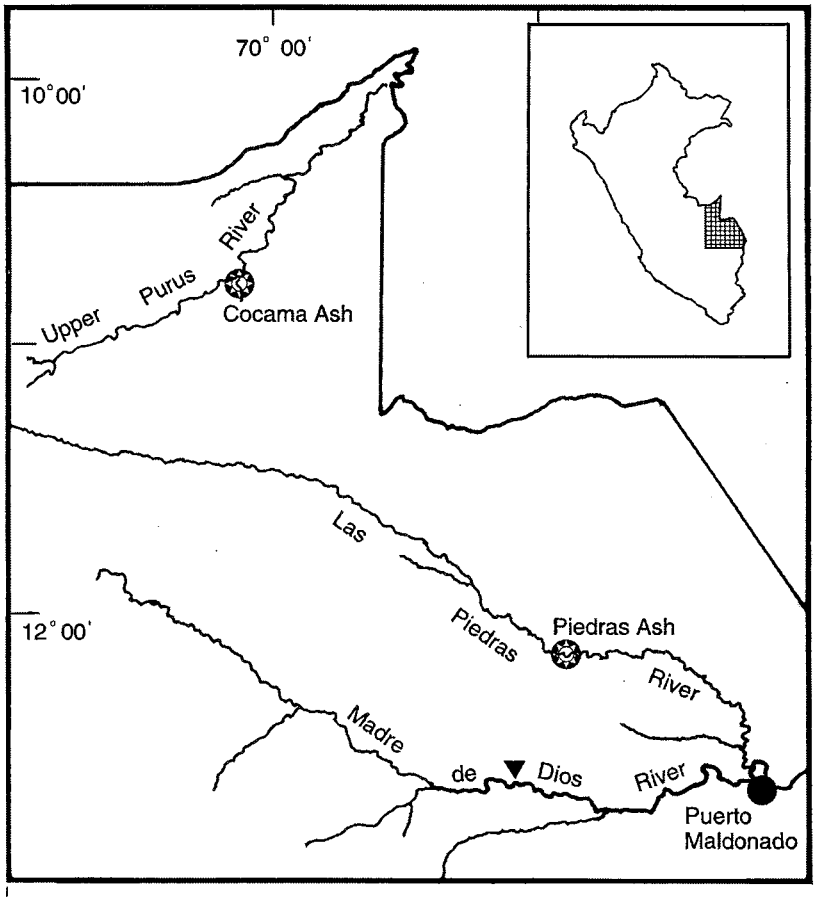

Figure 27. Map showing the location of the Cocama and Piedras ashes and their relationship to the holotypical locality for *Amahuacatherium peruvium* (indicated by triangle). From Campbell et al. (in press).

Unit "B," the latter appearing only after thermal demagnetization (D. Prothero, pers. comm.). Unfortunately, the seven samples between the two reversed zones, all of which demonstrated normal polarity under AF (alternating field) demagnetization, could not be thermally demagnetized because the loose sediments were collected in meltable plastic containers. Thus, we do not know if these samples would have shown reversed polarity if subjected to thermal demagnetization. The important result from this section, however, is that the base of Unit "A" once again falls into a zone of reversed polarity.

A third, very limited test for remnant paleomagnetism within the sediments of the Madre de Dios Formation was run on samples from two sites at a bluff cut by the Río Alto Purus at the town of Esperanza, Peru (9° 49' 51" S; 70° 46' 05" W), near the border with Brazil. Three samples were taken as blocks from each of two sites in the Madre de Dios Formation at this locality. The outcrop was poorly exposed, but the samples came from near the top of Unit "A" or the base of Unit "B." These samples revealed a zone of reversed polarity above a zone of normal magnetism (D. Prothero, pers. comm.), a result that may reflect the pattern seen at São Francisco, Brazil. Among other things, these three tests for remnant paleomagnetism have demonstrated that magnetostratigraphy has the potential to be an important tool in resolving the stratigraphic history of Amazonia.

The second $^{40}Ar/^{39}Ar$ date is from an ash deposit that crops out along the Río Las Piedras in the same outcrop from which came the first of the above-mentioned magnetostratigraphic data (Fig. 27). The ash came from low in Unit "C," the uppermost horizon of the Madre de Dios Formation. It is a fine-grained ash deposit approximately 0.5 m thick that extends over a distance of about 35 m. The ash horizon is overlain by nearly 5 m of silts and clays, out of a total estimated thickness of 31 m for the section. This section is cut into an uneroded portion of the Amazon planalto, thus, the top of the section represents the highest level of deposition in that part of the basin. The date of 3.12 ±0.02 Ma from this ash deposit marks a period near the end of the cycle of deposition that formed the Madre de Dios Formation, although most of Unit "C" was deposited after the ash horizon. Based on this date, and allowing time for accumulation of the overlying fine-grained deposits of Unit "C," deposition of the Madre de Dios Formation is estimated to have lasted until at least the middle late Pliocene, or until around 2.5 Ma. Thus, the two ash dates constrain the age of the Madre de Dios Formation to between the early late Miocene and the middle late Pliocene.

Our earlier interpretations of events in Amazonia were heavily influenced by a series of radiocarbon dates that seemed to indicate a late Pleistocene/Holocene age for

the entire Madre de Dios Formation (Campbell and Frailey, 1984; Campbell and Romero-P., 1989). The dates on the two ashes, in combination with the paleomagnetic results, falsify the hypothesis that the entire Madre de Dios Formation dates from the late Pleistocene. There remains the possibility, however, that, in localized situations, upper levels of Unit "C" may yet prove to be Pleistocene in age.

The Acre Conglomerate: The Acre Conglomerate is important for interpreting the age of the Madre de Dios Formation because it is basal in the formation, widespread, and quite fossiliferous at numerous localities. Within the Madre de Dios Formation the Acre Conglomerate is stratigraphically lower than the tuff dated at 9.01±0.28, thus we now have a minimum age for this deposit and its contained fossils. It is instructive, however, to review the history of how this horizon has been interpreted.

In our early field work the Acre Conglomerate always appeared to be a strictly basal, more-or-less horizontal feature of the Madre de Dios Formation. That is, we encountered no fossiliferous strata of similar lithology that did not rest directly upon the Ucayali Peneplane. In more recent field work, however, we have observed that similar fossiliferous lithologies do occur higher in the section, albeit rarely and still within the first 10 meters of section. This puts our observations into agreement with those of Simpson and Paula Couto (1981). Further, we now recognize that the Acre Conglomerate is not so much a single horizontal stratum as multiple, leading edge deposits of a prograding series, perhaps best characterized as foreset beds developed in shallow-water environments (see Miall, 1984). The Acre Conglomerate is, then, a series of numerous coarse-grained facies marking the advancing edge of deposition of Unit "A," and it should no longer be considered a distinct member of the Madre de Dios Formation, although the informal use of the term remains advantageous.

If, as we now interpret them, the basal conglomerates of Unit "A" are transgressive basin fill deposits, or in some instances channel deposits, this is important for interpreting the age of the Madre de Dios Formation based on its fossil content. The reason for this is that at a few localities these conglomerates have produced mammals interpreted to be Pleistocene in age because they represented lineages that were not thought to have been in South America until after the beginning of the Great American Faunal Interchange (GAFI) (Simpson and Paula Couto, 1981), an event thought to have been initiated in earnest at 2.5-2.0 Ma (Webb, 1985; Marshall and Sempere, 1993), or 2.7-2.5 Ma (Woodburne and Swisher, 1995). Despite the apparent mixing of fossils of two different ages, Simpson (in Simpson and Paula Couto, 1981:18) was of the opinion that although some of the fossils may have been reworked

from older deposits, most of the specimens are "unified as to age and essentially contemporaneous with 'Pleistocene Phase 1'..." As evidence for this he cites the unworn nature of most of the specimens and the fact that there were no known source beds underlying the conglomerate from which the "older" fossils could have come.

If the basal conglomerates are facies of a transgressive, aggradational, basin-fill depositional series, then this depositional episode would have been burying, rather than exposing, older Tertiary deposits upslope within the basin. It would have been unlikely for older Tertiary fossils to be eroded from within the basin from beneath Unit "A," carried downstream, and redeposited at the then leading edge of deposition of the basin-fill sediments. But this is not impossible, particularly if large river channels existed at the time and if they were cutting into the Contamana Group through previously deposited portions of Unit "A." However, the sedimentary structures observed at most of the fossiliferous localities within the basal conglomerate are not indicative of large-scale river channels. The exceptions are those localities where only remnants of the basal conglomerate remain, and these sites are exceptions only because it is not possible to put the deposit within a stratigraphic context, not because they appear within clearly demarcated paleochannels. For example, the clast size of the fossiliferous basal conglomerates is generally small, with clay pebbles smaller than 1 cm. Numerous paleochannel deposits indicative of large river channels with clay balls of much greater size have been observed, including some where the clast size is greater than 1 m, but these have always proved to be unfossiliferous. Older fossils may also have been eroded from channel cut banks in front of the leading edge of Unit "A," but it would have been unlikely for them to then be incorporated into Unit "A."

Unlike Simpson and Paula Couto (1981), we have located major fossiliferous deposits within the Contamana Group, directly underlying the Ucayali Peneplane, that hypothetically could be the source beds for reworked, older fossils. Nonetheless, we are in agreement with Simpson that most of the fossil vertebrates from the basal conglomerates are unified as to age and represent a single fauna, and we think the exceptions are very rare. An important consideration is that although Simpson cited the unworn nature of most of the fossil specimens from these deposits, he was unaware of the microfossil content of these deposits. We would add to his comments that, in most instances, the vertebrate microfauna of the basal conglomerates is far more abundant and diversified than the macrofauna, and it includes extremely delicate fish, amphibian, reptilian (e.g., dentulous small lizard jaws), and mammals (e.g., bats, primates, and rodents). The concentrations and unworn condition of these delicate microfossils argues strongly against their being reworked from older beds.

Another factor that must be recognized is that not all of the fossiliferous deposits of the Madre de Dios Formation found resting on top of the Ucayali Peneplane are necessarily contemporaneous, i.e., part of the same depositional horizon, or Unit "A," for the following reason. Although the contacts between Units "A," "B," and "C" of the Madre de Dios Formation may be conformable, these three horizons are generally fairly distinctive (Campbell et al., 1985), and they can be recognized at most good outcrops (see, e.g., Fig. 8). At the contacts between the horizons it is fairly common to note channels extending down into the lower units from above. Most of these channels are fairly small, but it is reasonable to assume that there were some fairly large rivers with deep channels crossing the Amazonian lowlands during the time Units "B" and "C" were being deposited. Depending on the base level of these rivers, they may well have eroded through underlying horizons of the Madre de Dios Formation to, or even into, beds of the Contamana Group. At this level they could have left deposits that could resemble in several respects the basal conglomerates of Unit "A" (see Figs. 22, 23). They may even have eroded fossils from Unit "A" and redeposited them, along with new skeletal debris. This would mean that some fossiliferous deposits found in the stratigraphic position lying directly upon the Ucayali Unconformity could be much younger than those of Unit "A." We must stress, however, that this situation is only a theoretical possibility. It has never actually been observed in the field.

In many instances it is possible to determine that a given fossiliferous deposit is *in situ* in Unit "A," as opposed to the possibility that it is a younger channel deposit of Unit "B" or Unit "C." This is because at many localities the entire thickness of the Madre de Dios Formation is exposed, from the Ucayali Peneplane to the planalto (as in Fig. 8), and it is possible to observe directly whether or not there are channels cutting into the lower beds from above. Also, with experience it is possible to identify the basal deposits of Unit "A" by their lithology and sedimentary structures, even though they are of a highly variable nature. However, if an outcrop consists solely of a partially consolidated, fossiliferous clay-pebble conglomerate resting unconformably on the Contamana Group with no surrounding stratigraphic context, it may well be impossible to position it positively within a stratigraphic sequence and the contained fossil taxa would have to be relied upon to yield its age. In this case, if Pleistocene taxa were found together with Tertiary taxa it would be necessary to consider the possibility that the latter were reworked at that locality.

Based on the presence of known mammalian indicator species, Frailey (1986:42) assigned a Late Miocene (Huayquerian; 9-6 Ma) age to the fauna (Table 6) from the conglomerates basal in Unit "A" exposed along the Río Acre in Peru, even though the available radiocarbon dates suggested that the deposit itself was upper Pleistocene/

Holocene in age. This age assignment was made on the basis of the presence in the fauna of such characteristic Huayquerian taxa as *Kiyutherium orientalis* Francis and Mones 1965, *Tetrastylus* sp. (Pascual et al., 1966), and possibly *Potamarchus murinus* Burmeister 1885. *Potamarchus murinus*, however, has a Chasicoan (12-9 Ma) and possibly Huayquerian distribution (Pascual et al., 1966). Broin et al. (1993) suggested that this fauna might be Chasicoan or Huayquerian (late Miocene - early Pliocene in their usage) in age. Their suggestion of a Chasicoan age was based in part on the presence of *Potamarchus* cited above, and that of an early Pliocene age was based on tentative biostratigraphic correlation with the "Mesopotamiense" of Argentina, which some authors (e.g., Paula Couto, 1978) had described as extending into the early Pliocene. However, the latest paper on this fauna (Noriega, 1995), and papers cited within, place the "Mesopotamiense" in the Upper Miocene.

Webb (1995) also suggested that the Acre fauna might date to the Chasicoan, his comments being based on the presence of small rodents (currently being described by CDF) and a primitive nothrothere sloth. However, at the time, Webb (1995) was writing in support of Räsänen et al.'s (1995) interpretation of the Madre de Dios Formation (Solimões Formation in their usage) as marine tidal deposits. From a paleogeomorphologic standpoint, an older age for the deposits would correlate with the postulated higher sea levels of the Serravallian stage (14.8-11.2 Ma) (Hardenbol et al., 1998; Berggren et al., 1995) more easily than a determination of an Huayquerian age, when sea levels were postulated to have been near or below modern levels.

The older age would also have allowed correlation of the postulated marine deposits of Räsänen et al. (1995) with those of the Paranense Sea of Paraguay and Argentina. In fact, however, the Paranense Sea probably correlates with the middle to upper Miocene Pebas beds of eastern Peru and western Brazil (Hoorn, 1994b). As noted above, the Pebas beds are part of the Contamana Group (Solimões Formation in Brazil), lie below the Ucayali Unconformity, and cannot correlate with any portion of the Madre de Dios Formation regardless of the origin of the latter (Fig. 21). Although Räsänen et al. (1995) attempted to make this correlation, it is not feasible.

An important component of Räsänen et al.'s (1995) hypothesis of marine tidal deposits in southwestern Amazonia was the presence of fossil sharks in the Acre VI local fauna, a vertebrate fauna that occurs in the Acre Conglomerate along the Rio Acre in Peru, locality LACM 4611. The four specimens of sharks (isolated teeth) from this locality known to these authors were collected by a field party led by KEC. They are referable to

a bullshark, *Carcharhinus* sp., a group well-known in the Amazonian river systems of today (Thorson, 1972) (Fig. 28). In support of their tidal hypothesis, Räsänen et al. (1995:389) stated that "... the absence of marine or semimarine mollusks shows that the water in this ebb-flow-dominated system may have had low salinity." In fact, *freshwater* molluscs of the family Mutelidae (J. McLean, pers. comm.) were collected at the same time and from the same deposits as the shark teeth, along with amphibians, another salinity intolerant group. These taxa, plus the presence of numerous taxa of freshwater fish, terrestrial reptiles and mammals (including primates and bats), combined with the complete lack of any marine or estuarine taxa from any of the numerous fossil sites from within the conglomerates of the Madre de Dios Formation collected by the authors, argue persuasively against any marine incursion or marine influence of any kind during the time of deposition of the Madre de Dios Formation.

The second component of the hypothesis of Räsänen et al. (1995) was the presence of sedimentary structures interpreted by them to be tidally-produced sand-mud couplets. However, as noted by Hoorn (1996), Paxton et al. (1996), and Marshall and Lundberg (1996), these sedimentary features are more likely to be the product of fluvial or fluvio-lacustrine depositional systems than tidal systems, an interpretation that was also presented earlier by Räsänen et al. (1992). To us, the observations and interpretations of the sedimentary features of the Madre de Dios Formation presented by Frailey et al. (1988) are a more accurate interpretation of these deposits. Thus, on both paleontological and sedimentological grounds, we reject the hypothesis of Räsänen et al. (1995) that there was a marine influence in the deposition of the Madre de Dios Formation. This conclusion is also supported by the study of molluscan isotopic signatures by Vonhof et al. (1998).

Although the margin of error of the Cocama ash date prevents definitive assignment of the faunas of the Acre Conglomerate to either the Chasicoan or Huayquerian SALMA, that date does corroborate the previous late Miocene age assignment for the fossil assemblage from the basal horizon of the Madre de Dios Formation. We recognize that strictly Huayquerian taxa remain small in number, and those taxa that suggest an older, or Chasicoan, age may yet prove to predominate in the faunas. On the other hand, because so few vertebrate faunas from Amazonia have been described, and none from independently well-dated strata, it may also prove to be the case that the time spans of taxa were different in the neotropics than in temperate South America [as noted by Goin (1997) *re* the La Venta local fauna of Colombia]. Based on our estimate for the age of initiation of deposition of the Madre de Dios Formation, or 9.5 Ma, we conclude that the faunas from the Acre Conglomerates are probably latest Chasicoan in age.

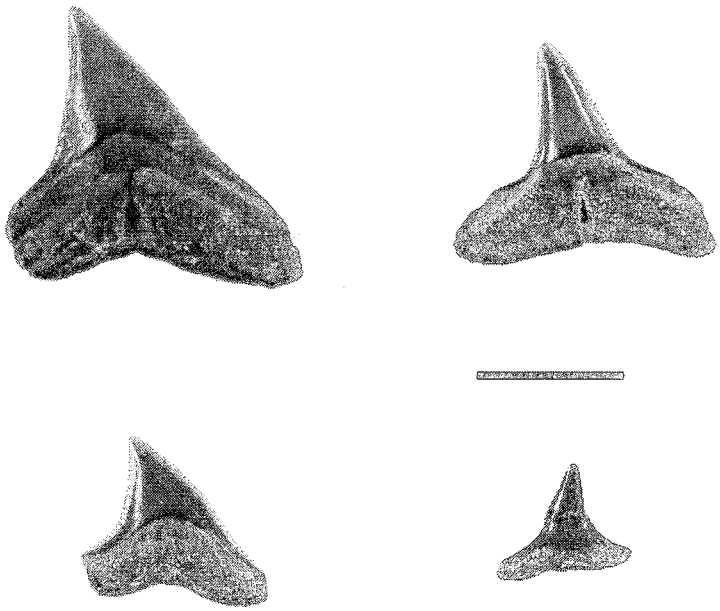

Figure 28. Four specimens of shark teeth referable to *Carcharhinus* sp. were found in the Acre Conglomerate along the Acre River in Peru; locality LACM 4611. Although these fossil sharks were used to support arguments for marine-induced tidal deposition of the Madre de Dios Formation (Räsänen et al., 1995), the presence of freshwater taxa intolerant of marine waters, such as molluscs and amphibians, in the same beds and collected at the same time as the shark teeth (all collected by KEC and party) clearly demonstrates that this interpretation is insupportable. Scale bar = 2 cm.

One final aspect of the fossil vertebrates from the Acre Conglomerate needs to be mentioned. Nearly four hundred cricetid-sized rodent teeth have been found among the microfossils collected from ten localities in the basal conglomerates of Unit "A." However, not a single cricetid rodent tooth is included in this sample. Although it is negative evidence, the absence of cricetid rodents in this large sample suggests that these deposits predate the arrival of those rodents in South America, an event that has been variously placed to "sometime in the Miocene" (Reig, 1980, 1986), to between 7.0-5.0 Ma (Marshall, 1979), to the base of the Montehermosan SALMA (~6 Ma) (Marshall and Cifelli, 1990), and to 2.5 Ma (e.g., Marshall and Sempere, 1993; Webb and Rancy, 1996).

Correlating the Madre de Dios Formation with Andean Tectonic Events: With the $^{40}Ar/^{39}Ar$ date of 9.01±0.28 on the Cocama ash it is possible to relate the deposition of the widespread Madre de Dios Formation to a specific Andean tectonic event. We estimate initiation of deposition of that formation at about 9.5 Ma, based on the fact that the Cocama ash lies above the basal conglomeratic facies of the formation. This date coincides with the beginning of the Quechua II tectonic event. Invoking the models of thrust deformation and lithosphere rheology presented by Quinlan and Beaumont (1984) and Flemings and Jordan (1990), compressive deformation in the Andes would have caused thrust-induced subsidence in the foreland basin. The subsiding basin would have filled rapidly with sediment from the newly uplifted terrain, and the depositional environment within the basin would have been aggradational fluvial upslope of the transgressing wave of basin-fill sediment, and more deltaic in nature at the leading edge of the basin fill. In this instance, because the floor of the basin would have been so near sea level, river gradients would have been extremely low, inevitably resulting in sluggish, meandering rivers and probably large lakes and swamps in the eastern portion of the foreland basin. This model would appear to accurately depict the sequence of events leading to the deposition of Unit "A" of the Madre de Dios Formation and the environments of deposition of that horizon.

A factor complicating the straight-forward application of these models, however, is that based on the date of 3.12±0.02 Ma for the Piedras tuff, deposition of the Madre de Dios Formation continued throughout the term of the Quechua II and Quechua III tectonic events. It is possible that the disconformities observed between the three horizons of the Madre de Dios Formation may be related in some way to events associated with these tectonic episodes. To determine if this is true a greater calibration of the chronology of deposition of the Madre de Dios Formation is required.

In central Peru, the Quechua III phase of tectonic activity led to the formation of the sub-Andean thrust and fold belt (STFB) at the eastern edge of the Andes, as well as the Contaya Arch and Serra do Divisor. The latter are partially thrust-bounded, anticlinal structures formed at a distance from the STFB farther to the east within the Amazonian llanos (Pardo, 1982; Mégard, 1984). Between the STFB and these structures, the Contaya Arch and the Serra do Divisor, there would have formed one basin, currently the Ucayali Basin (Fig. 24), receiving sediment from both the west (the STFB) and the east (the anticlinal structures). East of the Contaya Arch and Serra do Divisor there would have existed a second basin, possibly subsiding at a lesser rate than that to the west. South of the southern termination of the Serra do Divisor, at about 10E south latitude, the two separate basins would have been united as only one foreland basin to the east of the Andes. Despite this complication, the Madre de Dios Formation may still be considered a single depositional sequence. At least, this is the case until such a time as the three recognized horizons comprising the formation may be shown to be of different ages.

It should be noted that the Contaya Arch and Serra do Divisor (=Moa) are a direct continuation of the STFB in northern Peru, an offshoot trending northwest to southeast (Figs. 19, 24), and that the modern Río Ucayali cuts across this structure as it flows northward. The possibility that this flow direction was interrupted, assuming that northward flow was the ancestral pattern, by the uplift of the Contaya Arch should be considered. In this case the basin would have drained southward, around the end of the Serra do Divisor, before turning eastward. Under the hypotheses of Dumont (1989) and Räsänen et al. (1992), this scenario would not have been possible because of the presence of the Fitzcarrald Arch, a postulated, very poorly known subsurface structural arch trending NE-SW from Brazil to the Andes that they cite as forming a structural barrier separating the Ucayali Basin from the Madre de Dios-Beni Basin (Fig. 24). However, it is doubtful that the Fitzcarrald Arch has exerted any influence on Miocene or later depositional events in eastern Peru. Whether or not it did, however, is important because if so there could be significant differences in the ages of the strata on either side of this arch.

The Fitzcarrald Arch was described by Oppenheim (1975), who noted lithological differences between the outcrops in the vicinity of Fitzcarrald Pass and those in the rest of the Amazonian lowlands through which he had traveled. He also noted differences in the directions of the dips of the beds on either side of the Fitzcarrald Pass, i.e., south of the pass the beds dipped to the west and north of the pass they dipped to the north. However, his geologic sketch of the area does not clearly demonstrate the presence of an arch. Further, the area Oppenheim (1975) described is at the base of the Andes only a few tens

of kilometers east of the thrust zones of the STFB and the structural features he discussed may be related more to thrusting within the STFB than to any folding farther to the east.

There are only two other references of which we are aware that address the question of the existence of the Fitzcarrald Arch. Martinez (1975) cited evidence of Bouguer anomalies that demonstrate its presence and suggested that the formation of the structure may be related to the Pisco Inflexion. He presents no suggestion as to the age of its formation, nor are there any data describing the extent of the postulated arch. Mathalone and Montoya-R. (1995:426) state, without further comment, that "... [the Fitzcarrald] high is associated with a northeast trending normal fault system of Paleozoic origin..." If true, it is unlikely that it would have had any affect on late Tertiary deposition in the region.

In most maps that depict the presence of the Fitzcarrald Arch, the feature is shown as extending from western Brazil to the eastern Andes, the length of its eastern half almost directly underlying the Río Alto Purus (Fig. 24). If this arch were actively serving as a structural divide between the Ucayali Basin and the Madre de Dios-Beni Basin it is unlikely that a river would be coursing down the very top of the arch, trending in almost a straight line, but meandering back and forth across the crest of the "arch," for over 200 km. We traveled this portion of the Río Alto Purus in 1994 and our observations confirmed that the outcrops along this stretch of the river can be correlated to those observed elsewhere in western and southern lowland Amazonia. Moreover, we observed that as we traveled upstream, in a SW direction, the contact between the Contamana Group and the Madre de Dios Formation, i.e., the Ucayali Unconformity, remained more or less at the water line for the entire distance, or about 150 km upstream from the Peru-Brazil border. This indicates that the Río Alto Purus is descending the side of a gentle fold, or bulge, essentially following the level of the Ucayali Peneplane. It is possible that the slope our traverse covered was the eastern equivalent of the beds sloping to the west noted by Dumont et al. (1991) in the Ucayali Basin almost due west of the Río Alto Purus. This gentle fold, or bulge, the strike of which would be at nearly a right angle to the Fitzcarrald Arch, is strategically placed to be a southern extension of the Serra do Divisor. If so, this uplift would be a result of E-W compressional forces and it would have to be superimposed upon the SW-NE trending Fitzcarrald Arch, if that arch exists where it is commonly depicted.

We were unable to determine if the uplift noted along the Río Alto Purus affected all three horizons of the Madre de Dios Formation that we recognize, or just the older horizons. That is, we cannot comment on whether or not the uplift preceded or postdated the deposition of the younger members of the Madre de Dios Formation. At the very least

the uplift must postdate the formation of Unit "A" of the Madre de Dios Formation, or be younger than ~9.5 Ma. This uplift may correlate with the Quechua III tectonic event. There is also a possibility that this uplift resulted from the youngest Andean compressive phase (F6; ~2 Ma) recognized by Sébrier et al. (1988) and Sébrier and Soler (1991).

To arrive at a maximum possible date for *Amahuacatherium* it is necessary to relate Andean events older than the Quechua II phase to events in the Amazonian lowlands. As noted earlier, the last major E-W compressional event prior to the Quechua II phase was the Quechua I phase of ~15 Ma. It is unclear how the Quechua I phase may have affected the eastern Peruvian lowlands, but it can be assumed that at the very least any compression in the western portions of the foreland basin, resulting in thrust-induced subsidence and deposition in the central and eastern portions of the foreland basin, would have resulted in later isostatic readjustments in the affected areas. If the models of foreland basin deformation cited above, or some combination of the two, are correct, then subsidence followed by deposition would have occurred in eastern Peru during the Quechua I phase. In turn, following the end of the compressional phase and isostatic readjustment, extensional tectonics may well have occurred, which could have played a role in the formation of the Ucayali Peneplane. Once initiated, we postulate that peneplanation continued until the Quechua II compressional phase of the Andean orogeny began and deposition of the Madre de Dios Formation commenced at about 9.5 Ma.

Although Marshall and Lundberg (1996) and Lundberg et al. (1998) cited a "Quechua tectosedimentary episode" initiated along the Central Andes of Peru at about 11 Ma that brought about the deposition of marine sediments in the Andean Foreland Basin, there does not appear to be any record of such an event there at that time (Mégard, 1984, 1987; Ellison et al., 1989; Sébrier and Soler, 1991). Indeed, the suggested timing coincides with the lowest sea level stand of the Miocene (Hardenbol et al., 1998; Fig. 20), an event most unlikely to lead to marine transgressions. Marshall and Lundberg (1996) also proposed that this event lasted until 5 Ma, a several million year period that would be out of character for compressional events in the Andes, which are noted for their relatively short duration (Mégard, 1984, 1987; Ellison et al., 1989; Sébrier and Soler, 1991). Nor are there any published data or references known to us (and none were cited) of an ingression of marine waters into the Ucayali Basin or southward at that time (~11 Ma) or more recently (see, e.g., Rüegg, 1956; Kummel, 1948; Williams, 1949; Guizado, 1975; Seminario and Guizado, 1976; Pardo and Zuñiga, 1976; Cánepa and Rosado, 1980; Vanhof et al., 1998). The hypothesis of Marshall and Lundberg (1996) apparently depends upon the correlation of hypothetical events in eastern Peru with postulated events in southern

Bolivia (Marshall et al., 1993), an example of precisely the type of "...subjective long-distance correlations of events of assumed coeval tectonic origin based on rough synchroneity..." that Marshall and Sempere (1993:339) warned against. We must conclude, because there are no supporting data, that the "Quechua tectosedimentary episode" referred to by Marshall and Lundberg (1996) and Lundberg et al. (1998) cannot be substantiated.

From the above discussion it is possible to propose that the deposit that preserved *Amahuacatherium* was formed during one of two intervals. The first is sometime after the beginning of the Quechua I phase at ~15 Ma when the younger portion of the Contamana Group was being deposited, but prior to the period when erosion of the Contamana Group leading to the formation of the Ucayali Unconformity began. The second possible period would be during the late stages of formation of the Ucayali Peneplane, probably sometime shortly before initiation of the Quechua II event at about 9.5 Ma. Of these two possibilities, we consider the first to be less probable because it would put *Amahuacatherium* in South America well before passage across the water gaps of the Central American isthmus would seem possible (see below). In the latter case, *Amahuacatherium* would then possibly occupy a stratigraphic position similar to that of the Acre I local fauna, LACM locality 4418, which was interpreted by Frailey (1986) as a possible stream deposit at the top of the Contamana Group. In that several taxa are in common to the Acre I local fauna and the Acre VI local fauna from the Acre Conglomerate (Table 6), it is reasonable to conclude that the two faunas are of approximately the same age. Based on the date from the Cocama ash, these faunas would most likely be Chasicoan in age (earliest late Miocene). This correlation places the age of *Amahuacatherium* in the Chasicoan.

Therefore, on the basis of the above general correlation with Andean tectonic events, we conclude that *Amahuacatherium* dates from the late Chasicoan, i.e., to some time shortly before 9.5 Ma.

Sea Level Fluctuations: Before leaving the subject of dating geologic events of Amazonia, mention should be made of the possible role of sea level fluctuations on depositional and erosional events within lowland Amazonia. It should first be noted that, because the gradients of the rivers draining western Amazonia are so low over thousands of kilometers only major fluctuations in sea level with dramatic changes in ultimate base level would be expected to have any potential for influencing erosional and depositional events far inland. For example, the elevation of the Río Madre de Dios at Aurinsa, from whence came *Amahuacatherium*, is less than 250 m a.m.s.l. at about 2500 km, straight-line, from the mouth of the Río Amazonas, which gives a gradient of only 1 cm/km. To the

Table 6

Faunal list for western Amazonia for the younger (Upper Miocene) strata of the Contamana Group underlying the Ucayli Unconformity and the fossiliferous beds (Acre Conglomerate) of Unit "A" of the Madre de Dios Formation that overlie the Ucayali Unconformity. Only taxa for which the source beds are unequivocal are listed, and these taxa are found in Broin (1993), Campbell (1996), Czaplewski (1996), Frailey (1986), Gaffney et al. (1998), Kay and Frailey (1993), Mones and P. Mann de Toledo (1989), Santos et al. (1993); or based on personal observation in the case of undescribed taxa. Reports or descriptions of additional taxa of western Amazonia are found in Paula Couto (1956, 1981, 1982, 1983a,b), Rancy (1991), Simpson and Paula Couto (1981), Spillman (1949), and Willard (1966), but these are not listed here because their source beds are questionable. Most are described as coming from clay-ball conglomerates, and these were probably from the Acre Conglomerate of Unit "A." Nonetheless, their exact stratigraphic provenance could be called into question, as described in the text. From this restricted list, at least six taxa at the generic level and three at the species level are found both above and below the Ucayali Unconformity.

A. Contamana Group, including the Ipururo Formation and the Chambira Formation (corresponds to upper Solimões Formation in Brazil). Includes all specimens from below the Ucayali Unconformity. Age: Late Miocene (Chasicoan and older).

Chondrichthyes
- Batoidea
  - Potamotrygonidae

Osteichthyes

Reptilia
- Chelonia
  - Podocnemididae
    - Gen. et sp. indet.
    - *Stupendemys* sp.
    - cf. *Stupendemys* sp.
- Crocodilia
  - Gavialidae, indet.
  - Alligatoridae
    - *Purussaurus brasiliensis* Barbosa Rodrigues 1892

Mourasuchidae
Mourasuchus spp.
Mammalia
Edentata
Mylodontidae
Acretherium campbelli (Frailey 1986)
Nothrotheriidae, undescribed (2-3 spp.)
Orophodontidae
Octodontobradys puruensis Santos, Rancy, and Ferigolo 1993
Rodentia
Dinomyidae
Potamarchus murinus Burmeister 1885
Telicomys amazonensis Frailey 1986
Hydrochoeridae
Kiyutherium orientalis Frances and Mones 1965
Neoepiblemidae
Euphilus sp. cf. *E. ambrosettianus* Ameghino 1889
Litopterna
Macraucheniidae, indet.
Notoungulata
Toxodontidae, undescribed (2-3 spp.)
Proboscidea
Gomphotheriidae
Amahuacatherium peruvium Romero-Pittman 1996
Sirenia
Trichechiidae
?*Ribodon* sp.

B. Acre Conglomerate of Unit "A," Madre de Dios Formation (corresponds to the Içá Formation in Brazil). Includes all specimens from above the Ucayali Unconformity. Age: Late Miocene (latest Chasicoan or Huayquerian).

Chondrichthyes
Selachii
Carcharhinidae
Carcharhinus sp.
Batoidea
Potamotrygonidae

Osteichthyes
- Osteoglossidae
- Doradidae
- Pimelodidae
- Characidae
  - *Colossoma* sp.
- Callichthyidae

Reptilia
- Chelonia
  - Podocnemidae
    - *Stupendemys* sp.
    - cf. *Stupendemys* sp.
    - cf. *Peltocephalus* sp.
  - Testudinidae, indet.
- Crocodilia
  - Gavialidae, indet.
  - Alligatoridae
    - ?*Caiman* sp.
    - ?*Brachygnathosuchus* sp.
    - *Purussaurus brasiliensis*
  - Mourasuchidae
    - *Mourasuchus* spp.

Aves
- Anhingidae
  - *Anhinga fraileyi* Campbell 1996

Mammalia
- Marsupialia
  - Didelphidae, gen. (2) and sp. (2) indet.
- Edentata
  - Cingulata
    - Glyptodontidae, indet.
    - Dasypodidae, indet.
      - Dasypodinae, indet.
      - Pampatheriinae, indet.
    - Megatheriidae, indet.
    - Megalonychidae, indet.

Chiroptera
- Noctilionidae
  - *Noctilio lacrimaelunaris* Czaplewski 1996
- Molossidae, indet.

Rodentia
- Erethizontidae, undescribed (4+ taxa)
- Dinomyidae
  - *Potamarchus murinus* Burmeister 1885
  - *Tetrastylus* sp.
- Hydrochoeridae
  - *Kiyutherium orientalis* Frances and Mones 1965
- Caviidae
  - Cardiomyinae, undescribed (2 taxa)
- Neoepiblemidae, indet.
- Dasyproctidae, indet.
- Echimyidae
  - Heteropsomyinae, undescribed (4+ taxa)

Primates
- Cebidae
  - Allouattinae
    - *Stirtonia* sp.
  - cf. Cebinae, indet.

Litopterna
- Macraucheniidae, indet.
- Proterotheriidae, indet.

Notoungulata
- Toxodontidae
  - *Trigodon* sp.

Proboscidea
- Gomphotheriidae
  - *Haplomastodon* sp.

Sirenia
- Trichechiidae
  - ?*Ribodon* sp.

Caribbean, where the drainage of western Amazonia presumably flowed in the late Miocene (Hoorn et al., 1995), the distance is closer to 3000 km. The actual river channel length was, of course, probably close to double the straight-line distance.

The most significant drop in sea level, to ~-50 m, was reached ~11.4 Ma (Hardenbol et al., 1998; Fig. 20). Two subsequent lowstands in the late Miocene to below modern sea level occurred at ~8.8 Ma (~-14 m) and ~6.8 Ma (~-10 m) (Hardenbol et al., 1998). The first, and most significant, of these three sea level lowstands would appear, on the basis of current available geologic evidence and the date on the Cocama ash cited above, to be instrumental in initiating the formation of the Ucayali Peneplane. The second major sea level lowstand would appear to have occurred after deposition of the Madre de Dios Formation had begun. Its small amplitude, and that of the third and last major sea level lowstand, were arguably insufficient to have had much of an impact far upstream in western Amazonia.

In terms of sea level highstands, which would act to increase deposition within the basin, there appear to be only two in the late Miocene: ~7.5 Ma (~+25 m) and ~6.0 Ma (~+40 m) (Hardenbol et al., 1998; Fig. 20). It is unlikely that with their small amplitudes these highstands would have had any significant effect on deposition or erosion in western Amazonia, particularly in that the latter was such a brief event.

THE GREAT AMERICAN FAUNAL INTERCHANGE

The Great American Faunal Interchange (GAFI) is that event wherein portions of the faunas of North America and South America intermingled just prior to and following the establishment of the terrestrial link between the two continents. The GAFI brought to an end the long isolation of the South American fauna, which had endured since that continent broke away from Africa in the late Mesozoic. Although there were rare instances of new arrivals in South America from abroad during the pre-Miocene Tertiary (Simpson, 1950; Stehli and Webb, 1985; Marshall and Sempere, 1993; Wood, 1993), and similarly rare instances of South American taxa dispersing to North America (e.g., Gingerich, 1985; Gayet et al., 1992) and Eurasia (via Africa?) (e.g., Storch, 1993), the lack of a direct terrestrial connection to other continents allowed the South American vertebrate fauna to evolve, for the most part, in isolation.

Interpretations of the timing and the suites of taxa involved in the GAFI have changed over time, which is to be expected as new information is brought to bear on the subject. Previously, the first taxa known to make the journey between the continents did so in the late Miocene. These were the ground sloths going north, first known in North America from deposits in southwestern U.S. (below a tuff dated at 8.2 Ma) and Florida (Marshall, 1985), and procyonids (raccoons and related taxa) going south, first recorded in South America in Argentina in rocks dated at 7.5-7.0 Ma (Butler et al., 1984; Marshall, 1985). These early crossers are generally referred to as "waif" dispersers following a "sweepstakes" route (Simpson, 1940), i.e., the term suggesting that their crossings were more accidental and strokes of luck than normal patterns of dispersal. To this group of early dispersers we now add the proboscideans, represented by *Amahuacatherium peruvium*, known from deposits in southeastern Peru that we interpret to date to at least 9.5 Ma, and *Haplomastodon* sp. from the Acre Conglomerate exposed along the Rio Alto Juruá in Brazil (Simpson and Paula Couto, 1981), which dates to between ~9.5-9.0 Ma. Marshall and Sempere (1993) related this early interchange of "heralds," as they were referred to by Webb (1976), to a postulated, dramatic late Miocene lowering of sea

level at about 10 Ma (Haq et al., 1987), although the most recent revision of sea level fluctuations (Hardenbol et al. 1998) places this event at ~12.0 Ma. This lowering of sea level is presumed to have significantly reduced the size of the water gaps in the island chain that was to become the terrestrial link between the two continents. Modern taxa of the mammalian groups with representatives currently recognized as heralds are known to be particularly good swimmers on their own initiative, so the hypothesis that earlier members of these groups were able to cross water gaps or were able to survive being swept to sea until they somehow managed to arrive at a distant shore is reasonable. The time gap between the late Miocene period of low sea level and the first appearance of any of the heralds, including the proboscideans, in the fossil record is significant, but, considering the limited paleontological record of the tropics, perhaps not so great as to preclude the two events from being interrelated. Also, it must be noted that *Amahuacatherium* was found in the southwestern corner of the Amazon Basin, a long distance from where its ancestors presumably reached the South American continent. Based on the then known fossil record, Woodburne and Swisher (1995:350) suggested that the earliest crossings to the south may have occurred during low sea level stands at 8.9 Ma (TB3.2), 6.9 Ma (TB3.3), or 6.0 Ma (TB3.4).

The GAFI has been viewed as beginning in earnest in the late Pliocene, or ~2.7 Ma, coincident with a low sea level stand (TB3.7-8) (Woodburne and Swisher, 1995), to ~2.0 Ma (e.g., Stehli and Webb, 1985; Marshall and Sempere, 1993; Webb, 1991,1998; Webb and Rancy, 1996), when large numbers of savanna-adapted vertebrates moved north and south across the newly opened transtropical corridor, the Isthmus of Panama. This is considered the "real" GAFI by these authors, the earlier events being considered isolated, accidental occurrences. The dispersal corridor across the Isthmus of Panama was supposedly enhanced for savanna-adapted species by climatic deterioration in the late Pliocene that led to the postulated formation of savannas across the isthmus. Further, it has been postulated that later episodes of inter-continental migrations were pulsed by the appearance and disappearance of savanna habitats and newly emergent coastal lowlands during episodes of sea level lowering during glacial epochs (Webb, 1978, 1991; Marshall and Sempere, 1993). Proboscideans were considered as part of the initial wave of North American vertebrates moving southward after 2.5 Ma (2.0-1.9 Ma, Marshall, 1985) because they had not previously been recorded in South America from deposits thought to be older than the upper Pliocene/lower Pleistocene. In large part this interpretation of the timing of the GAFI is based on the first occurrence of numerous North American taxa in the Argentinian fossil record in the late Pliocene/early Pleistocene. Although the known fossil record may be a legitimate reflection of the arrival of savanna-adapted species into

South America, the actual pattern of inter-continental migration may be considerably at odds with this interpretation. In fact, we propose that tropical forest dwellers, not savanna dwellers, were probably the first to participate in the GAFI in significant numbers. Further, we expect future fossil discoveries in the tropics to support our hypothesis that an interchange of taxa was fairly continuous from the late Miocene on, interrupted only by sea level highstands..

Of particular significance to increasing our understanding of how the GAFI came about and the timing of various events associated with it have been the new geologic data coming from southern Central America and northeastern Colombia. We will briefly review the data bearing on the geologic underpinning of the GAFI, which give perhaps a new and slightly different twist to the physical aspects that made the interchange possible. We will then examine the biological ramifications of the geologic data and argue for an important, early role in the GAFI for tropical forest dwellers.

The Geological Connection

Prior to the acceptance of plate tectonics as a model for understanding the earth's mobile crust, the establishment of the connection between North and South America was viewed as the result of the gradual rise of a string of islands from beneath the sea and their interconnection into a complete terrestrial connection, the Central American isthmus, between the continents (Simpson, 1950). Sea level changes were also thought to have played a role in the timing of interchange events. In recent years, however, plate tectonics theory, with its moving plates, accreted terranes, and oceanic hot spots that create moving island arcs, has completely changed how we view the formation of the isthmian link.

The terrestrial and oceanic region encompassing southern Central America is extremely complex geologically, involving as it does the coming together of four major tectonic plates (the Caribbean, Cocos, Nazca, and South American) and numerous suspect terranes. We cannot review here all aspects of the many parts that created the isthmian link between North and South America, but instead refer readers to current works on the region and to references contained therein, e.g., Bonini et al., 1984; Burke, 1988; Pindell et al., 1988; Dengo and Case, 1990; Duque-Caro, 1990a, 1990b; Escalante, 1990; Mann et al., 1991; Mann, 1995a; Jackson et al., 1996. The following summary of events is derived primarily from those works.

As currently modeled, the Panama-Costa Rica Arc is a suspect terrane that may at one time have formed the western edge of the Caribbean Plate. It currently functions as a microplate that is being squeezed between the northeastward moving Cocos Plate and the relatively immobile Caribbean Plate (Kellogg and Vega, 1995). In the late Cretaceous/early Tertiary the northern end of this arc became attached to the Chortis Terrane, which now forms nuclear Central America. In the early Miocene the southern end of the arc came into contact with and began to accrete to northwestern South America (Pindell et al., 1988) (Fig. 29). The Panama-Costa Rica Arc later differentiated into the northern Chorotega Terrane and the southern Choco Terrane, with the boundary between the two occurring in the region of the Gatun Fracture Zone, wherein lies the Panama Canal Zone today. The origins of the Panama-Costa Rica Arc are still being debated (see Mann, 1995b), but this is not critical to our discussion here. What is important is that the eastern end of a island arc, the northern end of which was attached to Central America, was being moved northeastward by the combined movements of the Cocos and Nazca Plates. As a consequence of this movement, the Choco Terrane began colliding with what is now Colombia at approximately 5° N latitude in the early Miocene. In the course of this collision the Istmina Hills, within the Istmina Deformed Zone of western Colombia, were formed in the middle Miocene at the southern end of the Choco Terrane (Duque-Caro, 1990a) (Figs. 29, 30). Coates and Obando (1996) suggested that the point of collision of the Choco Terrane and the South American block was much farther north, but this would not appear to be possible in view of the data of Duque-Caro (1990a) and Mann and Corrigan (1990).

Continued northeastward movement of the Cocos Plate sutured the Choco Terrane to northwestern Colombia. The suture zone, i.e., the Atrato Suture (Fig. 29), is marked by the Uramita Fault Zone. Immediately to the west of the Uramita Fault Zone lies the Dabeiba Arch, which includes the Serranías de San Blas-Darién, the very low-lying, mostly subsurface Satuta Arch, and the northernmost western flanks of the Cordillera Occidental of the Colombian Andes. West of the Dabeiba Arch, the Atrato Basin and Chucunaque Basin extend nearly the length of the Choco Terrane, from central Panama to the Istmina Hills. The basins are two synclinal structures Duque-Caro (1990a) or fault-bounded depressions or grabens (Case et al., 1971) that are now separated by elevated terrain marking a transverse expansion of both the Serranías de San Blas-Darién and the Baudo Arch. This transverse range lies in the region of the Panama-Colombia border at the southern end of the Serranías de San Blas-Darién. The western portion of the Choco Terrane consists of the Baudo Arch, which is made up of the Serranías de Maji-Baudo, a series of ridges of markedly uneven crestline elevations that extend from central Panama to the Istmina Hills.

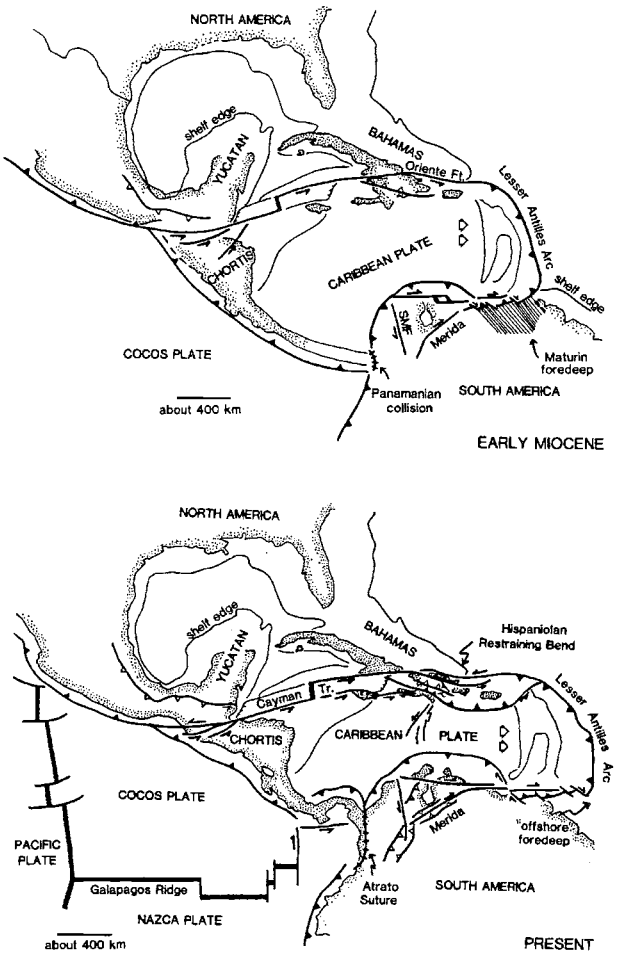

Figure 29. Central America originated as an island arc, the eastern end of which began colliding with South America at some depth below sea level in the early Miocene. This island arc, or suspect terrane, is differentiated as the Panama-Costa Rica Arc, a microplate that continued moving northeastward, being squeezed between the northeastward moving Cocos Plate and the relatively immobile Caribbean Plate. Attachment of the northern end of the Panama-Costa Rica Arc to the Chortis Terrane of Central America in the early Miocene allowed the passage of North American faunas to southern Panama at that time. The trailing southeast end of the Panama-Costa Rica Arc accreted to northwestern Colombia in the middle Miocene as this arc moved to the northeast, leading to the formation of a suture zone, the Atrato Suture. Continued movement of the Panama-Costa Rica Arc has led to the northward flexure, or bulge, of southern Central America. Modified from Pindell et al. (1988).

Marine Barriers and Currents: It has been known for some time that the last major marine barrier between North and South America existed in what is now South, not Central, America (Simpson, 1950; Whitmore and Stewart, 1965). Although this barrier, the "Bolivar Trough" (Whitmore and Stewart, 1965), has often been depicted as a simple water gap at the Panama -Colombia border (e.g., Marshall, 1979), based on the above reconstruction of events, it would appear that this water barrier was much more complex and that it may initially have occupied the combined Atrato-Chucunaque Basin, and subsequently just the Atrato Basin. The flow of marine waters into and through the "Bolivar Trough" was undoubtedly complex, with both subsurface and surface currents that would not necessarily have been flowing in the same direction at the same time, nor in the same direction through time.

Unfortunately, the role that surface water currents may have played in the success or failure of early waif dispersers has not been examined in any detail, and such a treatment is beyond the scope of this paper. It should be noted, however, that contrary to what may at first glance appear self-evident, i.e., that surface currents followed the trade winds and flowed east to west, the direct opposite appears to have occurred. Although Duque-Caro (1990b) suggested that surface flow across the Central American isthmus was from the Caribbean to the Pacific up until the time of final closure to passage of marine waters, others (Maier-Reimer et al., 1990; Cronin and Dowsett, 1996) argue that surface flow across the isthmus was from the Pacific to the Caribbean. The latter cite data showing a dilution of high salinity Caribbean waters caused by influxes of lower salinity Pacific water and the higher sea surface topography of the Pacific relative to the Atlantic as being important indicators of marine water flow direction. The direction of surface water currents is, of course, important to waif dispersers because if the flow was from the Caribbean to the Pacific the chances would probably have been greater that an animal attempting to cross a water gap, either by design or accident, would end up being lost at sea than if the opposite were true. But if the water flow was from the Pacific to the Caribbean, and if the last gaps in the terrestrial connection were located in the Choco Terrane, as detailed below, those animals moving southward and attempting to cross between islands of the rising Serranías de Maji-Baudo, but not succeeding, would have had a fair chance of surviving being carried eastward by water currents across the relatively narrow Atrato Basin to reach Colombia.

Winds of sufficient strength can, of course, move objects floating in water in directions other than prevailing water currents. At the present time northwestern South America is under the influence of northeasterly trade winds, which are more dominant during the

northern hemisphere winter when the intertropical convergence zone (ITCZ) is pushed south. During the austral winter the ITCZ moves northward, the northeasterly trade winds diminish, and strong southwesterly winds become dominant in the Choco region of Colombia. It is unclear, in the absence of polar ice caps comparable to those of today, what the position of the ITCZ might have been in the late Miocene, or whether there were any possible seasonal changes in its position at that time. It is reasonable to assume, however, that northeasterly trade winds were present in some form at some time of the year and their presence could certainly have assisted movement of early "heralds" across the narrow Atrato Basin from Colombia to the newly emergent Serranía de Baudo as "waif" dispersers.

Late entrance of marine waters from the Caribbean Sea into the Atrato Basin was from the Gulf of Uraba and across the northern extension of the low-lying Satuta Arch that connects the Serranías de San Blas-Darién with the northernmost western flanks of the Cordillera Occidental (Fig. 30). This is the course followed today by the Río Atrato, although the river flows in the opposite direction. The lowlands of the northern Atrato Basin represent the largest expanse of low elevation terrain between Central and South America and may well have been the last, i.e., most recent, portion of the Choco Terrane to emerge from beneath the sea.

If current topography can be used as a guide, which may be a big "if" because of the possibility of differential uplift along the Baudo Arch, there are three areas through which marine water may have entered the Atrato-Chucunaque Basin from the Pacific during the period just before the Baudo Arch was completely terrestrial. To the north, the Chucunaque Basin connects broadly with the Gulf of Panama and, through a narrow divide in the "trans-isthmian ridge" connecting the southern end of the Serranía de Darién and the northern end of the Serranía de Baudo, with the Atrato Basin (Fig. 30). Second, at about 6° 30' N latitude there exists a narrow stretch of low elevation crestline in the Serranía de Baudo through which Pacific marine water may have continued to enter the basin until near the end of the Miocene. Lastly, at the southern end of the Atrato Basin there exists a broad opening across the low Istmina Hills to the San Juan Basin and hence to the Pacific. Inasmuch as the Istmina Hills probably formed early in the course of accretion of the Choco Terrane to South America (Duque-Caro, 1990a), it is reasonable to suspect that perhaps this elevated area has formed a barrier to marine waters entering the Atrato Basin since near that time. Although elevations of a short section of the Istmina Hills may not exceed 100 m a.m.s.l., the other two areas cited as possible water gaps are currently between 100 m and 200 m a.m.s.l.

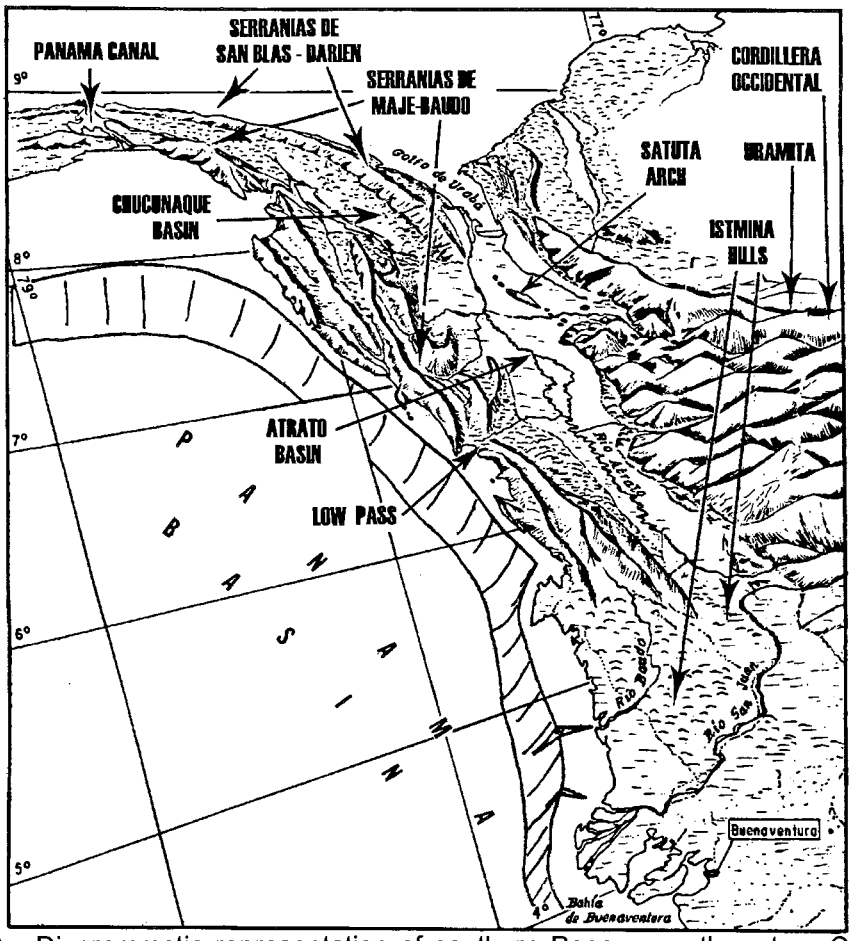

Figure 30. Diagrammatic representation of southern Panama-northwestern Colombia, wherein was located the last barrier to the movement of terrestrial faunas from North America to South America and vice versa, illustrating the various geographic features discussed in the text. The Istmina Hills occupy the Istmina Deformed Zone, which is where the Panama-Costa Rica Arc first began accreting to northwestern Colombia in the early Miocene. The Dabeiba Arch includes the Serranías de San Blas-Darién, the Satuta Arch, and the northernmost western flanks of the Cordillera Occidental. The Uramita Fault Zone extends north-northwest of the town of Uramita. An early Miocene fauna containing North American taxa from within the Panama Canal Zone at the western end of the Serranías de San Blas-Darién suggests that North American taxa were prevented from crossing to South America at that time only by the combination of the Atrato Basin and its interconnection with the Chucunaque Basin, which would have blocked passage between the southern end of the Serranía de Darién and the northern end of the Serranía de Baudo. Modified from Duque-Caro (1990a).

Chronology of Terrestrial Connections: According to Duque-Caro (1990a, 1990b), the major phase of accretion of the Choco Terrane to northwestern South America, i.e., its suturing to Colombia, and the formation of the Atrato Basin occurred during the middle Miocene, 12.9-11.8 Ma. He suggested that stability apparently existed during the period 11.8-8.6 Ma, followed by uplift since 8.6 Ma leading to the modern topography. His analysis was based primarily on stratigraphic and biostratigraphic data from the Atrato Basin, the basinal structure representing the middle, or longitudinal axis, of the southern one-half of the Choco Terrane. The low sea level stand between ~12.0-11.0 Ma may have been crucial to establishing enough of a terrestriality to the Choco Terrane such that the earliest dispersers were able to make the crossing between the continents. The tectonic activity initiated at 8.6 Ma, in conjunction with a sea level lowstand centered at ~8.8 Ma, may have been more important to the crossing of later dispersers, i.e., for the ground sloths going north and procyonids going south. This scenario would bring the timing of the early crossings more in line with the fossil record.

Although there are as yet no data pertaining to the relative heights between the floor of the Atrato Basin and the crestline of the Serranía de Baudo to the west at different points in time, it may be assumed that the relief in that area has decreased over time because of the weathering of the Serranía de Baudo and the infilling of the Atrato Basin with sediments from both the east and west. If so, then by the late Miocene, when the Atrato Basin had shallowed to less than 150 m depth (below sea level) (Duque-Caro, 1990a), the Serranía de Baudo must have already existed as a string of islands, if not an almost unified into a single island. These islands were gradually interconnected as uplift continued in the late Miocene, a process that led to the complete emergence of the Choco Terrane by the early late Pliocene.

There now seems to be considerable support for the hypothesis that a complete terrestrial connection was formed or nearly formed between North America and South America by ~3.5-3.1 Ma (Saito, 1976; Keigwin, 1978, 1982; Duque-Caro, 1990a,b; Coates et al., 1992; Collins et al., 1996), even though sea level reached a high stand during this period (Hardenbol et al., 1998; Dowsett and Cronin, 1990). Nonetheless, there are indications that short-lived flows of marine water across the Central American isthmus occurred as late as 2.0-1.8 Ma (Keller et al., 1989; Cronin and Dowsett, 1996). It is necessary to clearly understand that although the last marine barrier to the free intermingling of the terrestrial faunas of North and South America may well have occurred in the Choco region of Colombia, because of the tectonically unstable nature of the Central

American isthmus this does not mean that the last flow of marine waters between the Pacific and the Caribbean occurred in the Choco region.

Chronology of and Participants in Interchange Events

The timing of the major interchange events remains clouded by the lack of adequate geologic data and vertebrate faunas from the tropics, although current research is beginning to yield more precise dates for geologic events in the Central American isthmus (Mann, 1995a; Collins et al., 1996; Jackson et al., 1996). Unfortunately, most of the new data pertain to the Panama straits and surrounding regions rather than to what we view as the more critical areas of the southern half of the Choco Terrane. Nonetheless, from the recent new data that have appeared in print it is apparent that recent chronologies and interpretations of interchange events (Stehli and Webb, 1985; Webb, 1991,1998; Marshall and Sempere, 1993; Webb and Rancy, 1996; Woodburne and Swisher, 1995) are far from adequate. Some problems with these chronologies and interpretations have been noted above. It is not our intent here to propose a specific chronology for interchange events because we consider the field to be in such a state of flux that any specific scenario presented would rapidly be out of date. Rather, we will present our view of how the GAFI proceeded.

The oldest record of North American mammals in southern Central America is a fauna from exposures of the Cucaracha Formation within the former Panama Canal Zone (Whitmore and Stewart, 1965). This fauna, which includes a selenodont artiodactyl, equids, rhinocerotids, and oreodonts, was described as typical of North American herbivorous faunas found across the United States during the Miocene. The fauna did not include any South American taxa. The age of the fauna was put at early Miocene, or ~21 Ma (Whitmore and Stewart, 1965; Collins et al., 1996). The fossils were collected from deposits interpreted as having accumulated in a swamp (Whitmore and Stewart, 1965), just a short distance west of the Serranías de San Blas-Darién, which apparently also provided a terrestrial environment at that time (Woodring, 1957).

The importance of this fauna lies in the fact that it proves a terrestrial link between North America and southernmost Central America long before the Choco Terrane was sutured to Colombia, and during a period when sea level was probably much higher than it is today (Hardenbol et al., 1998). Without doubt, the terrestrial corridor linking southern Panama with North America through which this fauna passed was subsequently broken

many times by recurrent marine barriers that were established and disrupted again and again in the unstable regions of this tectonically active island arc. And it is not necessary that a single, complete terrestrial corridor from North America to Panama existed at this early point in time. Marine barriers may have simply disappeared in advance of a dispersing fauna even as they were being reestablished behind the advancing fauna. Documentation of the opening and closing of such marine straits is presented by Collins et al. (1996) and Cronin and Dowsett (1996).

In essence, the date of final, complete emergence of the Central American isthmus is not of any particular significance to the initial interchange of mammalian taxa between North and South America. The faunas were already poised to cross the final barrier, or water gap, millions of years before that barrier fell, even though marine barriers may have reformed behind them, isolating them between water gaps both north and south. And some taxa, e.g., proboscideans, ground sloths, and procyonids, probably crossed the final barrier when it was still in place. The crucial missing pieces of the puzzle are the location and nature of the final barrier. We suggest that it was located somewhere between the southern end of the Serranía de San Blas-Darién and the Istmina Hills, along the route traced by the Serranía de Baudo. The two most obvious possibilities for the most durable of marine barriers include the low pass between the Serranías de Darién and the Serranía de Baudo and/or a persistent gap in the Serranía de Baudo between the northern end of the Atrato Basin and the Istmina Hills. Our interpretation of the data leads us to suggest the route illustrated in Fig. 31 as the most likely path that was traveled by terrestrial faunas dispersing between the Americas. In this scenario, the key event for early dispersers is the uplift above sea level of the terrain between the Serranía de Darién and the Serranía de Baudo, which separated the Chucunaque Basin from the Atrato Basin. Although Duque-Caro (1990a, 1990b) suggested that the major phase of accretion of the Choco Terrane to northwestern Colombia occurred during the middle Miocene, i.e., 12.9-11.8 Ma, the final suturing of the northern end of the Choco Terrane to northwestern Colombia in the vicinity of the Gulf of Urabá may have occurred somewhat later. If so, the marine barrier extending southward into the Río Atrato valley would have been wider at the time the early North American dispersers were making their way into South America and a route through the Serranía de Baudo would have been more easily traversed. In this hypothesis, the terrestrial corridor between North and South America opened in earnest when all of the Serranía de Baudo and its connection to the Serranía de Darién were uplifted above sea level by continued tectonism involving the mobile Choco Terrane as it was crushed against the South American Plate.

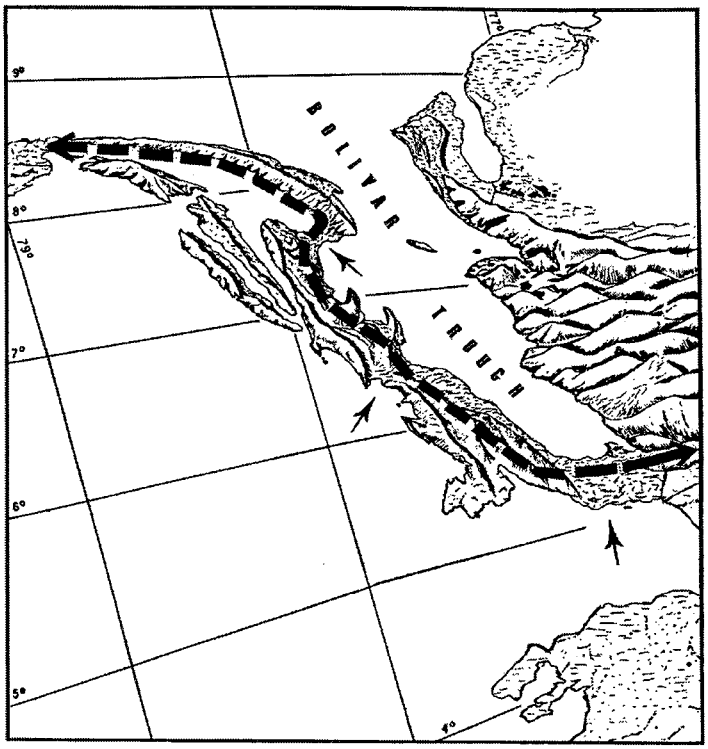

Figure 31. We illustrate here what we interpret to be the most likely path traveled by terrestrial faunas dispersing between North America and South America. We propose that as the marine connection between the Atrato Basin and the Chucunaque Basin was reduced and finally eliminated by uplift, the North American taxa resident in the Serranías de San Blas-Darién moved southwest into the Serranía de Baudo, then south to the Istmina Hills, and hence east into South America. This route obviates the need to cross the Atrato Basin when it was filled with marine waters, or the necessity of waiting until the basin filled sufficiently with sediment to permit crossing. This hypothesis does, however, make the assumption that the northern Atrato Basin was the longest-lived aquatic barrier between Central America and northwestern South America, which is not unexpected given that the Choco Terrane attached to Colombia first in the south and was then sutured onto the continent in a northerly direction. Although the major phase of accretion of the Choco Terrane to Colombia may have been well underway by the time *Amahuacatherium* and other North American mammals began dispersing into South America, the Gulf of Urabá may still have been as wide as is shown in this illustration. Hence, the northern Atrato Basin posed a formidable marine barrier to the passage of dispersing mammals in the late Miocene. Arrows indicate areas of low elevation that were possibly the sites of the last marine barriers to dispersal between the continents. Redrawn from Duque-Caro (1990a).

Savanna Corridor Hypothesis: We disagree with the arguments of Webb (1978, 1985, 1991, 1998), Stehli and Webb (1985), Marshall and Sempere (1993), MacFadden et al. (1993), and Webb and Rancy (1996) that the first large-scale interchange event began at ~2.6-2.5 Ma and that the first taxa to participate in the GAFI were savanna-adapted taxa that moved from north temperate to south temperate latitudes and vice versa. The combination of a significantly earlier date for the completion of the isthmian connection and accumulating data arguing against savannas dominating the isthmian landscapes (Bush et al., 1992; Colinvaux, 1996) would appear to falsify the two major tenets of those arguments. Further, we see no reason to assume that dwellers of the tropical forests would not have exploited the earliest opportunities to expand their ranges. As land emerged from the sea, in areas of low relief one would expect first the formation of estuarine conditions, then a successional series that may have led from brackish water swamp to freshwater swamp to semi-emergent forest to totally emergent forest. In areas of high relief, exposed ridges would probably have been covered by a successional series of dry land communities leading to a cover of tropical forest over a decadal time scale after exposure. As these habitats opened up across the final barrier, taxa specific to or adaptable to each stage would disperse through them. We find ourselves in agreement with early views of Webb (1976:22), who argued that the "faunal interchange at its acme was broad based" and that the nucleus consisted of "diversely adapted genera." We do not see how it could have been otherwise.

There are some other problems with the savanna corridor hypothesis, of which the following is representative. Marshall and Sempere (1993) suggested that there were major waves of savanna dispersants at 2.5-2.3 Ma, 1.5-1.2 Ma, 0.7 Ma, and possibly at 0.3 Ma. However, Webb and Rancy (1996) stated that the interchange of savanna vertebrates apparently ceased in the middle Pleistocene, leading them to suggest that at that time the savanna corridors were permanently cut by tropical forests, the presence of which finally allowed the intermingling of tropical forest taxa. If this were true it would be very puzzling because, based on oxygen isotope data (van Donk, 1976; Shackleton and Opdyke, 1976; Harland et al., 1990), it can be observed that the latter half of the Pleistocene saw longer periods of greater cooling than the first half. These data are supported by the observation of Cronin and Dowsett (1996) that suppression of North Atlantic deep water (NADW) formation was not as great during the late Pliocene as during the late Pleistocene glacial periods. NADW formation is greatest during periods of relative warmth and is turned off during cold periods. Indeed, none of the cooling events of the late Pliocene or early Pleistocene appear to have been equal to those of the later Pleistocene. If savanna formation were connected to cooling, one would expect that savannas would have been more prominent

during the glacial epochs of the mid- to late Pleistocene, rather than in the early Pleistocene or Pliocene.

Further, van Donk (1976) reported a very prominent high sea level at 1.4 Ma, a date that was also approximated by Hardenbol et al. (1998). A high sea level at 1.4 Ma would fall in the middle of the second period of savanna dispersal, i.e., 1.5 - 1.2 Ma, noted by Marshall and Sempere (1993), although a sea level lowstand at ~1.6 Ma proposed by Hardenbol et al. (1998) would seem to provide enough overlap to allow time for savanna dispersal early in that period. Woodburne and Swisher (1995) suggested that there was a sea level lowstand at ~1.8 Ma (TB3.9).

The latter two savanna dispersal episodes identified by Marshall and Sempere (1993), i.e., 0.7 Ma and 0.3 Ma, occurred during the last major sea level lowstand, although van Donk (1976) suggested periods of relative oceanic warmth and high sea levels at this time. Thus, there is no certainty that the last three periods of interchange Marshall and Sempere (1993) identified actually correlate with major marine regressions, although the first period (2.5-2.3 Ma) does appear to correlate with a short-lived sea level lowstand (Hardenbol et al., 1998). Marshall and Sempere (1993:365), noting Bush and Colinvaux's (1990) arguments regarding the permanency of tropical forests in Panama, suggested that the savannas in Panama "... apparently occupied the extensive continental shelf areas that were exposed during significant coeval sea level stands...". But, if it turns out that sea level was not significantly lower during these postulated periods of interchange, then, by their own arguments, the savanna corridors could not have existed at those times and there could have been no interchange of savanna-adapted vertebrates.

The final troubling point associated with the savanna dispersal scenarios to be mentioned here is presented as a question. If savanna-adapted taxa were limited to crossing the isthmian link only episodically because the presence of savanna habitats was limited to periods of cool global climates and low sea levels, why did tropical forest or eurytropic vertebrates not also cross episodically, but during interglacial periods when the opposite conditions prevailed? Is it not to be expected that during periods of warm global climates and high sea levels that tropical forests would dominate the isthmus? Is not the only other alternative a barren desert? What mechanism(s) could have come into play that would have prevented the interchange of tropical forest vertebrates under conditions when broad corridors of tropical forests existed between the Americas? These questions have yet to be addressed by proponents of the "savanna vertebrates first" version of the GAFI.

Fossil Data Bearing on Interchange Chronology: Virtually all interchange scenarios developed to date are based on fossil records from the north temperate and south temperate latitudes. An exception is the Inchasi local fauna of Bolivia (MacFadden et al., 1993), a high elevation, intramontane mammalian fauna composed of taxa commonly occurring in savanna paleofaunas of Argentina. The Inchasi local fauna is cited as a "pre-interchange" fauna supporting current interchange scenarios because of the absence of North American taxa. However, it is unlikely that tropical forest vertebrates would have occurred in this high mountain basin even in the Pleistocene after the "classic" GAFI had begun. It has perhaps been unavoidable that the absence of fossil vertebrates representing interchange taxa from forested tropical regions has been taken as negative evidence reinforcing the "savanna vertebrates first" scenarios. It must be remembered, however, that this negative evidence has not been the absence of interchange taxa from fossil vertebrate faunas of the forested tropics, but rather the more important historical lack of **any** fossil vertebrate faunas **at all** from the American tropics. With no fossil record, it is not surprising that tropical forest vertebrates and their role in the GAFI have been ignored.

This brings us back to proboscideans, the Acre Conglomerate, and paleofaunas of western Amazonia. In reporting on a series of fossils recovered from the Río Alto Juruá in western Brazil, Simpson and Paula Couto (1981) described the geology of the region and illustrated several outcrops. Two items of importance stand out in this paper. First, a conglomerate, the Acre Conglomerate in our terminology, was recognized as a basal facies of what they regarded as a series of Pleistocene lithologies overlying Tertiary "Puca-type" clays, with a "clear weathered and erosional unconformity" separating the two lithologies (Simpson and Paula Couto, 1981:16). This is the same stratigraphic sequence we recognize, although we use the terms Contamana Group for "Puca-type" clays, Ucayali Unconformity for the erosional unconformity, and Madre de Dios Formation for their "Pleistocene" beds. In all of their illustrations of actual sections they appear to recognize only two horizons in their "Pleistocene" beds overlying the basal conglomerate. However, in a composite diagram illustrating the complete Tertiary-Recent sequence in western Amazonia (reproduced here as Fig. 23) they illustrate a third, capping horizon that they refer to the Recent. This horizon lies in the position of, and must form, the planalto, and, as they illustrate, for this horizon to have been deposited at the planalto level all preexisting valleys must have been filled with sediments that date from the same depositional episode. The discrepancy between the presence of only two horizons in the actual sections illustrated and the three horizons in their composite diagram of the Madre de Dios Formation is readily explained by the fact that, as can be determined by viewing radar imagery of the

Río Alto Juruá, all of the sections they illustrated occur within, and completely exclude, the two extreme walls of the valley of the river. That is, none of their illustrated sections include the full stratigraphic sequence that exists outside the valley where the planalto remains. We interpret this to mean that within the valley walls the youngest horizon with which we are familiar, i.e., Unit "C," was removed by the river in the course of its downcutting to current levels. This view is reinforced by their comment (Simpson and Paula Couto, 1981:22) that at their Locality 4 (Parição) there is found an unusually high vertical cliff well back from the river low water margin. It can be seen in radar imagery that this cliff is cut into the far outside wall of the valley and into the planalto. In this case the section probably does include Unit "C," or their "Recent" beds. Unfortunately, they did not illustrate this section.

The stratigraphic diagram of Simpson and Paula Couto (1981) (Fig. 23) is also of significance in that it clearly demonstrates the authors' awareness of channeling of younger horizons into underlying beds. This is further shown by a section illustrated by Paula Couto (1983b: fig. 3). Knowing that the authors were aware of the possibility of channeling gives us confidence that no channeling was present in their illustrated sections in which no channeling is depicted. If channeling had been present, they certainly would have recognized and noted it. Thus, in those instances when they speak of a basal conglomerate, they are describing a conglomerate basal to the entire section, not a conglomerate that may owe its origin to channeling in the course of deposition of the younger, overlying beds.

The second item of importance in this paper is that within the identifiable fossil mammals from the sites they described were a group of typical Tertiary, i.e., Miocene, mammals, and a group of taxa derived from North American immigrants. It was the presence of the latter group, which included proboscideans, camelids, peccaries, and tapirs, that led Simpson and Paula Couto (1981) to the conclusion that the deposits overlying the Ucayali Peneplane were Pleistocene in age, an interpretation followed by Campbell et al. (1985) and Frailey (1986). The specimens of these taxa of North American immigrants were, in almost all instances, recovered from or thought to be derived from the basal conglomerate. The question is, was the fossil-producing conglomerate they described basal to the Madre de Dios Formation, i.e., coeval with the Huayquerian Acre Conglomerate, or is there a possibility that it was a product of channeling during deposition of overlying beds.

Unfortunately, the only site from which came more than one of the North American taxa, Cachoeira de Gastão, is one that lacks any stratigraphic context. This site, which

produced specimens of gomphotheres, tapirs, and a peccary, is an isolated patch of conglomerate resting on the Ucayali Peneplane within the river channel at some distance from the cutbank (Simpson and Paula Couto, 1981; fig. 2). Simpson and Paula Couto (1981) referred the gomphothere to the Pleistocene *Haplomastodon waringi* (Holland 1920) and the tapir and peccary to Recent taxa. However, Pedra Preta, a second locality that produced *H. waringi*, was illustrated by Paula Couto (1978; fig. 2; reproduced in Campbell et al., 1985; fig. 11), and it would appear that in this instance the conglomerate is a typical basal facies of Unit "A" of the Madre de Dios Formation. We have not visited this locality, but the illustration is strikingly similar to sections with which we are familiar. Unit "C" of the Madre de Dios Formation is absent from this figure, but this is not surprising given that this section occurs in the middle of the valley of the Río Alto Juruá, almost 4 km from the closest side of the valley where the planalto is present. Without actually visiting this locality, we are as sure as we can be that it represents a non-channelized sequence of the Madre de Dios Formation, minus an unknown portion of the top of the stratigraphic column removed by terracing. Furthermore, the fossiliferous conglomerate is basal in Unit "A," and thereby equivalent to the fossiliferous Acre Conglomerate of southeastern Peru. This would mean that all of the fossil vertebrates, including the *Haplomastodon* sp., date from the Chasicoan/Huayquerian (late Miocene). Of particular importance to this age assignment is the presence in the fauna from Pedra Preta of material that was referred to the late Miocene rodent *Phoberomys* Kraglievich 1926 (Paula Couto, 1978; 1979). If this interpretation is correct, then *Amahuacatherium* was not the only gomphothere roaming western Amazonia in the late Miocene, although it appears to have been the first.

In addition, the descriptions of two other localities producing gomphotheres listed by Simpson and Paula Couto (1981), their Locality 10 and Locality 14, suggest that at those localities the fossiliferous conglomerate is basal in the Madre de Dios Formation and that those deposits also date from the Chasicoan/Huayquerian. Additional sites along the Río Juruá producing gomphotheres were mentioned by Paula Couto (1956) and described in Simpson and Paula Couto (1957). Gomphotheres were also reported from western Amazonia by Moraes Rego (1930) and Benchimol and Santos Ferreira (1987), and unpublished records cited by Rancy (1991) are referred to in Webb and Rancy (1996). Unfortunately, there are no precise stratigraphic data available for any of these specimens, so their ages are unknown. It would be inappropriate, however, to automatically assume that they all represent Pleistocene occurrences, although some of them may very well be just that.

As for the other taxa of North American descent reported from these deposits, i.e., the camelids, tapirs, and peccaries (Simpson and Paula Couto, 1981), we cannot be absolutely certain that any of them were derived from the basal conglomerate of Unit "A," even though it is highly probable. The specimens are mostly fragmentary and lack good stratigraphic data (most were collected loose on riverbanks or sandbars), although the localities from which they came are known. There are three specimens of camelids, one referred to *Vicugna* sp. and two to *Lama* sp. Of the six specimens of tapirs, two were described as probably coming from the basal conglomerate, whereas the others did not have the same type of preservation as fossils from the conglomerate and they were considered to be younger.

Of special note is the single peccary specimen, a left lower jaw with an almost complete dentition from the basal conglomerates at Cachoeira de Gastão, which was referred to *Tayassu pecari* Fischer 1814 by Simpson and Paula Couto (1981). This specimen is currently under study, and preliminary analysis indicates that it is a new species, quite unlike *T. pecari*. The nature of fossilization is also typical of fossils from the basal conglomerates. Further, there is another series of peccary specimens of interest that was collected by Harvey Bassler in eastern Peru (Willard, 1966). Unfortunately, provenience data is limited to river valley for the respective specimens and there are no stratigraphic data, although the nature of the preservation of most of the specimens is typical of that of fossils from the basal conglomerate. Preliminary analysis of these specimens indicates that they represent two extinct taxa, one of which may be conspecific with the late Pliocene(?) *Dicotyles traunmulleri* Spillman 1949 from eastern Peru. The second species represented is a member of the genus *Tayassu*. Some of the Peruvian specimens are identical to the lower jaw from Cachoeira de Gastão collected by Simpson and Paula Couto (1981). Thus, there appear to be two species of peccary present in the basal conglomerates of the Madre de Dios Formation, placing this group of North American mammals in South America before 9 Ma.

It is also a very interesting question as to whether the evolution and dispersal of gomphotheres and camelids might not have had much in common. The camelids are another example of what has been assumed to be a rather straight-forward case of a North American lineage (represented by *Hemiauchenia* H. Gervais and Ameghino 1880) dispersing to South America and giving rise there to a new lineage (represented by *Palaeolama* P. Gervais 1867), which subsequently dispersed to North America. The problem with this evolutionary scenario is the time factor, which requires the *Hemiauchenia* lineage to arrive in South America about 2.0-1.9 Ma, give rise to a new lineage with a

quite different morphotype, and for that lineage to return to Florida where it is represented by *Palaeolama* by 1.4 Ma (Webb, 1974; Marshall, 1985). Perhaps it is more reasonable to consider the possibility that the camelids arrived in South America in the Miocene about the same time as the gomphotheres, thereby eliminating the need to postulate such extremely rapid rates of evolution. The possible presence of fossil camelids in the upper Miocene (Chasicoan/Huayquerian) Acre Conglomerate (Simpson and Paula Couto, 1981) would certainly seem to suggest that this was, indeed, the case.

We may summarize the above by saying that the available data suggests that *Amahuacatherium* was accompanied by, or closely followed by, *Haplomastodon* sp. and two species of peccaries in western Amazonia in the late Miocene, and we consider it probable that camelids and tapirs were also part of the late Miocene South American tropical fauna.

Thus, we see that the absence of interchange taxa from fossil vertebrate faunas of the tropics has not been as complete as assumed. Rather, the problem has been that any taxon derived from North American immigrants has automatically been assigned to the late Pliocene or Pleistocene, i.e., younger than ~2.5 Ma. We are confident that further collections in the tropics will finally bring to light a more accurate picture of the dynamics of the GAFI.

SUMMARY

Amahuacatherium peruvium is a primitive gomphothere from upper Miocene deposits of southeastern Peru. It was a tetrabelodont, brevirostrine gomphothere with lower tusks, the only gomphothere known with such a combination of characters. A unique mandibular cross-sectional shape at M_3 and characters of the M_2, M_3, and M^3, including, but not limited to, large numbers of conules that fill the lingual valleys, U-shaped valleys between cones, and slender rather than swollen primary cones, differentiate *A. peruvium* from all known gomphotheres. Although the mandibular symphysis is unknown, a brevirostrine condition is inferred from the curvature seen in the lateral side of the mandibular rami, the very shallow depth of the mandibular rami, the fact that the tooth row curved anterolaterally, and the presence of small lower tusks that rooted beneath the M_2. *Amahuacatherium peruvium* is strategically placed near the base of the ancestral lineage leading to the subfamily Cuvieroniinae, but the highly derived condition of some characters of the mandibles suggests that this lineage did not give rise to any of the later cuvieroniids. Possible scenarios for the role of *A. peruvium* in the history of South American gomphotheres are presented herein, but the lack of adequate data prevents precise placement of *A. peruvium* in the overall picture of evolution of later Cenozoic gomphotheres. It is reasonable to postulate, however, that much, if not all, of the evolution of the South American gomphotheres may have occurred in South America rather than North America, as previously assumed. Instead of having been a one-way, north-to-south range extension, one, two, or perhaps even three of the South American gomphotheres may have reinvaded North America during the Pliocene after diversification in South America.

Amahuacatherium peruvium came from Tertiary deposits exposed along the Río Madre de Dios in southeastern Peru. These deposits are interpreted as possible channel deposits left in the top of the Contamana Group during the late Miocene erosion of those strata that resulted in the widely recognized Ucayali Peneplane. Through a review of the tectonic evolution of the Peruvian Andes, a consideration of the biostratigraphy of eastern Peru, and a $^{40}Ar/^{39}Ar$ date of 9.01±0.28 Ma on an overlying ash deposit, *A.*

peruvium is securely dated to the late Miocene. Deposition of the overlying Madre de Dios Formation, which covers almost all of western Amazonia, is interpreted as having begun during the Quechua II compressional phase of Andean evolution within a thrust-induced subsiding basin between the rising Andes and the cratons to the east. In the absence of any supporting data, hypotheses of marine influence in the course of deposition of the Madre de Dios Formation are rejected.

The presence of a gomphothere in upper Miocene deposits of southeastern Peru suggests that the current paradigm for the Great American Faunal Interchange is in need of revision. A review of the current understanding of the geologic history of northwestern South America reveals that northwestern Colombia is an accreted island arc, the Choco Terrane, sutured onto the Western Cordillera of the Andes. Initial contact between the island arc and South America occurred in the early Miocene, and accretion began in earnest in the middle Miocene (12.9 - 11.8 Ma) in the region of the Istmina Hills and gradually proceeded northward. Uplift after 8.6 Ma completed the terrestrial link between central Panama and the South American continent. The last major marine barrier to a complete terrestrial link between Panama and South America appears to have been removed by 3.5-3.1 Ma, not at ~2.7-2.5 Ma as so often cited. This last marine barrier may have been located in the western portion of the Choco Terrane, but it may also have been located farther north on the Isthmus of Panama. Marine barriers may have come and gone at various times in the region of the Panama straits up until some time in the late Pliocene/ early Pleistocene, posing temporary restraints on the intermingling of faunas.

Proboscideans are now the earliest known North American mammals to arrive in South America as participants in the Great American Faunal Interchange (GAFI). Careful reconsideration of previously reported faunas of western Amazonia also gives strong support to the hypothesis that more than one gomphothere, as well as camels, tapirs, and peccaries, may well have been roaming throughout Amazonia in the late Miocene. There does not seem to be any support for the hypothesis that early participants in the GAFI were all savanna-adapted or savanna tolerant taxa that crossed the Central American isthmus during periods of climatic cooling or low sea levels. Indeed, some periods of postulated interchange of savanna vertebrates appear to coincide with periods of relative climatic warmth and high sea levels, which argue against the use of newly emergent coastlines as savanna corridors. Rather, we propose that the intermingling of the North American and South American faunas was a fairly continuous event that began in the late Miocene, interrupted only during periods of high sea level. As soon as members of any given taxonomic group were able to cross the last remaining barriers to their dispersal, they did so. If there was a

major initial interchange event after completion of the terrestrial link, it probably occurred between 3.5-3.1 Ma, or earlier, and it was probably dominated by tropical forest taxa. Savanna taxa followed later only as conditions permitted their passage. The existing fossil record may accurately reflect the movement of savanna vertebrates north and south across the Central American isthmus, but newly discovered vertebrate faunas and reinterpretation of long-known faunas of western Amazonia demonstrate that tropical forest vertebrates were active participants in the GAFI from the very beginning. The negative evidence of the absence of tropical forest vertebrates in the fossil record is proving to be invalid as paleontological research in the Amazonian lowlands continues to produce unexpected discoveries.

SUMARIO

Amahuacatherium peruvium es un gomphothere primitivo de los depósitos del Mioceno superior del sudeste del Perú. Este fue un gomphothere brevirostrino y tetrabelodonte con colmillos inferiores y es el único gomphothere conocido con semejante combinación de caracteres. *Amahuacatherium peruvium* está diferenciado de todos aquellos gomphotheres conocidos por la forma única de la sección transversal de su mandíbula debajo de M_3, los caracteres de M_2, M_3 y M^3, los numerosos grandes cónulos que llenan los valles linguales, valles formados en U entre los conos y conos delgados no gruesos. Aunque la sínfisis mandibular es desconocido, una condición brevirostrina es inferida de la curvatura vista en el lado lateral de la rama mandibular, la baja altura de la rama mandibular, el hecho que la fila de los dientes encorve anterolateralmente, y la presencia de pequeños colmillos inferiores que enraízan bajo los M_2's. *Amahuacatherium. peruvium* está estratégicamente situado cerca de la base del linaje ancestral que lo lleva a la subfamilia Cuvieroniinae, pero la condición altamente derivada de algunos caracteres de las mandíbulas sugiere que este linaje no dio lugar a los cuvieroniidos tardíos.

Se presentan posibles argumentos del rol de *Amahuacatherium peruvium* en la historia de los gomphotheres de sudamérica, pero la falta de datos adecuados impiden la colocación precisa de *A. peruvium* en el cuadro de evolución global de los gomphotheres del Cenozoico tardío. Sin embargo es razonable para postular, que muchos, si no todos de la evolución de los gomphotheres sudamericanos pueden haber ocurrido en América del Sur en lugar de América del Norte, como previamente se asumió. En vez de haber sido una ruta de expansión con dirección norte a sur, uno, dos, o quizás incluso tres de los gomphotheres sudaméricanos pudieron haber reinvadido América del Norte durante el Plioceno después de la diversificación en América del Sur.

Amahuacatherium peruvium provienen de los depósitos del Terciario expuestos a lo largo del río Madre de Dios en el sudeste del Perú. Estos depósitos son interpretados como posibles depósitos de canal dejados en el tope del Grupo Contamana, duran-

te la ultima erosión en el Mioceno tardío resultando la peneplanicie Ucayali que es ampliamente reconocida.

A través de una revisión de la evolución tectónica de los Andes Peruanos, una consideración de la bioestratigrafía del Perú oriental, y una datación $^{40}Ar/^{39}Ar$ de 9.01 ± 0.28 Ma sobre un depósito de ceniza sobreyaciente, el *Amahuacatherium peruvium* es asignado al Mioceno tardío.

La deposición de la sobreyacente Formación Madre de Dios que cubre casi toda la Amazonia occidental es interpretada como iniciada durante la fase compresional Quechua II de la evolución andina, dentro de una cuenca de subsidencia entre los Andes crecientes y el cratón hacia el este. En ausencia de cualquier dato de apoyo, se rechazan las hipótesis de influencia marina en el curso de deposición de la Formación Madre de Dios. La presencia de un gomphothere en los depósitos del Mioceno superior al sudeste del Perú sugiere que el paradigma actual para el Gran Intercambio Faunal Americano está en necesidad de revisión. Una revisión del actual conocimiento de la historia geológica del noroeste de América del Sur revela que el noroeste de Colombia es un arco de islas acrecionado, el terreno alóctono de Chocó que es suturado hacia la Cordillera Occidental de los Andes. El contacto inicial entre el arco de islas y América del Sur ocurrió en el Mioceno temprano, y la acreción empezó con más fuerza en el Mioceno medio (12.9 – 11.8 Ma) en la región de las colinas de Itsmina y gradualmente continuó hacia el norte. El levantamiento después de los 8.6 Ma, completó la conexión terrestre entre Panamá central y el Continente Sudamericano. La ultima barrera marina entre Panamá y América del Sur parece haber desaparecido hace 3.5 – 3.1 Ma, y no 2.7 – 2.5 Ma como tan a menudo es citado. Esta última barrera marina puede haber sido localizada en la parte oeste del terreno alóctono de Chocó, pero también se puede haber localizado, más al norte, en el istmo de Panamá. Las barreras marinas pueden haber venido y regresado varias veces en la región del estrecho de Panamá hasta hace algún tiempo en el Plioceno tardío a Pleistoceno temprano, proponiendo refrenamientos temporales en el entremezclar de faunas.

Los Probocideos son los primeros mamíferos norteamericanos conocidos que han llegado a Sudamérica como participantes en el Gran Intercambio Faunal Americano. La reconsideración cuidadosa de faunas previamente reportadas de la Amazonia occidental también da un fuerte sustento a la hipótesis que más de un gomphothere, así como los camellos, tapires y sajinos bien pudieron haber estado viviendo por toda la Amazonia en el Mioceno tardío. No parece ser apoyo alguno la hipótesis de que los participantes

tempranos en el Gran Intercambio Faunal Americano eran todos adaptados a sabanas o taxas tolerantes a la sabana que cruzaron el istmo centroamericano durante los periodos de enfriamiento climático o bajas del nivel del mar. Por cierto, algunos periodos del postulado intercambio de vertebrados de sabana al parecer coinciden con periodos de relativo calentamiento climático y subida del nivel del mar, que impidieron el uso de litorales recientemente como corredores de sabana.

Más bien, nosotros proponemos que el entremezclado de las faunas de América del Norte y América del Sur fue un evento bastante continuo que empezó en el Mioceno tardío y se interrumpió sólo durante los períodos de alto nivel del mar. Luego dado que los miembros de cualquier grupo taxonómico fueron capaces de cruzar las últimas barreras en su dispersión, ellos lo hicieron así. Si hubo inicialmente un evento de intercambio mayor después de completarse la conexión terrestre, es probable que ocurriera entre 3.5 – 3.1 Ma o más antes y fue probablemente dominado por taxa de selva. La taxa de sabana siguió después cuando las condiciones permitieron su transito. El registro de fósiles existentes puede correctamente reflejar el movimiento de los vertebrados de sabana del norte y sur cruzando el istmo de América Central; pero descubrimientos recientes de faunas de vertebrados y la reinterpretación de todas las faunas conocidas de la Amazonia occidental demuestran que los vertebrados de selva fueron participantes activos en el Gran Intercambio Faunal Americano desde el comienzo. Las investigaciones paleontológicas en la selva baja continúan produciendo descubrimientos inesperados que están probando la invalidez de la evidencia negativa o ausencia de vertebrados de selva en los registros fósiles.

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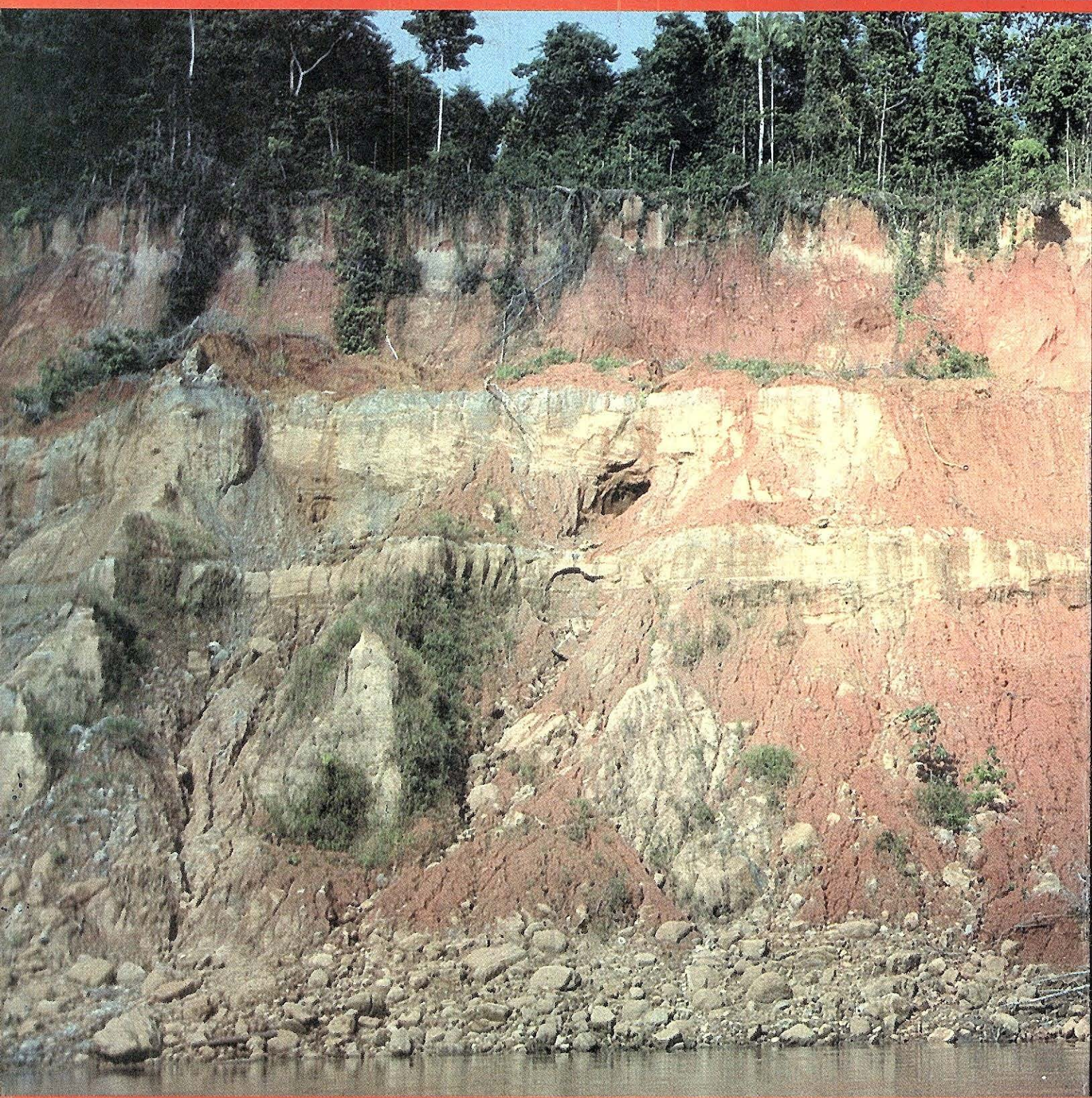

Carátula: View of Aurinsa, locality LACM6258, Madre de Dios River.
Vista de Aurinsa, localidad LACM6258, Río Madre de Dios.

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